PL-ISSN 1895-3123 (print), ISSN 2081-7487 (online) *Acta zoologica cracoviensia*, **54A**(1-2): 1-29, Kraków, July, 2011

doi:10.3409/azc.54a_1-2.01-29

Palaeoecology of Late Pliocene and Quaternary mammalian communities in the Carpathian Basin

Piroska PAZONYI

Received: 25 January 2011

Accepted: 9 March 2011

PAZONYI P. 2011. Palaeoecology of Late Pliocene and Quaternary mammalian communities in the Carpathian Basin. *Acta zoologica cracoviensia*, **54A**(1-2): 1-29.

Abstract. Late Neogene and Quaternary changes of climate and vegetation in the Carpathian Basin can be reconstructed using some ecological parameters of mammalian communities. This study is based on mammalian faunal data from 156 layers of 64 Upper Pliocene, Pleistocene and Holocene localities from the Carpathian Basin. Some of the applied methods analyse the species composition of mammalian faunas (cluster analysis, similarity and longevity studies, and reconstruction of evolutionary lineages). These methods allow the documentation of the first-, second- and third-order events in the mammalian fauna. The other group of analyses consists of taxon-free methods which are based on the ecological parameters (body size, trophic preferences, number of species) of mammalian species and communities. The distribution of ecotypes in a fauna (ecological variables) is primarily determined by the climate and vegetation. Therefore the ecological variables (distribution of body size and the trophic preferences, diversity index) together define the ecological unit which is characteristic to the community. In the Carpathian Basin 10 ecological units are distinguished and interpreted in the studied period. The succession of these ecological units provides a useful framework for tracking Late Pliocene and Quaternary changes in climate and vegetation.

Key words: Upper Pliocene, Quaternary, mammals, palaeoecology, taxon-free methods.

Piroska PAZONYI, Research Group for Paleontology, Hungarian Academy of Sciences–Hungarian Natural History Museum; POB 137, Budapest, H-1431 Hungary.
E-mail: pazonyi@nhmus.hu

I. INTRODUCTION

A large number of Quaternary localities have been excavated for vertebrate palaeontological investigations during the last 150 years in Hungary. Taxonomic composition and species abundance data were used to develop a biochronologic-biostratigraphic system, which has also been adopted by other workers internationally, beyond the Carpathian Basin. The very rich material allows palaeoecological investigation of the faunas. Such studies have so far been completed for either single faunas or single periods only. A comprehensive palaeoecological investigation of the whole Quaternary material is attempted here for the first time.

Much modern research of terrestrial mammals is based on examination of ecological characters of fossil communities (e.g. body size, trophic preferences, number of species). These taxon-free methods have been developed mainly for the African and Asian fossil large mammals (DAMUTH 1992), therefore some adaptations of methods were required before they could be applied to the Carpathian Basin mammalian faunas (PAZONYI 1999, 2004, 2006).

Aims of study are a comprehensive palaeoecological investigation of the whole Late Pliocene and Quaternary material and based on this study tracking changes in climate and vegetation in the Carpathian Basin.

II. MATERIAL AND DATABASE COMPILATION

II.1. Localities and their ages

The Pleistocene and Holocene are the two richest intervals of vertebrate faunas in the Carpathian Basin. Localities were selected for quantitative palaeoecological investigations on the basis of three basic criteria: (1) stratigraphic position, (2) number of species and (3) lack of anthropogenic effects. Mixed faunas were excluded, as well as those localities were either small or large mammals were found exclusively.

The age of localities is expressed in years for the practical purposes of this article (Table I). The numerical ages are based on the earlier biochronologic-biostratigraphic systems (KRETZOI 1941, 1953; JÁNOSSY 1986; FEJFAR & HEINRICH 1990; KORDOS 1994), the malacological (FŰKÖH et al. 1995), palynological (MAGYARI 2002), and archaeological data (KORDOS & RINGER 1991; RINGER & MESTER 2001), the climatostratigraphic system (MIS) (SHACKLETON et al. 1990, VOGELSANG 1990; DEMENOCAL 1995), the „arvicolid thermometer" method (KRETZOI 1956; KORDOS 1978), the palaeomagnetic investigations of travertines (SCHEUER & SCHWEITZER 1979; KORPÁS et al. 2004) and the radiometric dates (KROLOPP 1977; SZÖŐR & KORDOS 1981; SCHWARCZ & SKOFLEK 1982; RINGER 2002; ADAMS 2002; PAZONYI 2006).

II.2. Databases

Following the selection and age determination of localities, the data was organized into databases. Different databases were needed for different methods, but all of them are based on specimen numbers of mammalian taxa from the selected localities. Data on Chiroptera were excluded because bats present problems in many respects: (1) the analysis of bat fauna is not uniform, (2) the bats' cave habitat is different from habitats of other members of the vertebrate fauna, (3) specimen count of bats is difficult to interpret, because these animals live in colonies in different parts of caves.

Table I

List of localities and their ages in the database

Locality	Age (ka)	Locality	Age (ka)
Rigó-lyuk layer 1	0.2	Kőlyuk II. layer 15–17	7.6
Rigó-lyuk layer 2	0.3	Rejtek I. kőfülke layer 5	7.8
Nagy-oldali-zsomboly layer 0	0.3	Ocsisnya-tető	8.6
Nagy-oldali-zsomboly layer 1–2	0.4	Rejtek I. kőfülke layer 6	8.8
Rigó-lyuk layer 3	0.5	Rejtek I. kőfülke layer 7	9.4
Nagy-oldali-zsomboly layer 3	0.7	Tücsök-lyuk	9.5
Rigó-lyuk layer 4	0.8	Petényi-barlang layer 5	9.5
Rigó-lyuk layer 5	1.2	Rejtek I. kőfülke layer 8	9.8
Nagy-oldali-zsomboly layer 4	1.5	Jankovich-barlang layer 4	9.8
Petényi-barlang layer 1	1.5	Peskő-barlang layer 1	10
Rigó-lyuk layer 6-7	1.8	Peskő-barlang layer 2	10.2
Nagy-oldali-zsomboly layer 5	2	Peskő-barlang layer 3	10.4
Rigó-lyuk layer 8-9	2.2	Peskő-barlang layer 4–5	10.8
Nagy-oldali-zsomboly layer 6	2.5	Peskő-barlang layer 6	11
Kis-kőháti-zsomboly layer 4	2.5	Peskő-barlang layer 7–8	11.4
Petényi-barlang layer 2	3	Jankovich-barlang layer 5	11.4
Rejtek I. kőfülke layer 1	3	Peskő-barlang layer 9	11.6
Petényi-barlang layer 3	4.5	Peskő-barlang layer 10	11.8
Rejtek I. kőfülke layer 2	4.5	Peskő-barlang layer 11	12
Jankovich-barlang layer 1	4.5	Peskő-barlang layer 12	12.2
Kőlyuk II. layer 1	5	Peskő-barlang layer 13	12.4
Kőlyuk II. layer 2	5.2	Peskő-barlang layer 14–15	12.8
Baradla-barlang	5.5	Peskő-barlang layer 16	13
Rejtek I. kőfülke layer 3	5.5	Peskő-barlang layer 18	13.4
Kőlyuk II. layer 3	5.5	Peskő-barlang layer 19	13.6
Hosszú-hegyi-zsomboly layer 2	5.5	Peskő-barlang layer 20	13.8
Kőlyuk II. layer 4	5.8	Jankovich-barlang layer 7	15
Kőlyuk II. layer 5	6	Bivak-barlang yellow layer	15.5
Jankovich-barlang layer 2	6	Bivak-barlang yellowish grey layer	17
Hosszú-hegyi-zsomboly layer 3	6	Jankovich-barlang layer 8	17
Rejtek I. kőfülke layer 4	6.5	Jankovich-barlang layer 9	17.5
Kőlyuk II. layer 6-7	6.5	Jankovich-barlang layer 10	18
Hosszú-hegyi-zsomboly layer 4	6.5	Jankovich-barlang layer 11	20
Kőlyuk II. layer 8	6.8	Függő-kői-barlang layer 4	22
Petényi-barlang layer 4	7	Függő-kői-barlang layer 5	22.5
Kőlyuk II. layer 9–11	7	Függő-kői-barlang layer 6	23.3
Hosszú-hegyi-zsomboly layer 5	7	Függő-kői-barlang layer 7	23.8
Kőlyuk II. layer 12–14	7.3	Függő-kői-barlang layer 8	24.2
Hosszú-hegyi-zsomboly layer 6	7.5	Függő-kői-barlang layer 9	24.6

Table I cont.

Locality	Age (ka)	Locality	Age (ka)
Függő-kői-barlang layer I	25.5	Uppony I. kőfülke layer 4–5	200
Gencsapáti	26	Uppony I. kőfülke layer 6	205
Függő-kői-barlang layer II	26.2	Budapest, Vár-hegy, Hotel Hilton	220
Függő-kői-barlang layer III	27	Nagyharsány-hegy 6	250
Istállós-kői-barlang	30	Hórvölgyi-barlang	250
Tokod I	40	Kőrös-barlang layer 5–7	255
Szeleta-barlang	45	Solymári-ördöglyuk	260
Diósgyőr-Tapolca-barlang layer II/4	50	Pongor-lyuk	270
Suba-lyuk layer 10-16	64	Szuhogy-Csorbakő	270
Érd	73.5	Tar-kői-kőfülke layer 1	290
Diósgyőr-Tapolca-barlang layer II/5	77	Tar-kői-kőfülke layer 2–3	300
Tokod II	80	Budapest, Vár-hegy, Fortuna str. 16–18.	310
Lambrecht Kálmán-barlang	82	Budapest, Vár-hegy, Fortuna str. 25.	310
Tar-kői-kőfülke locality IV	97	Budapest, Vár-hegy, Országház str. 16.	320
Tata	100	Vértesszőlős II	320
Bajót Rock shelter 3	101	Tar-kői-kőfülkelayer 4–7	320
Poros-lyuk	104	Tar-kői-kőfülke layer 8–14	350
Tatabánya, Kálvária-hegy Rock shelter 4	105	Vár-hegy, Táncsics M. str. 23., Úri str. 72.	400
Süttő 9	109	Tar-kői-kőfülke layer 16	440
Uppony, Horváti-lik layer 7	110	Nagyharsány-hegy 4	500
Uppony, Horváti-lik layer 8	111	Uppony I. kőfülke layer 10	500
Uppony, Horváti-lik layer 9/A	112	Villány 6	640
Eger, Dobó-bástya	112	Kövesvárad	700
Uppony, Horváti-lik layer 10	113	Villány 8	800
Uppony, Horváti-lik layer 11	114	Somssich-hegy 2	900
Uppony, Horváti-lik layer 12	114.5	Betfia 9	1000
Uppony, Horváti-lik layer 13	115	Villány 5	1100
Uppony, Horváti-lik layer 14	115.5	Osztramos 8	1200
Uppony, Horváti-lik layer 15	116	Újlaki-hegy	1200
Uppony, Horváti-lik layer 16	116.5	Osztramos 2	1400
Uppony, Horváti-lik layer 18	117	Včeláre layer 3+3B	1500
Uppony, Horváti-lik layer 20	118	Koliňany layer 1–3	1700
Uppony, Horváti-lik layer 21	120	Villány 3	2000
Por-lyuk	120	Osztramos 3	2000
Süttő 6 layer 1–5	128	Osztramos 7	2300
Süttő 6 layer 6–10	132	Beremend 15	2700
Uppony I. kőfülke layer 1	170	Beremend 11	3000
Uppony I. kőfülke layer 2	175	Beremend 5	3100
Uppony I. kőfülke layer 3	180	Beremend 26	3200

The „raw database" consists of the localities or fossiliferous layers ranked according to their assigned ages and the number of specimens of mammalian species. Because of differences in the species and specimen number at different localities, and to eliminate taxonomic inconsistencies, the „raw database" needed further processing, amendment and standardization. The first step was to convert specimen numbers into percent proportion within faunas in all localities. If the age of two or more localities was equal, the percent proportions of their mammalian species needed averaging. In these cases weighted average values were entered in the database for the given age. If a species is missing from individual localities for taphonomic reasons, but is present in other temporally and geographically adjacent localities, the average of number of specimens at the two closest localities is entered into the database. Since the aim was to reconstruct the entire mammalian fauna of the Carpathian Basin in the studied period, the database also includes species which were not present at any of the selected localities. These species are registered in the database from faunas of localities which were unsuitable for quantitative studies. Following these additions to the database, proportion values of all ages were normalized. This „enhanced database" served as a basis for similarity and longevity studies (Fig. 1).

The database for cluster analysis differs from the „enhanced database", because it consists of normalized proportion values of small mammals (<1 kg body weight) only. The database used for examination of evolutionary lineages is similar to the database for cluster analysis. In this case values of arvicolids of same evolutionary lineage were extracted from the „enhanced database". Separate databases were constructed for all evolutionary lineages.

The „enhanced database" also served as the basis for ecological investigations' databases, but in these cases values were sorted by different ecological characters of species. The database that was used to calculate the diversity index consists of non percental proportion of species within faunas. Databases used for determination of body size distribution and the trophic preferences contain percent proportion values within faunas of various ecotypes. The body size categories follow those of ANDREWS et al. 1997, the trophic categories were distinguished by a cluster analysis with respect to the main food sources for mammalian species.

The database of ecological units consists of 15 variables (6 trophic and 8 body size categories, and the diversity index). Faunas of the same ecological character were distinguished by cluster analysis from this database. Other databases were used for characterization of ecological units. These databases in all cases consist of values of one variable only. Cluster analysis for each variable helped to determine range for their low, medium and high values.

III. METHODS

The applied methods fall into two categories. Some of them are based directly on the species composition of mammalian faunas (cluster analysis, similarity study, longevity studies and investigation of evolutionary lineages). The other group of applied methods

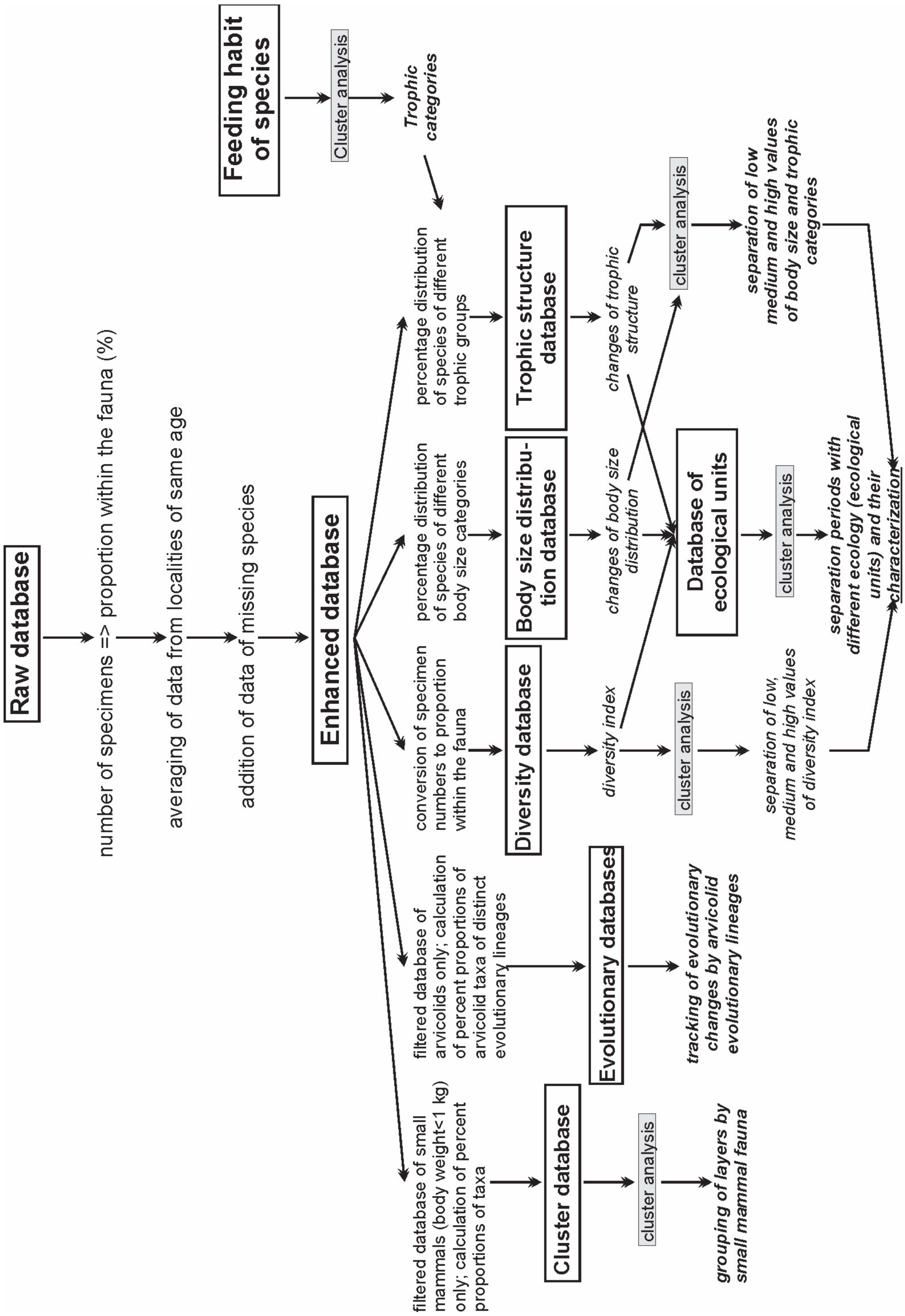

Fig. 1. Summary of the databases and flow chart of the analyses performed.

consists of taxon-free methods, which are based on ecological parameters (body size, trophic preferences, number of species) of mammalian species and communities. The distribution of ecotypes in a fauna (ecological variables) is primarily determined by the climate and vegetation. Ecological variables (distribution of body size and the trophic preferences, diversity index) together define the ecological unit which is characteristic to the community.

The purposes of the two groups of methods are different. Methods in the first group are suitable to demonstrate changes of mammalian faunas, to separate time periods, and to characterize the fauna of these periods. On the other hand, taxon-free methods permit the ecological characterization of these periods and the identification of periods of very similar ecological characters, but of different species composition (PAZONYI 2004).

III.1. Methods based on species composition

III.1.1. Cluster analysis

Cluster analysis provided equally useful results both as a separate examination method and as a part of the taxon-free methods. The database for cluster analysis consists of small mammals (<1 kg body weight) only, because we have far more data of small mammals. This way, changes of small mammal faunas were distinguished from changes of the whole mammalian faunas. Cluster analysis as a part of taxon-free methods also played an important role in characterization of ecological variables and in separation of ecological units.

III.1.2. Similarity study

Percentage similarity is an index that measures the common part of two temporally or spatially adjacent communities. Faunal changes can thus be demonstrated using similarity. Low similarity indicates faunal changes, whereas high values indicate stability of communities. Percentage similarity is calculated as follows (KREBS 1989):

$$P = \sum \text{minimum} (p_{1i}, p_{2i});$$

where P is the percentage similarity between community 1 and community 2, p_{1i} is percentage of the ith species of community 1, and p_{2i} is percentage of the ith species of community 2.

Similarity study was based on whole faunas. Moving average calculation was applied for smoothing the data and to obtain curves. High density of data in the last 30 ka required that a 1000 year sliding window was shifted in 400 year increments. The preceding interval (300-30 ka) also has a significant amount of data, thus a 10000 year sliding window with 5000 year increment was adequate. Between 500 and 300 ka, where data are sparser, a 50 ka window and shift was suitable. For all older data a 500 ka window and 100 ka increments were used. Through smoothing, the interfering peaks that masked the actual changes could be filtered out, allowing a better interpretation of the curves.

III.1.3. Longevity studies

III.1.3.1. First Occurence Datum–Last Occurence Datum studies

Distribution of longevity within a population is influenced by stability of environment. In periods characterized by stable environmental conditions the long-ranging species were common and the number of appearance and disappearance events was low. But an increase in the number of short-ranging species and appearance and disappearance events suggests changes of environmental conditions (e.g. climate, vegetation) (BARRY et al. 1995).

Because the aim was to study the mammalian fauna of the Carpathian Basin, first and last appearances of individual species apply to this area only (Fig. 2a-2b) (PAZONYI 2006).

Contrary to other methods, results of longevity studies are applied to intervals. Intervals' lengths were determined by density of data and frequency of events. Four different interval lengths were used: (1) 5 ka in the intervals with the highest density of data (Holocene and Late Pleistocene), (2) 10 ka in the early Late Pleistocene (faunas older than 30 ka), (3) 50 ka in the later Middle Pleistocene and (4) 100 ka interval with the lowest density of data (Early and early Middle Pleistocene).

Turnovers of faunas were calculated by the number of the first and last occurrences in all intervals.

III.1.3.2. Distribution of longevity

Apart from turnovers, the distribution of longevity was also found to be useful. The longevity is based on the first and last occurrence datum of species. Species were divided into three groups (short, medium or long longevity) by cluster analysis.

III.1.4. Investigation of evolutionary lineages

Beside the analysis of the whole mammalian fauna, a separate study focusing on arvicolids (Arvicolidae), that are the most abundant family, is also justified (Fig. 3). Arvicolids became the dominant group of mammalian faunas in Quaternary, after they replaced the previously very abundant cricetids and murids. Owing to their very fast evolutionary and reproductive rates, they appear in great diversity and abundance in the material of Quaternary localities. The rate of species appearence and longevity is indicative of the stability of environment.

Four evolutionary lineages of Arvicolidae are traceable in the Carpathian Basin:

(1) *Mimomys–Arvicola* lineage,

(2) *Propliomys–Pliomys* lineage,

(3) *Borsodia–Lagurodon–Lagurus* lineage,

(4) *Microtus* lineage (KORDOS 1995).

III.2. Taxon-free methods

The taxon-free examination of communities is based on ecotypes that are established on the basis of the number of species in the communities, and the body size and trophic preferences of the species in a community. The distribution of the ecotypes is an ecological variable characteristic to the community.

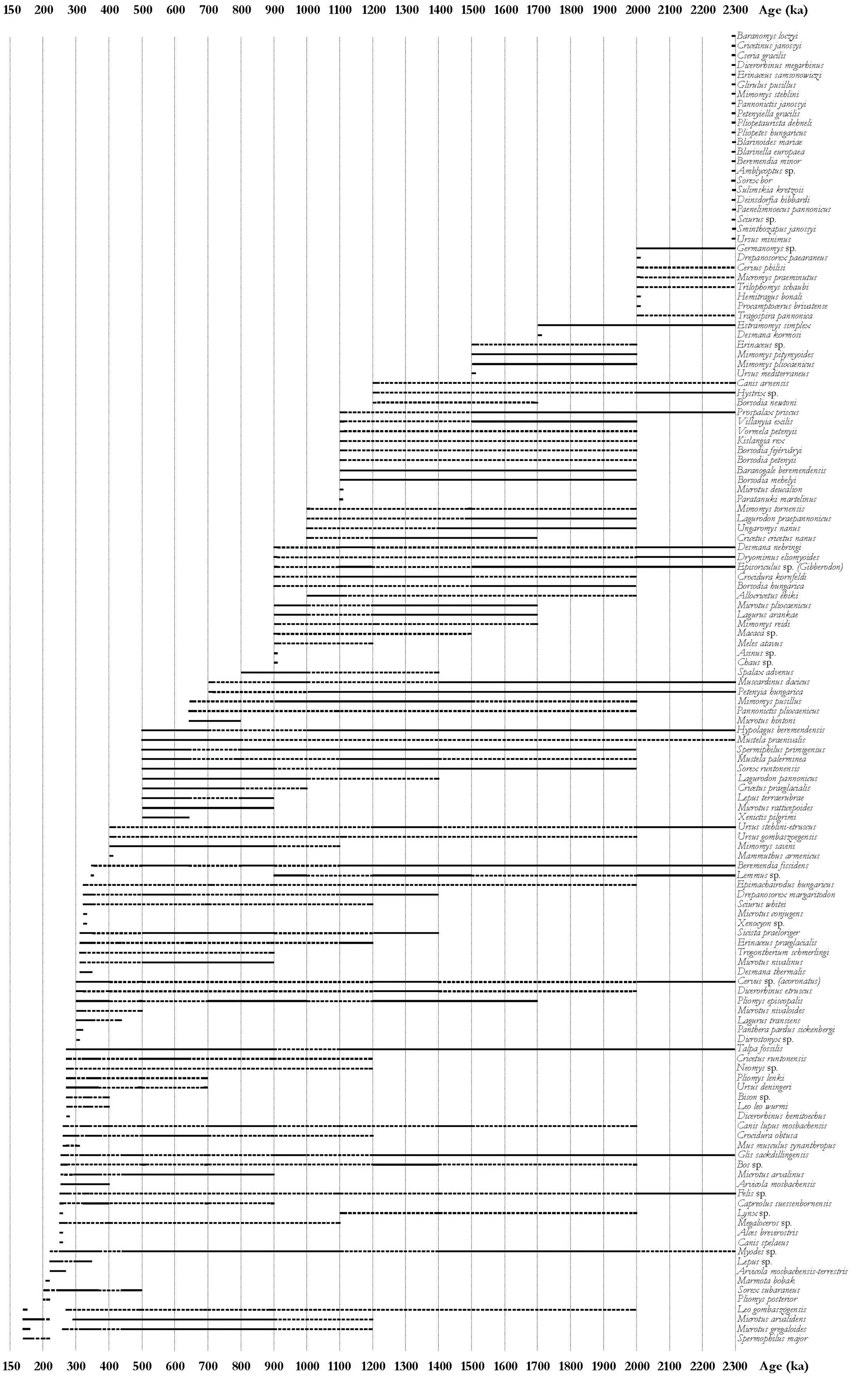

Fig. 2a. Ranges of the Quaternary mammals in the Carpathian Basin (part 1).

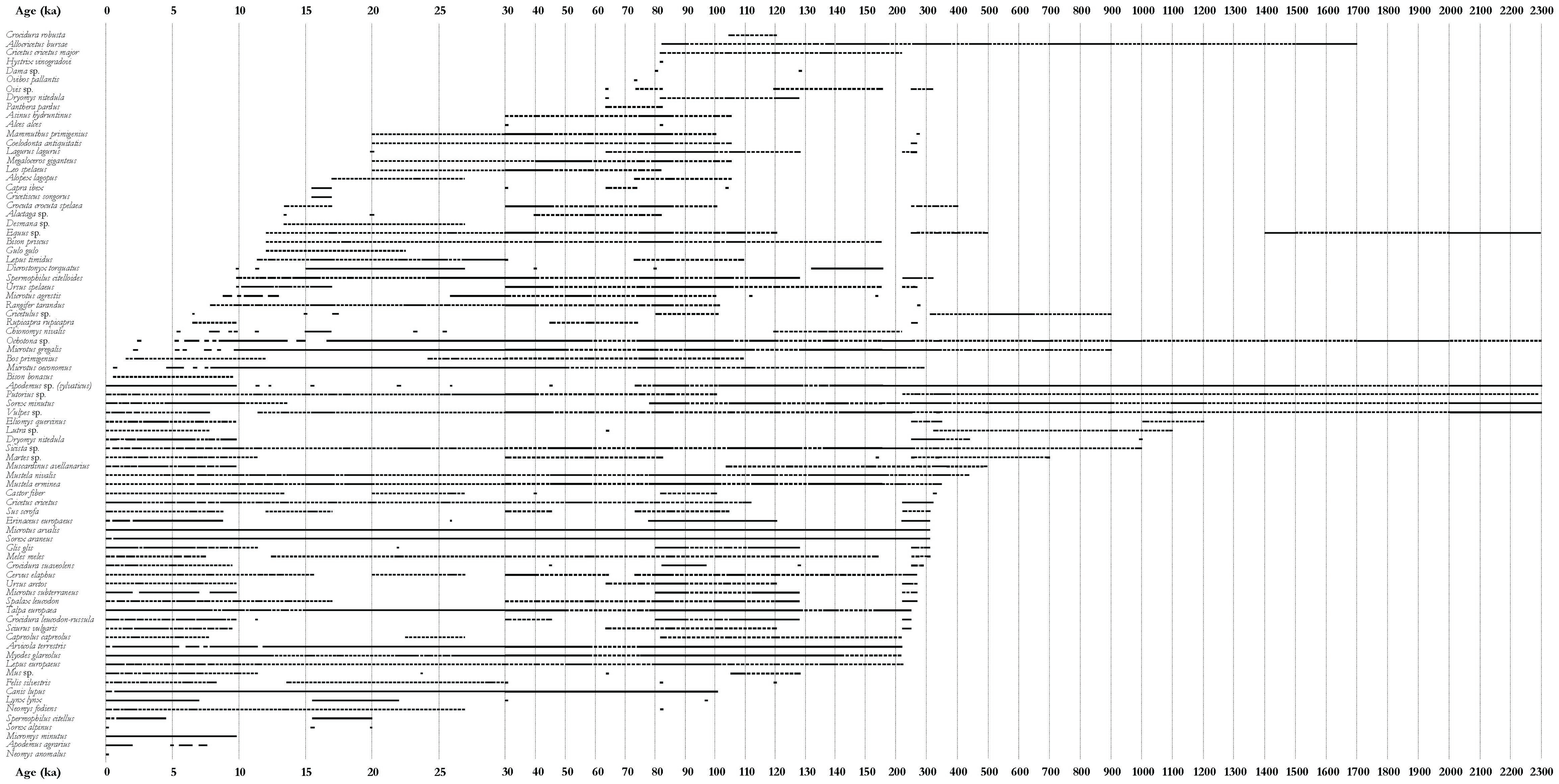

Fig. 2b. Ranges of the Quaternary mammals in the Carpathian Basin (part 2).

Fig. 3. Changes in proportion of arvicolid species in the Carpathian Basin in the past 3.5 Ma.

The diversity index determined by the number of species, the distribution of body size, and the trophic preferences are defined as ecological variables. These ecological variables together define the ecological unit characteristic to the community, which can be used for stratigraphic studies (Fig. 4).

In case of extinct species, this model is based on ecological preferences of their extant relatives and on tooth morphology. Body size was determined by extant relatives of species, and trophic preferences were determined by tooth morphology and by analogy of extant relatives.

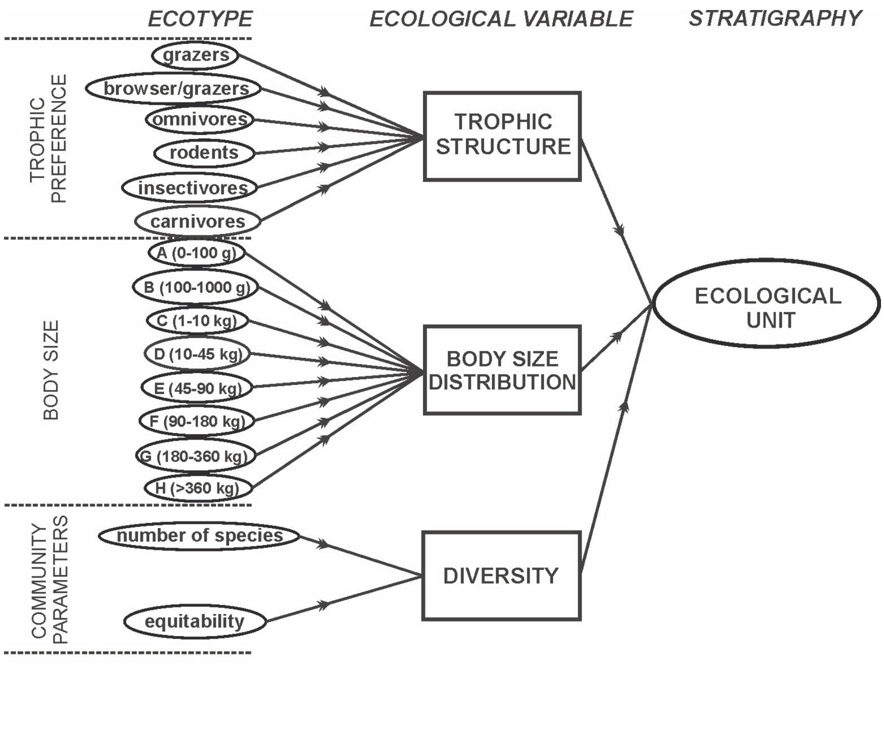

Fig. 4. Flowchart of the taxon-free method (PAZONYI 2004).

III.2.1. Ecotypes

The ecotypes serve as the primary basis of the taxon-free methods but they also provide information on the environment. Changes in the number of species and the body size in communities depend on the environment. Trophic preference of animals is primarily determined by the vegetation.

III.2.1.1. Number of species

The number of species is primarily determined by the environmental conditions and the vegetation. In adverse circumstances and less complex environments (such as the tundra), the number of species is lower than in a more balanced and complex environment (e.g., in tropical rainforests), because the number of available niches is lower (ANDREWS 1995).

Determination of number of species was based on the „enhanced database", in order to eliminate biases resulting from taphonomic differences.

III.2.1.2. Body size

Estimation of body size can be made by comparing the data of extant and fossil species, or by using the correlation between tooth and body sizes (LEGENDRE & ROTH 1988). For the studied period, the comparative method yields good results, since the majority of the species included in the database still exists today, and reliable information is available on the extinct species.

For the comparative method, the body size categories of ANDREWS et al. (1997) were adopted. Species were classified into eight categories: (A) 0-100 g, (B) 100-1000 g, (C) 1-10 kg, (D) 10-45 kg, (E) 45-90 kg, (F) 90-180 kg, (G) 180-360 kg and (H) over 360 kg. (Note that the original categories were defined in pounds, rather than in kilograms).

III.2.1.3. Trophic preferences

Performing a cluster analysis, the following six trophic groups were distinguished with respect to the main nutrition sources for mammalian species: (1) sprout, root, seed and fruit eaters with no animal food (granivores), (2) frondage eating grazers (browsers/grazers), (3) grazers (grass only), (4) carnivores (animal food only), (5) insectivores, (6) omnivores (with dominance of vegetal food) (PAZONYI 1999, 2004, 2006).

III.2.2. Ecological variables

III.2.2.1. Diversity index

The concept of diversity takes into account two independent variables: the number of species and the distribution of specimens among the species. A diversity index quantifies the diversity of the fauna on the basis of both independent variables. The value of a diversity index is high if at least one of the variables takes a high value. Generally, faunas with high diversity index are of high number of species and equitability of specimens distribution. However, it can also be high with relatively low number of species, if the specimens are very evenly distributed among species. Both high turnover (rate of material flux), which is characteristic of tropical forest, and environmental heterogenity can lead to high values of diversity index (ANDREWS 1995).

Diversity is calculated using the Shannon-Weaver diversity index (SHANNON & WEAVER 1949):

$$H' = -\sum_{i=1}^{N} p_i * \ln p_i$$

where H' is the Shannon-Weaver index, and p_i is the ratio of the i^{th} species in the fauna. The ratio of the i^{th} species was determined on the basis of number of M1.

III.2.2.2. Body size distribution

Among modern mammalian faunas, size structure changes along vegetation and climatic gradients. Species of large (8-250 kg, categories C-G) and very large (>250 kg, categories G-H) size are more common in areas with more open vegetation (woodland and grassland) than in forests, because large herbivores can subsist on plants with relatively low nutrition value (such as grass). In forests, small and medium-sized mammals (typically <8 kg in body size, categories A-C) dominate, since a wide variety of easily digestible food is available (e.g. fruits, seeds). Many mammals adapted to an arboreal mode of life, which also favours small size. Areas with more open vegetation may lack species of medium size (0.5-8 kg, categories B-C), whereas environments with closed vegetation are characterized by the presence of all categories (EISENBERG 1981; FLEAGLE 1985; LEGENDRE 1989). However, these observations are true in tropical areas only. In contrast, tundra is an open area, but it can only support a limited number of large mammals, so the body size distribution of this habitat is dominated by small mammals (categories A-B).

Herein the body size distribution of a given fauna is obtained through ranking the body size categories by size, followed by a graphical illustration of the percentage of species within each category. This representation method differs from the cenogram, where the body size pattern of the fauna is established through ordering the members of the fauna by size (excluding carnivores and bats) (LEGENDRE 1986, 1989).

III.2.2.3. Trophic structure

Similarly to the body size distribution, the trophic distribution of modern mammalian faunas also changes along vegetation and climatic gradients. More open areas (savanna, woodland) are characterized by a higher percentage of herbivores (~55%) and carnivores (~20%). On the other hand, in forests and gallery forest the percentage of these groups decreases, while omnivores and insectivores are more common (GUNNELL et al. 1995).

Temporal patterns of trophic distribution of the studied faunas, similarly to the body size distribution, allow the interpretation of vegetation and climatic changes within the studied period.

III.2.3. Ecological units

The ecological units, which are characterized by diversity index, distribution of body size and trophic preferences, are the units of highest rank in the taxon-free method. These units are thought to be controlled by climate and vegetation conditions, and they can also be used for stratigraphic purposes.

Determination of ecological units is based on 15 variables (6 trophic preference types, 8 body size categories, and the diversity index). In the first step, faunas with similar ecological characteristics were separated by a cluster analysis. In the second step, the separated groups were characterized by these variables. Cluster analyses were performed using each distinct variable (percent proportions of variables of body size and trophic preferences). Based on these cluster analyses, ranges of low, medium and high values were defined for each variable (Table II). The limits of these ranges are different for each variable, their values depend on frequency of the given variable in a mammalian fauna and deviation of these values.

Because data from all Quaternary localities suitable for statistics were used in the analyses the obtained ranges are applicable for the entire Quaternary. Ten ecological units were distinguished and characterized by this method in the examined period.

Table II

Ranges of high, medium and low values of the ecotypes

Ecotype	Low	Medium	High
granivores	<45%	45-70%	70%
browsers/grazers	<5.7%	5.7-14%	14%
grazers	<5%	5-10%	10%
carnivores	<7.5%	7.5-12%	12%
insectivores	<20%	20-35%	35%
omnivores	<4%	4-8%	8%
A (0-100 g)	<45%	45-72%	72%
B (100-1000 g)	<17%	17-25%	25%
C (1-10 kg)	<2.5%	2.5-5.6%	5.6%
D (10-45 kg)	<2.5%	2.5-4.5%	4.5%
E (45-90 kg)	<4%	4-8%	8%
F (90-180 kg)	<7%	7-12%	12%
G (180-360 kg)	<7%	7-22%	22%
H (360 kg)	<2.5%	2.5-7.5%	7.5%
diversity index	<2.45	2.45-2.85	2.85

IV. RESULTS

IV.1. Determination of ecological units

IV.1.1. Results of the cluster analysis (Fig. 5)

Cluster analysis as an independent method resulting in grouping the small mammal faunas of different localities on the basis of abundance distribution of species within each fauna. Eight groups were separated within the small mammal fauna of the examined localities by this method. These results show that the Early and Middle Pleistocene small mammal faunas differ significantly from that of the Late Pleistocene, and groups which are characterized with different composition of small mammal fauna were cyclically alternating within the Late Pleistocene owing to the significant climatic changes.

The cluster analysis demonstrates that the first significant change in the small mammal fauna happened at 950 ka. By this time the small mammal fauna, which was mainly characterized by extinct arvicolids (*Mimomys* and *Microtus* species) (type 1), disappeared. This type of small mammal fauna was typical during the whole Early Pleistocene and in early Middle Pleistocene. Following a smaller change, when the type 1 of small mammal fauna recurred at a single locality (750 ka), the next great change within the small mammal fauna occured at 280 ka. In this time the small mammal fauna, which was mainly characterized by arvicolids (*Microtus*, *Lagurodon* and *Pliomys*) and a significant proportion of insectivores and glirids (type 2), was replaced by the small mammal fauna dominated by *Microtus* species, which was typical in the whole Late Pleistocene and Holocene.

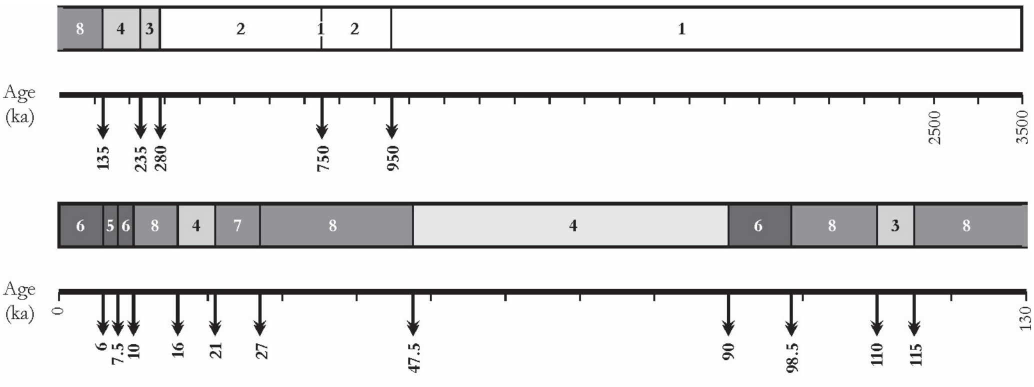

Fig. 5. Temporal ranges of groups identified as a result of cluster analysis. The upper scale begins at 3.5 Ma. Note that the scale changes at 2.5 Ma. Spacing of tick marks is 500 ka before, 100 ka after 2.5 Ma. On the lower scale, tick marks are spaced at 10 ka. Cold intervals are light grey, warm intervals are dark grey and the transition intervals of medium shade. For explanation of the numbers of groups, see text.

Later changes in the small mammal fauna were closely connected with climate changes. Small mammal assemblages which were adopted to the cold and warm periods alternated cyclically, reflecting changes of climate and vegetation.

Six different types of small mammal faunas were distinguished in the Late Pleistocene and Holocene periods on the basis of the cluster analysis. Two types characterize the cold periods, two other types are restricted to the rather warm periods, whereas yet two more types appeared in the „transitional" periods. Both types of small mammal faunas which were typical for cold periods appeared in two intervals: (1) between 280 ka and 235 ka, and (2) between 115 ka and 110 ka. The dominance of *Microtus arvalis* characterized this type of small mammal fauna (type 3). The other type of cold-adapted small mammal fauna appeared several times in the Late Pleistocene and Holocene: (1) between 235 ka and 135 ka, (2) between 90 ka and 47 ka and (3) between 21 ka and 16 ka. This type of small mammal fauna was characterized by the abundance of not only *Microtus arvalis* but also other arvicolids, *Microtus gregalis* and *Microtus oeconomus*. Moreover, other cold-adopted species (*Lagurus lagurus*, *Dicrostonyx torquatus*, *Ochotona pusilla*) also constituted a significant proportion of the assemblage (type 4).

The two types of small mammal faunas which were adapted to the warm periods differ from each other in proportion of *Apodemus sylvaticus*, *Myodes glareolus*, glirids and insectivores. The first one is characterized by the dominance of *Apodemus silvaticus* and a high proportion of glirids (type 5), whereas the other one has nearly equal proportions of *Apodemus sylvaticus* and *Myodes glareolus* as well as a high proportion of insectivores (type 6). While the type 5 was typical in Holocene between 7.5 and 6 ka only, the type 6 appeared also in the Late Pleistocene (98.5-90 ka) and Holocene (10-7.5 ka and 6-0 ka).

One of the two „transitional" types of small mammal fauna was typical between 27 and 21 ka only. This type is characterized by nearly equal proportions of *Microtus arvalis* and *Microtus gregalis* as well as a high proportion of *M. oeconomus* (type 7). The other „transitional" type is characterized by *M. arvalis*, accompanied by mainly steppe species such as *Spermophilus*, *Spalax*, *Alactaga*, *Sicista* and *Cricetus* (type 8). This community type appeared three times, between 110 and 98.5 ka, between 47.5 and 27 ka, and between 16 and 10 ka.

There is one interval which is not easily classifiable into any type of small mammal fauna. For the interval between 135 and 115 ka, the cluster analysis classified a significant part of faunas to the type 8, but assignment to the types 7 and 5 also appeared. Despite the ambiguity, this interval was classified to the type 8.

IV.1.2. Results of similarity study (Fig. 6)

Contrary to cluster analysis, the similarity study indicated changes in the complete mammalian fauna. Therefore changes which affected the large mammal fauna only were detected as well. The similarity study is significantly more sensitive than the cluster analysis. Not only changes of the fauna, but also the magnitude of changes was detected by this method. Large changes were observed mainly in the Early and Middle Pleistocene, which is explicable by sparse data as well as the temporal distance between the localities. The significantly more dense data of Late Pleistocene allowed for detection of smaller changes.

The first significant change of mammalian fauna occured 950 ka ago according to the cluster analysis. However, based on similarity study, prior to this event there were other large and small changes in the mammalian fauna. Ages of the big changes were: (1) 3.15 Ma, (2) 2.85 Ma and (3) 1.45 Ma, while the smaller change was 1.15 Ma ago.

The next big change in the small mammal fauna occured at 280 ka according to the cluster analysis. Following the change at 950 ka, one big and two smaller changes were detected by the similarity study up to this time. The big change of mammalian fauna at about 700 ka can probably be correlated with a small change (750 ka) which appeared in the cluster analysis. The smaller changes were at 475 ka and 305 ka.

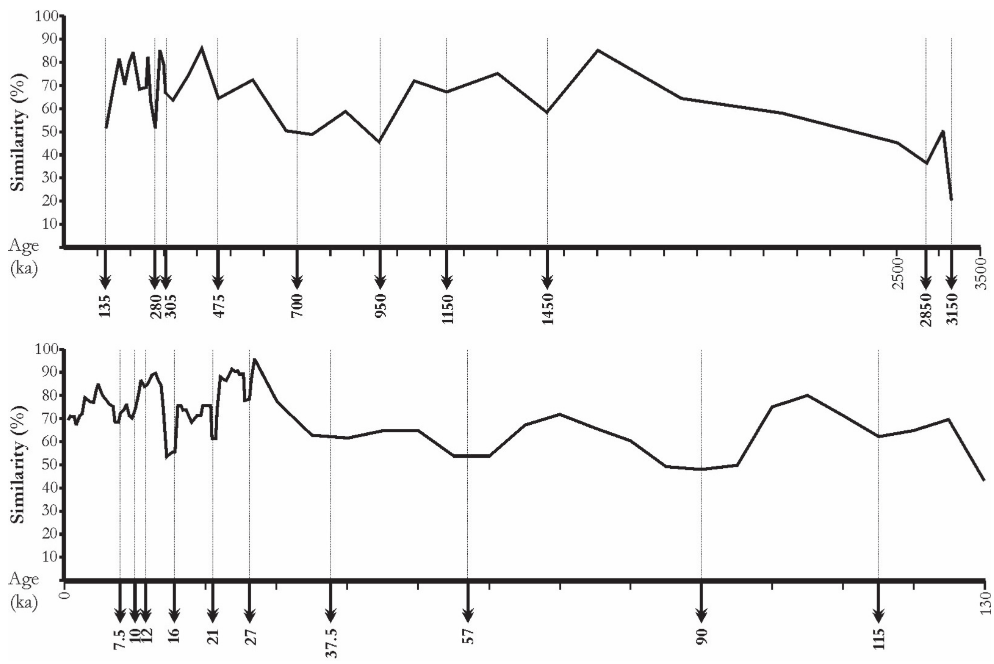

Fig. 6. Faunal changes inferred from the similarity study. The upper scale begins at 3.5 Ma. Note that the scale changes at 2.5 Ma. Spacing of tick marks is 500 ka before, 100 ka after 2.5 Ma. On the lower scale, tick marks are spaced at 10 ka.

Following the large change at 280 ka, results of cluster analysis corresponded roughly with results of the similarity study. Based on the similarity study only two significant faunal changes happened in this period (135 to 90 ka), the other changes were smaller. Differences of results from the two methods were the following: (1) changes at 110 ka and 98.5 ka couldn't be detected by similarity study; (2) the similarity study indicated faunal changes at 57 ka and 37.5 ka, while the results of cluster analysis put the change between these two dates to 47.5 ka; (3) similarity study indicated a significant change 12 ka, but results of cluster analysis suggest that this change didn't affect the small mammal fauna; (4) similarity study couldn't detect the change of small mammal fauna 6 ka.

These results demonstrate that the similarity study provided a higher resolution for the examined period, but the ages of significant changes of fauna were similarly identified by both methods.

IV.1.3. Results of longevity studies

Longevity studies are based on two independent methods: (1) examination of appearance and disappearance events based on the first and the last occurrence datum of species (FOD-LOD), and (2) examination of distribution of longevities.

IV.1.3.1. Appearance and disappearance events (FOD-LOD) (Fig. 7)

Appearance and disappearance events of species form cycles, where maxima of appearance events generally precede the maxima of disappearance events, but in several cases the two kinds of maxima coincide. The first appearance maximum was 3.3 Ma in the examined period in the Carpathian Basin. The cycle started before the beginning of the examined pe-

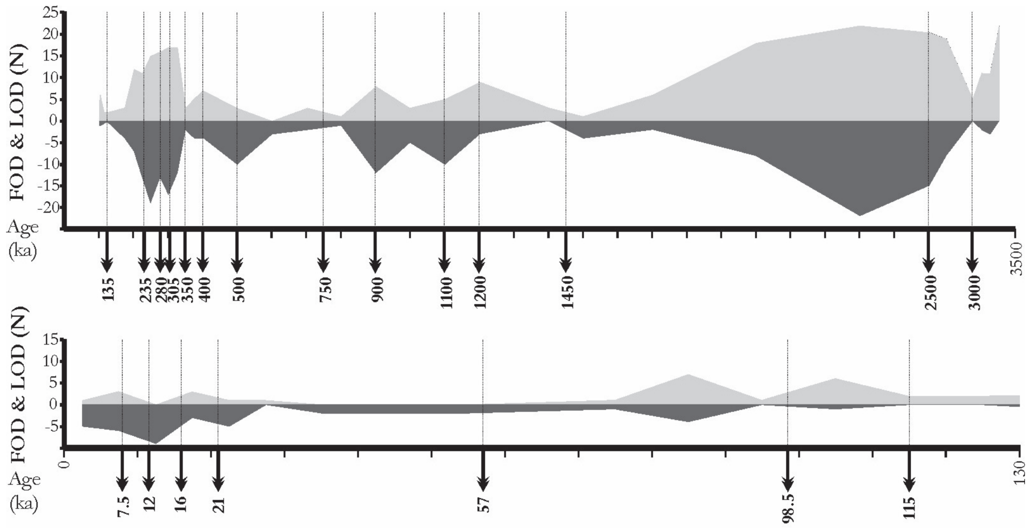

Fig. 7. Appearance and disappearance events during the last 3.5 Ma. Appearance events are in light grey, disappearance events are in dark grey. The upper scale begins at 3.5 Ma. Note that the scale changes at 2.5 Ma. Spacing of tick marks is 500 ka before, 100 ka after 2.5 Ma. On the lower scale, tick marks are spaced at 10

riod, its end was 3 Ma. The next large appearance and disappearance cycle occured between 3 and 1.45 Ma, its maximum was between 2.5 and 2.3 Ma. Both in terms of appearances and disappearances this was the largest maximum in the examined period. The next big cycle was between 1.45 Ma and 750 ka. Within this cycle there were two appearance maxima (1.2 Ma and 900 ka) and two disappearance maxima (1.1 Ma and 900 ka). The first appearance peak preceded the disappearance peak by about 100 ka, the other two peaks were synchronous. In the following cycle (between 750 and 350 ka) besides several appearances there were a relative large number of species disapperances (10 species). In this cycle there was also a temporal shift between the two events, however in this case the disappearance peak (500 ka) preceded the appearance peak (400 ka) by 100 ka. In the following cycle (between 350 and 135 ka) the appearance and disappearance events were nearly simultaneous. There was a conspicuous appearance maximum between 305 and 235 ka, whereas within this interval there was a downturn of disappearances 280 ka. The last 135 ka make up one cycle, subdivided into smaller subcycles. Within the whole cycle the maximum of appearances was about 85 ka and the maximum of disappearances was about 12 ka. However, the density of data made possible subdivision of this cycle into two subcycles. These are as follows: (1) between 135 and 57 ka; (2) from 57 ka to the present. The first subcyle was dominated by appearances, while the second one – by disappearances. Appearance events are clustered between 115 and 75 ka, although there was a downturn 98.5 ka. Disappearances also occured in two waves, both of them were followed by a rise of appearance events. The first peak of disappearance was 21 ka, this was followed by a small peak of appearance events 16 ka. The second maximum of disappearance was 12 ka, whereas the following maximum of appearance was 7.5 ka.

IV.1.3.2. Distribution of longevities in the examined period (Fig. 8)

Distribution of longevity was determined by species of short (0-500 ka), medium (500 ka-1.2 Ma) and long (>1.2 Ma) longevities. Species longevity is controlled by the body size and by the stability of environment, so species with long longevities indicate stable environment, whereas volatile environments are characterized by species with short longevities.

The examined period is divided in three parts. At the start of the Pleistocene (between 2.5 and 2.15 Ma) long-lived species were dominant in the fauna with a relatively small number of species (25 species), however number of short longevity species was also significant (15-20 species). At the end of this cycle number of species with middle and short longevities decreased to only a few (3-5) species.

The next cycle started at 2.15 Ma and lasted until about 475 ka. This cycle was generally characterized by dominance of species with long and medium longevities. The number of species with long longevities increased to 45 by 2.05 Ma, then remained at this value till 950 ka, when it began to decrease gradually. Species with medium longevities also began a slow increase but this increase accelerated about 1.45 Ma. Number of species of medium longevities decreased about 950 ka, too. Changes in number of species with short longevities were opposite to the above mentioned trends. At the start of the cycle there was a moderate decrease in number of these species, followed by an intense decrease 1.45 Ma, then there was a gradual increase till 950 ka. This cycle was characterized by a high stability of environment.

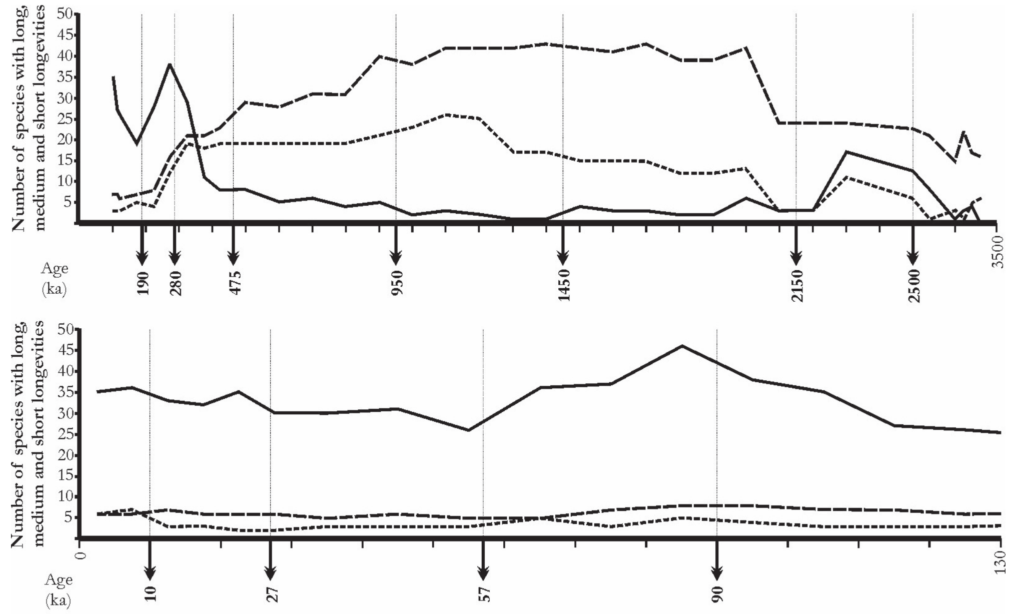

Fig. 8. Changes in the number of species with long (long dashed line), medium (short dashed line) and short (solid line) longevities during the last 3.2 Ma. The upper scale begins at 3.5 Ma. Note that the scale changes at 2.5 Ma. Spacing of tick marks is 500 ka before, 100 ka after 2.5 Ma. On the lower scale, tick marks are spaced at 10 ka.

A significant change in distribution of longevity occured between 475 and 280 ka. Apart from a more drastic decrease in number of species with long and medium longevities, the number of species with short longevities drastically increased and it exceeded the number of long-lived species for the first time in the examined period. From this point onward the fauna was characterized by the dominance of species with short longevities, consequently an instable environment is inferred. However, longevities in this period are constrained as they cannot extend beyond the present, so the results are distorted, as the increase in number of species with short longevities is an artefact.

The Late Pleistocene could be divided into smaller units because of the density of data. Between 280 and 190 ka, all categories showed a significant decrease. The number of species with medium and long longevities decreased from 20-25 to 5-10 species, while the number of species with short longevities decreased from 37 to 20 species. After this interval the number of species with medium and long longevities showed no significant changes, although the number of species with medium longevities reached and exceeded the number of species with long longevities 10 ka. The number of short longevity species increased between 190 and 90 ka, then gradually decreased till 57 ka and remained steady at a value of about 30 species. Following this period of stagnation a subsequent slow increase is observed till 27 ka.

IV.1.4. Results of evolutionary lineages study

Similarly to other methods of investigation, analysis of arvicolids evolutionary lineages also provides information on the stability of environment. Appearances or disappearances of a large number of species within the given evolutionary lineage indicate unstable environment. Evolutionary lineages were adapted from the works of KORDOS (1994, 1995).

Mimomys-Arvicola lineage (KRETZOI 1969; JÁNOSSY & VAN DER MEULEN 1975; CHALINE 1987; CHALINE & SEVILLA 1990; FEJFAR & HEINRICH 1990; FEJFAR et al. 1990). – Only one *Mimomys* species occured in the Late Pliocene material (*Mimomys stehlini*) then, following two appearance events, the group became predominant among the Early Pleistocene arvicolids. The first significant appearance event of this group was 2.7 Ma, when four species appeared (*Mimomys pitymyoides*, *M. hajnackensis*, *M. reidi*, *M. pusillus*). However, the group reached the greatest species richness 2 Ma, when two other species appeared (*Mimomys tornensis*, *M. pliocaenicus ostramosensis*). The great diversity of *Mimomys* ended between 1.1 Ma and 900 ka, when all of the species disappeared except *M. pusillus* and *M. savini*. The latter species was replaced by *Arvicola mosbachensis* 400 ka, which coexisted with a transitional species (*A. mosbachensis-terrestris)* between 270 and 250 ka. Finally, the transitional form gave rise to the extant *Arvicola terrestris* 220 ka (Fig. 3).

Propliomys-Pliomys lineage (RABEDER 1981; MALEZ & RABEDER 1984; CHALINE 1990). – This evolutionary lineage showed much less diversity than the former one. Though *Propliomys hungaricus* – which was typical of the Pliocene – episodically appeared 3.2 Ma, following this event taxa of this evolutionary lineage were missing from the material for a long time. The next species to appear already belonged to the genus *Pliomys* (*Pliomys episcopalis*), it appeared 1.7 Ma. This single species represented the evolutionary lineage till 700 ka, when *Pliomys lenki* appeared. *P. episcopalis* eventually disappeared 340 ka, *P. lenki* was present in the material till about 270 ka. A new species (*P. posterior*) appeared for a short interval (20 ka) about 220 ka. Following the very short occurrence of this species, this evolutionary lineage was no longer present in the Carpathian Basin (Fig. 3).

Borsodia-Lagurodon-Lagurus lineage (ZAZHIGIN 1980; RABEDER 1981; HORÁČEK 1990). – The oldest member of the evolutionary lineage (*Borsodia hungarica*) appeared 2,7 Ma. The group reached the greatest species richness 2 Ma, when another four species appeared (*B. fejervaryi*, *B. petenyii*, *B. mehelyi*, *Lagurodon praepannonicus*). Following the appearances of two other species, *Lagurodon arankae* (1.7 Ma) and *Lagurodon pannonicus* (1.4 Ma), the older forms became subordinate, and they disappeared entirely between 1.1 Ma and 900 ka. *Lagurus pannonicus* was replaced by *Lagurus transiens* 450-500 ka, which disappeared about 340 ka. After this time only *Lagurus lagurus* occurs in the materials of cold periods (Fig. 3).

Microtus lineage (KRETZOI 1969; RABEDER 1981; MALEZ & RABEDER 1984; HORÁČEK 1990). – The evolutionary lineage of the presently most widely dispersed arvicolids started 1.7 Ma, when *Microtus pliocaenicus* appeared. From this form two *Microtus* species (*M. arvalidens*, *M. gregaloides*) evolved first 1.2 Ma, then simultaneously with the disappearance of *M. pliocaenicus*, several new *Microtus* species appeared 900 ka (*M. hintoni*, *M. ratticepoides*, *M. arvalinus*, *M. nivalinus*, *M. gregalis*). The next great turnover, at the time of development of the extant arvicolids, was between 310 and 220 ka. At this time *M. arvalis*, *Chionomys nivalis*, *M. oeconomus* and *M. subterraneus* appeared, meanwhile a large part of the earlier species disappeared (Fig. 3).

Changes in the proportions of species of evolutionary lineages show an interesting pattern (Fig. 9). The predominant part of the arvicolid fauna was composed of members of the *Mimomys-Arvicola* lineage till 1.45 Ma. However, from this time onward the proportion of these species gradually decreased. They were replaced first by representatives of the *Borsodia-Lagurodon-Lagurus* lineage (between 1.45 Ma and 950 ka; between 700 and 475 ka), then later the species of the *Microtus* lineage (between 950 and 700 ka; from 350 ka to present). The largest proportion of species from the *Propliomys-Pliomys* lineage is registered between 475 and 350 ka.

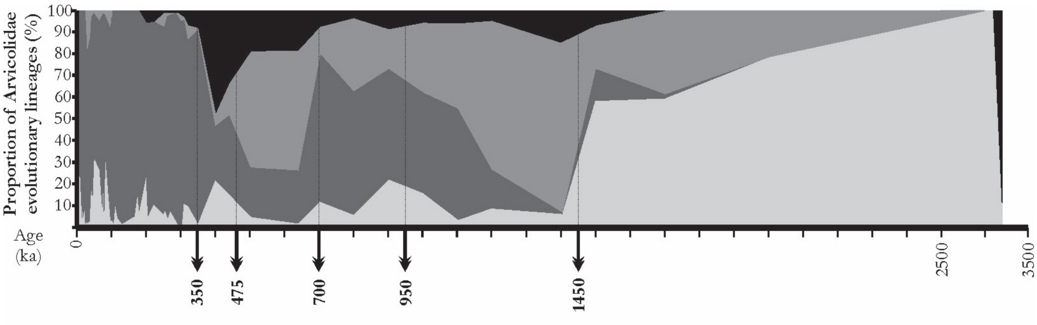

Fig. 9. Changing proportion of species in the different evolutionary lineages. Legend: light grey = *Mimomys-Arvicola* lineage; dark grey = *Microtus* lineage; medium grey = *Borsodia-Lagurodon-Lagurus* lineage; black = *Propliomys-Pliomys* lineage. The scale begins at 3.5 Ma. Note that the scale changes at 2.5 Ma. Spacing of tick marks is 500 ka before, 100 ka after 2.5 Ma.

IV.1.5. Results of ecological clustering

The first step of ecological investigation was the separation of faunas which had similar ecological characteristics by cluster analysis. Based on this investigation, ten distinct ecological units were separated; many of those recurred at multiple occasions in the examined period (Fig. 10). Resolution of this method was the best among all of the applied methods. Similarly to the previously discussed methods, resolution in the Late Pleistocene and Holocene, when there were more data, was far better than in the Early and Middle Pleisto-

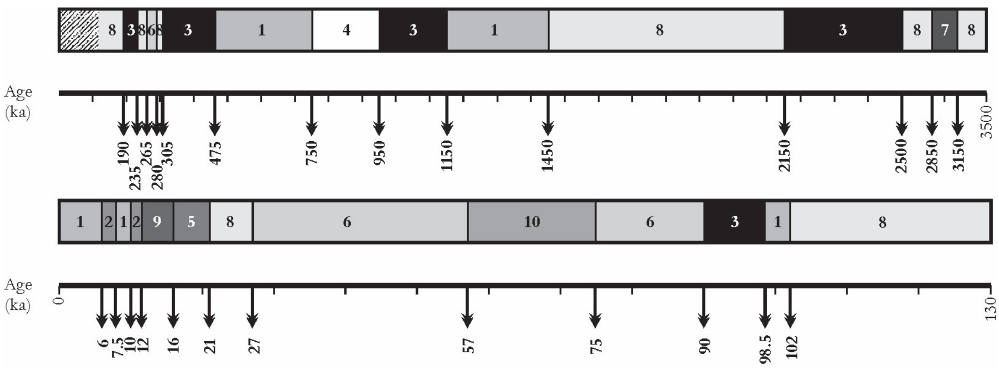

Fig. 10. Temporal ranges of ecological units. The upper scale begins at 3.5 Ma. Note that the scale changes at 2.5 Ma. Spacing of tick marks is 500 ka before, 100 ka after 2.5 Ma. On the lower scale, tick marks are spaced at 10 ka. For characterization of the ecological units (marked by arabic numbers), see text.

cene. The majority of the boundaries, which were identified with this method, coincided with the previously established ones, however, there were some events (265, 102 and 75 ka) which were demonstrable by this method only.

Ecological characteristics of mammalian fauna in the Carpathian Basin changed often during the Pleistocene and Holocene, as the mammalian fauna adapted to the changing conditions of climate and vegetation. Similar environmental conditions were reflected in similar ecological characteristics of mammalian faunas accounting for periodic reappearances of the same ecological units.

IV.1.6. Summary of the results discussed so far

Every above reviewed method allowed the subdivision of the examined period on the basis of different characteristics of the mammalian fauna. Although the resolution of methods differs, the boundaries and events demonstrated by them coincide more or less. A significance is attached to the events (limits) on the basis of how many of the above reviewed six methods detected them. Based on this concept the events are categorized into three groups: (1) primary events (identified by at least four methods); (2) secondary events (demonstrable with 2-3 methods); and (3) tertiary events (demonstrable with one method only). Results of the six methods are summarized in Fig. 11.

Thirteen primary events were demonstrated in the examined period. These were as follows: (1) 1.45 Ma; (2) 950 ka; (3) 750 ka; (4) 475 ka; (5) 280 ka; (6) 235 ka; (7) 90 ka; (8) 57 ka; (9) 27 ka; (10) 21 ka; (11) 16 ka; (12) 10 ka; and (13) 7.5 ka. More than half of the events are in the Late Pleistocene-Holocene, which is explicable by the unevenness of data density. Beside the primary events, 15 secondary and 8 tertiary events were also identified.

IV.2. Characterization of ecological units

Based on palaeoecological analysis of the whole mammalian fauna, ten ecological units were distinguished in the Carpathian Basin in the examined period. Separation and characterization of the units is based on 15 ecotypes as well as ecological variables (distribution of body size and the trophic preferences, diversity index).

Parameters of the ten ecological units are the following:

Ecological unit 1. Proportions of ecotypes mainly fall into the medium and low ranges. Regarding the trophic preferences, proportion of granivores is low, proportions of browsers/grazers, carnivores and insectivores are medium-low, while proportions of grazers and omnivores are low within a community. Distribution of body size is also relatively balanced: proportion of category A is medium, proportions of categories B, D and H are medium-low, while proportions of categories E, F and G are low within a community. Category C could not be estimated because of its large deviation. Value of diversity index is medium-high in this unit.

Ecological unit 2. Several ecotypes (carnivores, body size categories C, D and E) could not be estimated because of their large deviation. Among groups of trophic preferences, proportions of granivores and browsers/grazers are medium, proportions of grazers and insectivores are low, while proportion of omnivores is medium-high. Distribution of body size is the following: proportions of categories A and H are medium, proportion of category G is medium-low, while proportions of categories B and F are low. Value of the diversity index is medium-high in this unit.

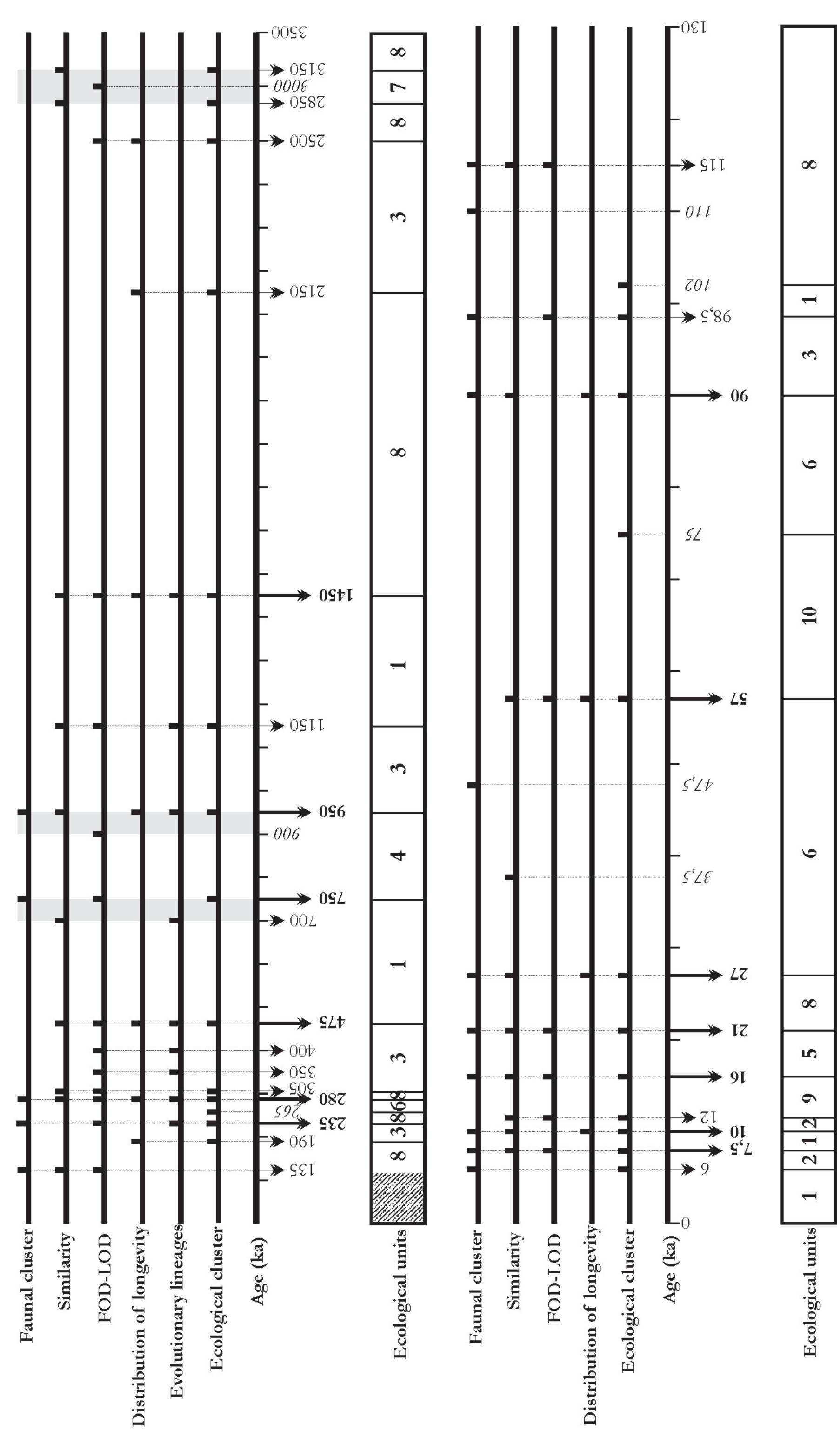

Fig. 11. Dates and significance of the events identified by the different methods applied. Legend: thick arrow = primary event; fine arrow = secondary event; italics = tertiary event. The events in the grey zones are probably synchronous. The upper scale begins at 3.5 Ma. Note that the scale changes at 2.5 Ma. Spacing of tick marks is 500 ka before, 100 ka after 2.5 Ma. On the lower scale, tick marks are spaced at 10 ka. For characterization of the ecological units (marked by arabic numbers), see text.

Ecological unit 3. Among groups of trophic preferences, proportion of insectivores is the highest (medium-high), proportion of granivores is medium-low, while proportions of the other groups are low. Distribution of body size is relatively even. Although the small mammals are dominant, proportion of category A is medium-high and proportions of categories B and C are medium-low, but proportion of category H is also medium-low. Proportions of the other body size categories are low. Value of the diversity index is medium-high in this unit.

Ecological unit 4. Dominance of granivores and small mammals is typical in this unit. Among groups of trophic preferences, only the proportion of granivores is high, proportions of all the other categories are low. Distribution of body size is similar: proportion of category B is high, proportions of categories A and C are medium and proportions of all the other categories are low. Value of the diversity index is low in this unit.

Ecological unit 5. Omnivores could not be estimated because of their large deviation. Among groups of trophic preferences, proportion of browsers/grazers is high, while proportion of granivores is medium. Proportions of the other trophic preference groups are low. Regarding the distribution of body size, proportion of category B is high, proportions of categories A and F are medium, while proportions of the other categories are low. Value of the diversity index is medium-low in this unit.

Ecological unit 6. Although several ecotypes could not be estimated because of their large deviation (omnivores, body size categories B, D and E, diversity index), both the distribution of trophic preferences and distribution of body size show a specific pattern. Among groups of trophic preferences, proportions of grazers and carnivores are medium-high, proportions of granivores and browsers/grazers are medium-low, while proportion of insectivores is low within a community. Distribution of body size shows dominance of the medium-sized and large mammals: proportion of category C is high, proportion of category H is medium-high, proportion of category G is medium, while proportions of categories A and F are low within a community.

Ecological unit 7. Among groups of trophic preferences, insectivores and carnivores are dominants, while the distribution of body size shows dominance of the small and medium-sized mammals. Proportion of insectivores is high, proportion of carnivores medium-high, proportion of browsers/grazers medium-low, while proportions of the other groups are low within a community. Among categories of body size, proportions of categories B and D are high, proportions of the other categories are low. Category C could not be estimated because of its large deviation. Value of the diversity index is low in this unit.

Ecological unit 8. Granivores and small mammals are dominant. Among groups of trophic preferences, proportion of granivores is high, proportion of insectivores is medium-low, while proportions of the other groups are low within a community. Among categories of body size, only the proportion of category A is high, proportions of the other categories are low. Value of the diversity index is medium-low in this unit.

Ecological unit 9. This unit is characterized by dominance of the medium- and large-sized browsers/grazers, carnivores and omnivores. Among groups of trophic preferences, proportion of browsers/grazers is high, proportions of carnivores and omnivores are medium, while proportions of the other groups are low within a community. Distribution of body size shifts to the larger mammals: proportion of category F is high, proportion of category D medium-high, proportions of categories E and H are medium, while proportions of the other categories are low. Value of the diversity index is medium in this unit.

Ecological unit 10. Among groups of trophic preferences, proportions of grazers, carnivores and omnivores are equally high. Proportion of browsers/grazers is medium, while proportions of the other groups are low within a community. Among categories of body size, two categories, E and G, show high values. Proportion of category C is medium, proportions of the other categories are low. Categories D and H could not be estimated because of their large deviation. Value of the diversity index is medium in this unit.

Parameters of the above described ecological units are summarized in Table III.

Table III

Parameters of the different ecological units

	1	2	3	4	5	6	7	8	9	10
granivores	medium	medium	medium-low	high	medium	medium-low	low	high	low	low
browser/grazers	medium-low	medium	low	low	high	medium-low	medium-low	low	high	medium
grazers	low	low	low	low	low	medium-high	low	low	low	high
carnivores	medium-low	*	low	low	low	medium-high	medium-high	low	medium	high
insectivores	medium-low	low	medium-high	low	low	low	high	medium-low	low	low
omnivores	low	medium-high	low	low	*	*	low	low	medium	high
A (<100 g)	medium	medium	medium-high	medium	medium	low	low	high	low	low
B (100-1000 g)	medium-low	low	medium-low	high	high	*	high	low	low	low
C (1-10 kg)	*	*	medium-low	medium	low	high	*	low	low	medium
D (10-45 kg)	medium-low	*	low	low	low	*	high	low	medium	*
E (45-90 kg)	low	*	low	low	low	*	low	low	medium	high
F (90-180 kg)	low	low	low	low	medium	low	low	low	high	low
G (180-360 kg)	low	medium-low	low	low	low	medium	low	low	low	high
H (>360 kg)	medium-low	medium	medium-low	low	low	medium-high	low	low	medium	*
diversity index	medium-high	medium-high	medium-high	low	medium-low	*	low	medium-low	medium	medium

• low ● medium-low ● medium ● medium-high ● high * indeterminate

IV.3. Interpretation of ecological units

Interpretation of ecological units is presented in order of logic and methodology. At first those units are discussed in which the typical vegetation was determined on the basis of habitat preferences of the extant mammals. Next the units of the mammoth steppe are discussed as well as the ecological units connected with this type of vegetation. Finally two ecological units are discussed which are characterized mainly by investigations of clay minerals.

IV.3.1. Interpretation of ecological units 1, 2, 3, 5, 8 and 9 – the last 27 ka

The last 27 ka is the best known interval, on the one hand because of a high number of localities, on the other hand because of the presence of numerous extant plant and animal species. It is possible to infer changes of climate and vegetation in the examined interval from archeology, paleobotany, malacology and mammalian fauna research, but because various methods differ in sensitivity, they may yield slightly different results.

Since in this interval the mammalian fauna mainly consisted of extant species, interpretation of ecological units was based on habitat preferences of these species. Occurrence of ecological units 1, 2, 3, 5, 8 and 9 in the examined period is demonstrated by cluster analysis. At first extant mammals were sorted according to their habitats, then habitat preferences were expressed as percentages calculated from abundance distribution in the given ecological unit (Table IV).

Table IV

Percent distribution of habitat preferences of extant mammalian species in the distinguished ecological units

Habitat preference (%)	1	2	3	5	8	9
forest taxa	14.65	15.13	14.42	1.36	3.41	2.52
forest. scrub taxa	34.68	31.44	38.99	1.89	11.65	5.32
woody steppe taxa	1.33	1.79	0	0	0.55	1.05
field taxa	22.19	22.73	27.7	17.95	32.99	35.44
eurytopical taxa	3.78	7.09	4.5	3.07	3.03	7.82
steppe taxa	16.39	11.11	7.17	41.28	34.88	15.92
tundra taxa	2.74	3.54	3.59	29.71	9.62	28.09
waterfront taxa	4.24	7.17	3.64	4.75	3.87	3.84
total	100	100	100	100	100	100

Thus the above mentioned ecological units are divided into two groups. Ecological units 1, 2 and 3 constitute the first group, while ecological units 5, 8 and 9 make up the second one. In the first three units the distribution of habitats indicate more closed vegetation, while the other group suggests more open.

In ecological unit 1, beside species which prefer woody scrub vegetation, other species which prefer open vegetation (field) as well as steppe species also appear in significant proportions. Based on distribution of habitat preferences woody steppe was the typical vegetation in this unit. Since modern mammalian communities of the Carpathian Basin be-long to this ecological unit according to the cluster analysis, interpretation of this unit is the most solid.

Ecological unit 2 shows similar pattern in distribution of habitats, but in this unit proportion of steppe species is lower, while proportion of species which prefer woody vegetation is higher than in ecological unit 1. Based on distribution of habitat preferences deciduous forest which was dotted with open areas (field) was the typical vegetation in this unit. Ecological unit 2 appeared in the early Holocene, when the pollen analysis suggests warm temperate mixed-oak woody steppe and mixed-oak closed forests in which hazel was a significant element (MAGYARI 2002). These results agree well with the ecological analysis.

In ecological unit 3 the proportion of steppe species is lower, while proportion of species which prefer woody scrub vegetation is higher than in ecological unit 2. This unit is very similar to ecological unit 2 in the distribution of habitat preferences, but it was characterized by a more open, mainly woody scrub vegetation. Since the cluster analysis assigned only a single fauna from the last 27 ka to ecological unit 3, the result cannot be compared with results of the other methods.

In ecological unit 5 more than 70% of the fauna consist of steppe and tundra species. Apart from these, only some species which prefer open (field) habitat have significant proportions. These characteristics suggest that probably tundra steppe was the typical vegetation in this unit. The tundra steppe (or mammoth steppe) was a mixture of grassy vegetation dotted with patches of scrubs and a moss-lichen vegetation, with no known recent analogue. Ecological unit 5 appeared during the last glaciation, its vegetation was similar to the transitional zone of taiga and woody tundra in NE Europe and West Siberia, based on palynological investigations (MAGYARI 2002). Differences between the two results were produced probably by differences between the two examined areas. Vegetation is reconstructed as open tundra steppe with patches of taiga-woody tundra.

Ecological unit 8 is dominated by species which prefer open areas (field, steppe). Steppe vegetation was typical in this unit, as indicated by the distribution of habitat preferences. Ecological unit 8 appeared prior to the last glaciation during the last 27 ka, when an extremely dry climate and cold continental steppe vegetation characterized this area, according to the malacological investigations (SZÖÕR et al. 1991; SÜMEGI & KROLOPP 1995).

Such interpretation of this unit holds true only for the Middle and Late Pleistocene as well as the Holocene, when dominance of small granivores is simultaneous with dominance of arvicolids. Interpretation of this unit is different for the Pliocene and Early Pleistocene. In the Pliocene, dominance of small granivores within a fauna is accompained by dominance of murids instead of arvicolids, while the Early Pleistocene lacked significant cold periods, the climate became drier only. Based on clay minerals, a warm and dry climate was typical of the Late Pliocene and Early Pleistocene (VICZIÁN 2002), thus the areas with open vegetation in this period were not identical to the modern cold, continental steppe.

Ecological unit 9 was dominated also by species which prefer open areas, however, contrary to the previous unit, beside the field species, the proportion of the tundra rather than the steppe species was more significant. Based on distribution of habitat preferences, the vegetation of this unit cannot be classified to any given type, but the area of tundra vegetation was probably significant. Ecological unit 9 appeared after the Last Glacial

Maximum, when pollen analysis and malacological investigation suggest a mosaic vegetation with forest, woody steppe and tundra patches (SÜMEGI & KROLOPP 1995; SÜMEGI & HERTELENDI 1998).

IV.3.2. Interpretation of ecological units 6 and 10 – the mammoth steppe

For faunas which are older than 27 ka, and for the corresponding ecological units, the use of modern analogies is not possible, because of the increased number of extinct mammalian species in communities. In these cases the interpretation of ecological units is based on both the ecological parameters and literature data.

Animals of the mammalian community of mammoth steppe are not only known from skeletal material of paleontological sites, but also from the nearly intact frozen finds. Knowledge of stomach material of the frozen animals, as well as the pollen analysis allowed the environmental reconstruction for this type of community.

Herbaceous plants (grass, sedge, forb and horsetail) characterized the vegetation of the mammoth steppe, which was composed of short lawn. Such type of vegetation did not allow the spread of browsers, so the large grazers became dominant in communities. There is no actual analogue of mammoth steppe vegetation among modern ecosystems. Moist calcareous tundra is the closest analogue of mammoth steppe, which occurs in a narrow belt between polar deserts and mossy acidic tundra (GUTHRIE 2001; WALKER et al. 2001).

The significant proportion of large grazers and carnivores is the main ecological parameter of mammoth steppe community, which is typical of ecological units 6 and 10. These two units differ in the proportions of omnivores, large grazers and carnivores, all of which are higher in unit 10 than in unit 6. In ecological unit 6 the proportion of medium size (body size category C) mammals is also significant. Ecological unit 6 may be regarded as the mammoth steppe in general, while ecological unit 10 represents probably the maximum extent of mammoth steppe. High proportion of omnivores is explained by the spread of cave bear (*Ursus spelaeus*) in ecological unit 10.

IV.3.3. Interpretation of ecological units 4 and 7

Similarly to ecological unit 8, the interpretation of ecological units at the older, Late Pliocene - Middle Pleistocene localities, is aided by clay mineral studies. Clay minerals allow the determination of composition of original bedrock, geomorphological, hydrogeological and climate parameters of weathering and pedogenesis, as well as depositional environment (VICZIÁN 2002). Based on both the climatic parameters inferred from clay minerals and the ecological parameters, interpretation of ecological units is relatively reliable.

Two localities, Somssich-hegy 2 and Villány 8 were assigned to ecological unit 4 by the cluster analysis. At locality Somssich-hegy 2 the main clay mineral component is illite, whereas smectite, clorite and kaolinite occur in smaller amounts. The sediment differ from the typical Pliocene kaolinite-rich red clays both in its colour and composition. Its high calcite- and low goethite content and light yellow colour are loess-like parameters (KORDOS in JÁNOSSY 1999; VICZIÁN 2002). The Biharian scarlet montmorillonitic terra rossa gradues into loess sediment at localities of Villány (e.g. Villány 8, KRETZOI 1969). The occurrence of loess unambiguously indicates cold, dry climate. Ecological parameters of this unit are similar to those suggested for ecological unit 8, the difference is that the dominant granivores are bigger. The extant steppe species make up a significant part of the fauna, which supports the assumption that this unit is interpreted to be similar to the steppe.

In ecological unit 7 there are also two localities, Beremend 5 and 11, as determined by the cluster analysis. Clay minerals of the Late Pliocene-Early Pleistocene sediments contain mainly kaolinite, which indicates warm, humid (subtropical) climate (VICZIÁN 2002). This ecological unit is characterized by the dominance of small and middle size insectivores and carnivores. Since modern insectivores prefer almost exclusively the more closed, forested environment, results of clay mineralogical and ecological examinations are in good agreement; ecological unit 7 is best interpreted as a subtropical forest. Now such climate and vegetation occur at the Atlantic coast of Portugal (KAISER 1999) and also in Southeast-Asia (KOLOSZÁR et al. 2000).

V. CONCLUSIONS

Joint application of a suite of methods allowed a complex paleoecological analysis of Late Neogene mammalian faunas in the Carpathian Basin. Contrary to the previously applied methods, faunas of different age and species composition became comparable, so the whole available fossil material (that is suitable for ecological analysis) was analysed by a standardized methodology. Methods which are based directly on species composition of mammalian faunas helped to document the small- and large-scale changes (events) in the mammalian fauna. These changes mark the limits of ecological units. Ten different ecological units are distinguished in the studied period, most of them appear several times. Interpretation of ecological units and their temporal changes permit to track changes of climate and vegetation in the Carpathian Basin.

A c k n o w l e d g e m e n t s. I would like to thank László KORDOS for all the help which he gave me for my work in the last 13 years. This is MTA-MTM Paleo contribution number 143.

REFERENCES

ADAMS B. 2002. New radiocarbon dates from Szeleta and Istállós-kő caves, Hungary. *Praehistoria*, **3**: 53-55.

ANDREWS P. 1995. Mammals as palaeoecological indicators. *Acta Zoologica Cracoviensia*, **38**(1): 59-72.

ANDREWS P., BEGUN D. R., ZYLSTRA M. 1997. Interrelationships between Functional Morphology and Paleoenvironments in Miocene Hominoids. [In:] D. R. BEGUN, C. V. WARD, M. D. ROSE (eds) – Function, Phylogeny, and Fossils: Miocene Hominoid Evolution and Adaptations. Plenum Press, New York, Pp: 29-58.

BARRY J. C., MORGAN M. E., FLYNN L. J., PILBEAM D., JACOBS L. L., LINDSAY E. H., RAZA S. M., SOLOUNIAS N. 1995. Patterns of faunal turnover and diversity in the Neogene Siwaliks of Northern Pakistan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **115**(1-4): 209-226.

CHALINE J. 1987. Arvicolid data (Arvicolidae, Rodentia) and evolutionary concepts. [In:] M. K. HECHT, B. WALLACE, C. T. PRANCE (eds) – Evolutionary biology. Plenum Publishing Corporation, New York, Pp: 237-310.

CHALINE J. 1990. An approach to studies of fossil arvicolids. [In:] O. FEJFAR, W.-D. HEINRICH (eds) – International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia). Geological Survey, Prague, Rohanov, Pp: 45-84.

CHALINE J., SEVILLA P. 1990. Phyletic gradualism and developmental heterochronies in a European Plio/Pleistocene *Mimomys* Lineage (Arvicolidae, Rodentia). [In:] O. FEJFAR, W.-D. HEINRICH (eds) – International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia). Geological Survey, Prague, Rohanov, Pp: 85-98.

DAMUTH J. D. 1992. Taxon-free characterization of animal communities. [In:] A. K. BEHRENSMEYER, J. D. DAMUTH, W. A. DIMICHELE, R. POTTS, H.-D. SUES, S. L. WING (eds) – Terrestrial ecosystems through time: evolutionary palaeoecology of terrestrial plants and animals. The University of Chicago Press, Chicago, Pp: 183-203.

DE MENOCAL P. B. 1995. Plio-Pleistocene African climate. *Science*, **270**: 53-59.

EISENBERG J. F. 1981. The mammalian radiations: An analysis of trends in evolution, adaptation, and behavior. University of Chicago Press, Chicago, 610 pp.

FEJFAR O., HEINRICH W.-D. 1990. Proposed biostratigraphical division of the European continental Neogene and Quaternary based on muroid rodents (Rodentia: Mammalia). [In:] O. FEJFAR, W.-D. HEINRICH (eds) – International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia). Geological Survey, Prague, Rohanov, Pp: 115-124.

FEJFAR O., MEIN P., MOISSENET E. 1990. Early arvicolids from the Ruscinian (Early Pliocene) of the Teruel Basin, Spain. [In:] O. FEJFAR, W.-D. HEINRICH (eds) – International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia). Geological Survey, Prague, Rohanov, Pp: 133-164.

FLEAGLE J. G. 1985. Size and adaptation in primates. [In:] W. L. JUNGERS (ed.) – Size and Scaling in Primate Biology. Plenum Press, New York, Pp: 1-19.

FŰKÖH L., KROLOPP E., SÜMEGI P. 1995. Quaternary malacostratigraphy in Hungary. *Malacological Newsletter*, Suppl. 1. FŰKÖH L. (ed.), Gyöngyös, 219 pp.

GUNNELL G. F., MORGAN M. E., MAAS M. C., GINGERICH P. D. 1995. Comparative paleoecology of Paleogene and Neogene mammalian faunas: Trophic structure and composition. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **115**(1-4): 265-286.

GUTHRIE D. 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. *Quaternary Science Reviews*, **20**(1-3): 549-574.

HORÁČEK I. 1990. On the context of Quaternary arvicolid evolution: changes in community development. [In:] O. FEJFAR, W.-D. HEINRICH (eds) – International Symposium evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia). Geological Survey, Prague, Rohanov, Pp: 201-222.

JÁNOSSY D. 1986. Pleistocene vertebrate faunas of Hungary. Akadémiai Kiadó, Budapest, 208 pp.

JÁNOSSY D. 1999. Újabb adatok a villányi Somssich-hegy 2. lelőhely leleteihez. [New data of locality 2 of Somssich Hill, Villány Mountain]. *Manuscript*, Budapest, 1-10 pp. [In Hungarian].

JÁNOSSY D., MEULEN VAN DER A. J. 1975. On *Mimomys* (Rodentia) from Osztramos-3, North Hungary. *Koninklijke Nederlandse Akademie van Wetenschappen Proceedings*, Series B **78**(5): 381-391.

KAISER M. 1999. Jelentés a Tengelici Formáció rétegtani helyzetének vizsgálatáról. [Report about investigation of stratigraphic position of Tengelic Formation]. *Manuscript*, MÁFI, Budapest, 7 pp. [In Hungarian].

KOLOSZÁR L., MARSI I., CHIKÁN G. 2000. A Mórágyi-rög keleti részének kainozoos fedőképződményei [Cenozoic sedimentary cover of the eastern part of Mórágy Hills]. *A Magyar Állami Földtani Intézet Évi Jelentése az 1999. évről*, Budapest, 117-135 pp, 137-148 pp.

KORDOS L. 1978. Changes in the Holocene climate of Hungary reflected by the „vole-thermometer" method. *Földrajzi Közlemények*, **26**(1-3): 222-229.

KORDOS L. 1994. Revised Biostratigraphy of the Early Man Site at Vértesszölös, Hungary. *Courier Forschungs-Institut Senckenberg*, **171**: 225-236.

KORDOS L. 1995. Arvicolid biostratigraphy of Europe: a zoogeographical outline. *Annales Géologiques des Pays Helléniques*, **36**: 551-564.

KORDOS L., RINGER Á. 1991. Climatostratigraphic and archeostratigraphic correlation of Arvicolidae stratigraphy of the Late Pleistocene in Hungary. *A Földtani Intézet Évi Jelentése az 1989. évről*, Budapest, 523-534 pp.

KORPÁS L., KOVÁCS-PÁLFFY P., LANTOS M., FÖLDVÁRI M., KORDOS L., KROLOPP E., STÜBEN D., BERNER Zs. 2004. Sedimentology, geochemistry, chronology and palaeokarst evolution of Quaternary thermal lacustrine travertine. An integrated case study from Vár-hegy, Budapest, Hungary. *Földtani Közlöny*, **134**(4): 541-562.

KREBS J. R. 1989. Ecological methodology. Harper and Row Publishers, New York, 654 pp.

KRETZOI M. 1941. Ősemlősmaradványok Betfiáról. – Die unterpleistozäne Säugetierfauna von Betfia bei Nagyvárad. *Földtani Közlöny*, **81**: 384-417.

KRETZOI M. 1953. A negyedkor taglalása gerinces fauna alapján. [Subdivision of Quaternary based on the vertebrate faunas]. *Alföldi Kongresszus* (Az Alföld földtani felépítésének kérdései), Budapest, 89-97 pp. [In Hungarian].

KRETZOI M. 1956. A Villányi hegység alsó-pleisztocén gerinces-faunái. [Lower Pleistocene vertebrate faunas of Villány Mountain]. *Geologica Hungarica series Palaeontologica*, **27**: 1-264. [In Hungarian and in German].

KRETZOI M. 1969. A magyarországi quarter és pliocén szárazföldi biosztratigráfiájának vázlata. [Biostratigraphical sketch of the Hungarian Quaternary and Pliocene]. *Földrajzi Közlemények*, **17**: 179-204. [In Hungarian].

KROLOPP E. 1977. Absolute chronological data of the Quaternary sediments in Hungary. *Földrajzi Közlemények*, **35**(1-3): 230-233.

LEGENDRE S. 1986. Analysis of mammalian communities from the late Eocene and Oligocene of southern France. *Palaeovertebrata*, **16**: 191-212.

LEGENDRE S. 1989. Les communautés de mammiferes du Paléogene (Eocene supérieur et Oligocene) d'Europe occidentale: structures, milieux et évolution. *Münchener Geowissenschaftliche Abhandlungen* Reihe A, **16**: 1-110.

LEGENDRE S., ROTH C. 1988. Correlation of carnassial tooth size and body weight in recent carnivores (Mammalia). *Historical Biology*, **1**: 85-98.

MAGYARI E. 2002. Climatic versus human modification of the Late Quaternary vegetation in Eastern Hungary. *Manuscript* (PhD Thesis), Department of Mineralogy and Geology, University of Debrecen, Debrecen, 150 pp.

MALEZ M., RABEDER G. 1984. Neues Fundmaterial von Kleinsäugern aus der altpleistozänen Spaltenfüllung Podumci 1 in Norddalmatien (Kroatia, Jugoslawien). *Beiträge zur Paläontologie Österreichs*, **11**: 439-510.

PAZONYI P. 1999. A Kárpát-medence késő-neogén és kvarter emlősfauna közösségeinek paleoökológiai és rétegtani vizsgálata. [Paleoecological and stratigraphical investigations of the Late Neogene and Quaternary mammalian communities in the Carpathian Basin]. *Manuscript*, ELTE Őslénytani Tanszék, Budapest, 100 pp. [In Hungarian].

PAZONYI P. 2004. Mammalian ecosystem dynamics in the Carpathian Basin during the last 27,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **212**(3-4): 295-314.

PAZONYI P. 2006. A Kárpát-medence kvarter emlősfauna közösségeinek paleoökológiai és rétegtani vizsgálata. [Paleoecological and stratigraphical investigations of the Quaternary mammalian communities in the Carpathian Basin]. Manuscript (PhD Thesis), Magyar Természettudományi Múzeum, Budapest, 115 pp. [In Hungarian with English abstract].

RABEDER G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. *Beiträge zur Paläontologie Österreichs*, **8**: 1-373.

RINGER Á. 2002. The new image of Szeleta and Istállós-kő caves in the Bükk Mountains: a revision project between 1999-2002. *Praehistoria*, **3**: 47-52.

RINGER Á., MESTER Zs. 2001. A Szeleta-barlang 1999-2000. évi régészeti revíziójának eredményei. [Results of archeological revision of the Szeleta Cave in 1999-2000]. [Lake-marsh and tetarate types travertines in the Eastern Gerecse Mountain]. A Miskolci Herman Ottó Múzeum Évkönyve, Vol.40. Miskolc, 5-19 pp. [In Hungarian].

SCHEUER G., SCHWEITZER F. 1979. Tavi-mocsári és tetarátás típusú édesvízi mészkőösszletek a Kelet-Gerecsében. *Földrajzi Közlemények*, **27**: 116-125.

SCHWARCZ H. P., SKOFLEK I. 1982. New dates for the Tata, Hungary archaeological site. *Nature*, **295**: 590-591.

SHACKLETON N. J., BERGER A., PELTIER W. R. 1990. An alternative astronomical calibration of the lower Pleistocene timescale based on ODP Site 677. *Transactions of the Royal Society of Edinburgh-Earth Sciences*, **81**: 251-261.

SHANNON C. E., WEAVER W. 1949. The mathematical theory of communication. University of Illinois Press, Urbana, 117 pp.

SÜMEGI P., HERTELENDI E. 1998. Reconstruction of microenvironmental changes in the Kopasz Hill loess area at Tokaj (Hungary) between 15 and 70 ka B.P. *Radiocarbon*, **40**(2): 855-863.

SÜMEGI P., KROLOPP E. 1995. A magyarországi würm korú löszök képződésének paleoökológiai rekonstrukciója Mollusca-fauna alapján. [Paleoecological reconstruction of formation of the Hungarian wurm loesses based on Mollusc fauna]. Földtani Közlöny, **125**(1-2): 125-148. [In Hungarian with English abstract].

SZÖŐR G., KORDOS L. 1981. Holocén gerinces anyag paleobiogeokémiai módszerrel történő abszolút kronológiai és paleoklímatológiai értékelése. [Absolute chronological and paleoclimatological evaluation of Holocene vertebrate material with paleobiogeochemical method]. Földtani Közlöny, **11**(3-4): 472-486. [In Hungarian with English abstract].

SZÖŐR G., SÜMEGI P., HERTELENDI E. 1991. Őshőmérsékleti adatok meghatározása malakohőmérő-módszerrel az Alföld felső pleisztocén-holocén klímaváltozásaival kapcsolatban. [Determination of paleotemperature data with malaco-thermometer method in connection with the Upper Pleistocene-Holocene climatic changes of the Hungarian Great Plain]. Acta Geographica Debrecina, 1989-1990, **28-29**: 217-229. [In Hungarian].

VICZIÁN I. 2002. Clay mineralogy of Quaternary sediments covering mountainous and hilly areas of Hungary. *Acta Geologica Hungarica*, **45**(3): 265-286.

VOGELSANG E. 1990. Paläo-Ozeanographie des Europäischen Nordmeeres an Hand Stabiler Kohlenstoff- und Sauerstoffisotope. *Berichte aus dem Sonderforschungsbereich 313. Sedimentation im europäischen Nordmeer*, Vol. 23. Universität Kiel, 1-136 pp.

WALKER D. A., BOCKHEIM J. G., CHAPIN F. S., NELSON F. E., PING C. L. 2001. Calcium-rich tundra, wildlife, and the „Mammoth Steppe". *Quaternary Science Reviews*, **20**(1-3): 149-163.

ZAZHIGIN V. S. 1980. Late Pliocene and Anthropogene rodents of the south of Western Siberia. Academy of Sciences of the USSR, Moscow, 1-159 pp. [In Russian].