

Origin and History of the Present Rodent Fauna in Poland Based on Fossil Evidence¹

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On the basis of study of ca. 16000 rodent remains belonging to at least 25 species, obtained from 21 faunal assemblages of the Late Quaternary age from Poland, an analysis of rodent communities, their species diversity and succession during 60—70 thousand years was undertaken. Communities of rodents from the Pleni-Vistulian are characterized by a mixture of tundra (*Microtus gregalis*, *Lemmus lemmus*, *Dicrostonyx gulielmi*) and steppe elements (*Spermophilus citelloides*, *S. superciliosus*, *Lagurus lagurus*, *Cricetulus migratorius*) with minor additions of sylvan species (e.g. *Clethrionomys glareolus*). During cool periods (stadials), an increase in frequency of *M. gregalis*, *Lemmus* and *Dicrostonyx* is observed, while mild phases (interstadials) are characterized by a distinct predominance of *Microtus arvalis*. The present rodent communities with *Clethrionomys glareolus*, *Apodemus (Sylvaemus)*, *Pitymys subterraneus*, *Microtus agrestis*, *Glis glis* and *Muscardinus avellanarius* have emerged during the Late Vistulian and the Holocene, following considerable changes in climate and vegetation. A gradual disappearance of steppe-tundra species starts towards the end of Vistulian 3; however, *Dicrostonyx* and *M. gregalis* has survived as a relic form until the beginning of the Neoholocene. It is only in the Sub-Atlantic period of the Holocene that a wide expansion of *M. arvalis* and *Apodemus agrarius* accompanied by synanthropic species was possible due to human activity.

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1. INTRODUCTION

The most direct evidence of rodent history in Poland comes from fossil and sub-fossil remains. The present rodent communities have formed around the Pleistocene/Holocene boundary; however, some species reached Central Europe much earlier, creating similar rodent communities already during previous interglacials of the Pleistocene. Crucial for the origin of the present rodent fauna of Middle Europe was the Pliocene/Pleistocene boundary (ca. 1.6—1.7 My BP) when, following the first distinct cooling of the climate, which had entailed changes in the vegetation of the Northern Hemisphere, there appear the genus *Microtus*

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and several modern taxa among other groups of rodents. Our knowledge about the succession of rodents during the Lower Pleistocene (Biharian) of Poland is sufficiently precise, while we lack information concerning fossil rodents from the Middle Pleistocene. On the other hand, the relatively numerous material from the Late Quaternary provided an opportunity to study the history of particular species and changes in community structure of rodents throughout the last glaciation up to the recent times. Some problems under discussion were earlier summarized by Madeyska (1981, 1982) and Nadachowski (1982) with special reference to palaeoenvironmental changes during the Late Quaternary.

The primary objective of this study was to analyse the structure of rodent communities, their species diversity and succession during the last 60—70 thousand years in the territory of Poland and, on the basis of such evidence, to reconstruct the history of the extant rodent fauna. Moreover, the Late Quaternary history of 30 species of rodents is briefly reviewed.

2. MATERIAL AND METHODS

The material for this study was collected from caves or rock shelters during archaeological investigations (cf. Madeyska, 1981; Nadachowski, 1982). The excavated samples bear a complex relationship to the five animal communities (e.g. Birks & Birks, 1980). The small mammal remains, including rodents, are thought to have been mainly accumulated by owls as pellets. Studies of food composition of owls show some differences in periods of high density of rodents and under condition of prey deficiency. Also, it has been shown that the dissimilarity of food composition for particular owl species is greatly determined by the type of habitat in which the owls hunt (cf. Glutz von Blotzheim & Bauer, 1980). Moreover, a composition of thanatocoenose (death assemblage) shows some inherent bias in comparison to a live community caused by taphonomic factors. Taking into account all the above limitations, however, it seems that changes in relative frequency in prey remains, especially that of predominant forms, are likely to reflect real changes in the rodent community structure.

This objective can be attained by the analysis of two elements: (1) the number of species (species richness or diversity) calculated from the equation $d = S - 1/\ln N$, where S = number of species and N = number of individuals, and (2) the degree to which individual species are evenly represented (dominance or, conversely, equitability), computed from the equation $e = H/\ln S$. Usually, both elements are combined to give an indication of general diversity, such as the Shannon index, calculated from the equation $H = -\sum P_i \ln P_i$ where $P_i = n_i/N$ = relative frequency for each species (cf. Avery, 1982; Emlen, 1973).

The present paper reviews results of the study of ca. 16000 rodent remains belonging to at least 25 species, obtained from 21 faunal samples of Late Quaternary age, mainly from the Cracow Upland, with a minimum count of 100 individuals per sample. The number of individuals (N) was determined on the basis

of the highest number of first lower molars (M1) for vole remains, or the maximum number of the most common category of molars for other species of rodents. Table 1 shows the percentage representation of the species in various samples arranged in the order from the earliest to the latest ones, together with the total number of individuals (N) and species (S), including values of community composition indices.

The correlation of successive samples with the geological age was made on the basis of archaeological and lithological materials as well as, in some cases, of radiometric methods (Bocheński *et al.*, 1985; Madeyska, 1981, 1982; Nadachowski *et al.*, 1989). The stratigraphical subdivision of the last glaciation (synonymes Vistulian, Wisła, Würm, Weichselian, Valdai, Devensian) was based on climato-stratigraphic units (Table 2) using a combination of either Polish (Madeyska, 1982) or Dutch nomenclature (Hammen *et al.*, 1967; Kolstrup & Wijmstra, 1977), while subdivision of the Holocene was assumed according to Starkel (1977).

3. LATE QUATERNARY HISTORY OF PARTICULAR SPECIES OF RODENTS

The present fauna of rodents of Poland consists of 31 species including the introduced taxa (Pucek, 1981). Particular species show a different history depending on climatic, environmental and historical factors. On the basis of relatively abundant fossil evidence (*e.g.* Bocheński *et al.*, 1983, 1985; Chmielewski *et al.*, 1967; Kowalski, 1961, 1972; Nadachowski, 1976, 1982) one can describe the Late Quaternary history of particular species of rodents as follows (species recently introduced are excluded):

(1) *Sciurus vulgaris* Linnaeus, 1758: remains of this species were only found during warmer phases. It accidentally appears at the end of V1 and then, after a long gap, in milder periods of V3, LV and during the Holocene.

(2) *Spermophilus citelloides* (Kormos, 1916): probably the immediate ancestor of the recent European species *Spermophilus citellus* (Linnaeus, 1766), appears during V1/2 phase as a result of the cooling of the climate and survives up to interstadial V2/3, at least in the southern part of the Cracow Upland.

(3) *Spermophilus superciliosus* (Kaup, 1839): another fossil species of sousliks, is believed to be closely related to the recent *Spermophilus major* Pallas, 1778. It occurs, though rarely, during V2—V2/3 period and definitively disappears from Poland towards the end of the V3 phase.

The occurrence of the genus *Spermophilus* has been lately confirmed in the Carpathians, at least during V2/3 interstadial (Nadachowski & Wolsan, 1987).

(4) *Marmota marmota* (Linnaeus, 1758): is known as a fossil only from one locality (Ujazd near Jasło) from sediments of uncertain stratigraphic position (Kadyi & Kowalski, 1975).

Table

Percentage representation of rodent taxa in successive samples of the Late groups: A — species of tundra environment, B — species of open country and Samples: RA 1—3 — Raj Cave layers 1, 2 and 3; NI 10—11 — Nietoperzowa layers 5 and 6; RA 7—8 — Raj Cave layers 7 and 8; RA 10 — Raj Cave layer Cave layers 9 and 9/10; MM 7—3 — Mamutowa Cave layers 7, 4 and 3; MM Cave layers 5, 6, 7 and 8; MM 2—2g — Mamutowa Cave layers 2 and 2g; MM 7 and 7 spag; BR 5 — Bramka layer 5; ND 4 — Nad Jaskinią Niedostępną MS 4, 3 and 2 — Nad Mosurem Starym Duża Cave layers 4, 3 and 2; DS — (1985), Nadachowski (1982) and

| Eg | Species | Sample | RA 1—3 | NI 10—11 | RA 4 | RA 5—6 | RA 7—8 | RA 10 | KZ 13—11 |
|----|-----------------------------------|--------|--------|----------|------|--------|--------|-------|----------|
| A | <i>Dicrostonyx gulielmi</i> | | 2.0 | 1.0 | — | 6.8 | 13.6 | 29.2 | 32.4 |
| | <i>Lemmus lemmus</i> | | 5.9 | 4.0 | 2.7 | 10.9 | 32.6 | 10.3 | 1.3 |
| | <i>Microtus gregalis</i> | | 16.7 | 5.0 | 5.6 | 59.5 | 46.0 | 54.9 | 64.4 |
| B | <i>Spermophilus superciliosus</i> | | — | — | — | 0.2 | 0.4 | 0.1 | — |
| | <i>Spermophilus citelloides</i> | | 3.9 | — | 1.5 | 1.4 | 0.8 | — | — |
| | <i>Cricetulus migratorius</i> | | — | — | — | — | — | — | — |
| | <i>Cricetus cricetus</i> | | — | — | — | — | — | — | 0.1 |
| | <i>Lagurus lagurus</i> | | 2.0 | — | 0.3 | 0.5 | 0.8 | 0.1 | — |
| | <i>Microtus cf. arvalis</i> | | 54.9 | 68.3 | 77.1 | 13.1 | 0.8 | 0.5 | — |
| C | <i>Arvicola terrestris</i> | | 2.9 | 4.9 | 2.1 | 1.0 | 0.8 | 0.2 | 0.1 |
| | <i>Microtus cf. agrestis</i> | | 3.9 | 5.9 | 7.4 | 2.9 | 1.9 | 2.1 | — |
| | <i>Microtus oeconomus</i> | | 3.9 | 8.9 | 2.7 | 3.2 | 1.9 | 1.2 | 1.5 |
| | <i>Pitymys subterraneus</i> | | — | — | — | — | — | — | — |
| | <i>Micromys minutus</i> | | — | — | — | — | — | — | — |
| D | <i>Sciurus vulgaris</i> | | — | — | — | — | — | — | — |
| | <i>Castor fiber</i> | | 1.0 | — | — | — | — | — | — |
| | <i>Clethrionomys glareolus</i> | | 2.9 | 2.0 | 0.3 | 0.3 | 0.4 | 1.4 | 0.2 |
| | <i>Apodemus (Sylvaemus) sp.</i> | | — | — | 0.3 | 0.2 | — | — | — |
| | <i>Glis glis</i> | | — | — | — | — | — | — | — |
| | <i>Muscardinus avellanarius</i> | | — | — | — | — | — | — | — |
| | <i>Eliomys quercinus</i> | | — | — | — | — | — | — | — |
| | <i>Sicista betulina</i> | | — | — | — | — | — | — | — |
| E | <i>Apodemus agrarius</i> | | — | — | — | — | — | — | — |
| | <i>Mus musculus</i> | | — | — | — | — | — | — | — |
| | <i>Rattus norvegicus</i> | | — | — | — | — | — | — | — |
| | Total no. of individuals (N) | | 102 | 101 | 338 | 586 | 258 | 1169 | 1328 |
| | Number of species (S) | | 11 | 8 | 10 | 12 | 11 | 10 | 7 |
| | Shannon index of gen. div. (H) | | 1.58 | 1.19 | 0.95 | 1.39 | 1.34 | 1.17 | 0.79 |
| | Species diversity (d) | | 2.16 | 1.52 | 1.55 | 1.73 | 1.80 | 1.27 | 0.83 |
| | Equitability (e) | | 0.66 | 0.57 | 0.41 | 0.56 | 0.56 | 0.51 | 0.41 |

(5) *Castor fiber* Linnaeus, 1758: very rarely found in fossil cave assemblages; up to now it has been recorded thrice in Tunel Wielki Cave (V1) (Nadachowski, 1988), Raj Cave (V1/2) (Kowalski, 1972) and in the Holocene layers of Ciasna Cave (Nadachowski, 1982). Abundant subfossil

1

Quaternary age and values of community composition indices. Eg — ecological steppe, C — eurytopic species, D — forest species, E — synanthropic species. Cave layers 10 and 11; RA 4 — Raj Cave layer 4; RA 5-6 — Raj Cave 10; KZ 11-13 — Koziarnia Cave layers 11, 12 and 13; NI 9 — Nietoperzowa II-VI — Mamutowa Cave layers II, III, IV, V, and VI; NI 5-8 — Nietoperzowa VII-IX — Mamutowa Cave layers VII, VIII and IX; ZL 7 — Zalas layers Rock-shelter layer 4 and 4k; SW 3 — Saspowska Zachodnia Cave layer 3; Dużej Sowy Cave. Quantitative data original or adopted after Bocheński *et al.* Nadachowski *et al.* 1989).

| NI 9 | MM 7-3 II-VI | NI 8-5 | MM 2-2g VII-IX | ZL 7 | BR 5 | ND 4 | SW 3 | MS 4 | MS 3 | MS 2 | DS |
|---------|--------------------|-----------|----------------------|---------|---------|---------|---------|---------|---------|---------|------|
| 14.6 | 7.8 | 1.5 | 16.0 | 23.7 | 6.0 | 9.7 | 1.2 | 1.9 | — | — | — |
| 0.7 | 8.5 | 1.8 | 6.0 | — | 2.3 | 3.7 | — | — | — | — | — |
| 68.6 | 59.7 | 2.9 | 58.8 | 3.0 | 4.6 | — | 0.9 | 1.9 | — | — | — |
| — | 0.2 | 0.4 | 0.1 | — | — | — | — | — | — | — | — |
| — | — | 0.4 | — | — | — | — | — | — | — | — | — |
| 0.7 | — | — | 0.1 | 1.3 | — | — | — | — | — | — | — |
| — | — | — | 0.1 | 2.6 | 0.7 | 0.9 | 27.1 | 4.7 | 17.0 | 1.3 | 0.2 |
| — | 1.1 | — | 0.1 | — | — | — | — | — | — | — | — |
| 6.0 | 2.5 | 42.0 | 2.2 | 1.3 | 3.0 | 4.6 | 6.1 | 0.9 | 1.9 | 5.8 | 73.4 |
| 0.7 | 1.2 | 6.6 | 0.7 | 10.9 | 6.8 | 12.7 | 24.0 | 14.9 | 36.9 | 10.3 | 9.2 |
| 0.7 | 2.5 | 7.3 | 3.4 | — | 5.3 | 10.6 | 8.6 | 30.0 | 6.6 | 4.5 | — |
| 8.0 | 14.6 | 36.4 | 11.9 | 7.0 | 14.4 | 3.2 | 6.1 | 12.1 | 1.9 | 2.6 | — |
| — | — | — | — | — | 5.3 | 8.8 | 1.2 | — | 3.8 | 12.2 | 0.1 |
| — | — | — | — | — | 0.7 | — | — | — | — | — | 0.4 |
| — | — | — | — | — | 0.7 | 0.7 | 0.6 | — | 0.9 | 1.3 | 0.1 |
| — | — | — | — | — | — | — | — | — | — | — | — |
| — | 1.9 | 0.7 | 0.5 | — | 38.4 | 37.5 | 22.1 | 31.8 | 16.0 | 41.6 | 0.1 |
| — | — | — | — | — | 12.0 | 3.0 | 1.8 | 0.9 | 8.5 | 17.3 | 10.5 |
| — | — | — | — | — | 0.7 | — | — | — | 2.8 | 1.9 | 0.1 |
| — | — | — | — | — | 0.7 | — | — | — | 0.9 | 0.6 | 0.1 |
| — | — | — | — | — | — | — | — | — | 0.9 | 0.6 | — |
| — | — | — | 0.1 | — | — | — | 1.2 | 1.9 | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | 4.2 |
| — | — | — | — | — | — | — | — | — | — | — | 1.4 |
| — | — | — | — | — | — | — | — | — | — | — | 0.2 |
| 150 | 567 | 272 | 2787 | 156 | 133 | 434 | 163 | 107 | 106 | 156 | 7157 |
| 8 | 10 | 10 | 13 | 7 | 15 | 12 | 11 | 10 | 13 | 12 | 13 |
| 1.05 | 1.37 | 1.42 | 1.32 | 1.31 | 2.04 | 2.01 | 1.85 | 1.32 | 1.93 | 1.81 | 0.96 |
| 1.40 | 1.42 | 1.61 | 1.51 | 1.19 | 2.86 | 1.81 | 1.96 | 1.93 | 2.57 | 2.18 | 1.35 |
| 0.51 | 0.60 | 0.62 | 0.52 | 0.67 | 0.75 | 0.80 | 0.77 | 0.57 | 0.75 | 0.73 | 0.37 |

remains were described from numerous archaeological localities all over Poland from Roman and Medieval times (*e.g.* Chmielewski, 1973).

(6) *Cricetus cricetus* (Linnaeus, 1758): probably appears during the Eemian (evidence from Nietoperzowa Cave; Kowalski, 1961; Nadachow-

Table 2

Possible climatostratigraphic correlations of the Late Quaternary in different parts of Europe with estimated duration for major climatic phases (after Stuart, 1982; Hammen *et al.*, 1967; Kolstrup & Wijmstra, 1977; Madeyska, 1982; Velichko *et al.*, 1983, modified). Chron. — chronology, Interstad. — interstadials.

| ky | England | Netherlands | Poland | USSR European Part | Poland |
|----|-------------------|-------------------------------------|--------------------------------|--------------------|--------------------|
| BP | Chron. Interstad. | Chron. Interstad. | Chron. Interstad. | Chron. Interstad. | Chron. Interstad. |
| 10 | Flandrian | Holocene | Holocene | Holocene | Holocene |
| 20 | Late Allerød | Late Allerød Weichselian Bølling | Late Vistulian | Late Valdai | Late Vistulian |
| 30 | Middle Devensian | Middle Weichselian Dencamp Hengelo | Younger Pleniglacial Vistulian | Valdai | Vistulian 3 |
| 40 | Upton Warren | Moershoofd | Inter-Pleniglacial Vistulian | Middle Valdai | Vistulian 2/3 V2/3 |
| 50 | Devensian | Odderade | Older Pleniglacial Vistulian | Valdai | Vistulian 2 |
| 60 | Early Chelford | Early Weichselian Bratup Amersfoort | Early Vistulian | Early Valdai | Vistulian 1/2 V1/2 |
| 70 | Devensian Wretton | Eemian | Vistulian B | Valdai | Vistulian 1 |
| | Ipswichian | Eemian | Eemian | Mikulino | Eemian |

ski, 1982), while during almost the whole Vistulian it is very rare and only occurs in stadials V2 and V3. Towards the end of glaciation it regularly appears as an accidental element. In some phases of the Holocene, this species becomes very frequent, being a subdominant element for example during the Sub-Boreal phase (Nadachowski *et al.*, 1989).

(7) *Cricetulus migratorius* (Pallas, 1773): a very rare representative of steppe fauna, probably occurred at the beginning of the last glaciation (Ciemna Cave) (Nadachowski, 1982) and reappeared once more during interstadial V2/3 and cold period V3. Its last appearance date lies within the cooler phase of LV, most probably the Older Dryas (Bocheński *et al.*, 1985).

(8) *Dicrostonyx gulielmi* (Sanford, 1870): a typical representative of the steppe-tundra rodent community in Europe during the last glaciation, is the immediate ancestor of the recent arctic form — *D. torquatus* Pallas, 1779. Its immigration around the Eemian/Vistulian boundary to Central Europe indicates the first wider expansion of the non-forest environments. Fluctuations in frequency of this species are connected with climatic and vegetational changes. It is especially frequent in V2 and V3 stadials while during milder phases it becomes rare yet always present in the rodent community. It has survived, as a Pleistocene relic form, until the beginning of the Neoholocene, at least in the Cracow Upland (Nadachowski *et al.*, 1989).

(9) *Lemmus lemmus* (Linnaeus, 1758): another species of the lemming also connected with steppe-tundra environments appears in Poland probably together with *Dicrostonyx* in the stadial V1. It dominates over *Dicrostonyx* in milder phases while it becomes less frequent during climatic minima. Its last appearance date lies probably around the Vistulian/Holocene boundary, at least for the Cracow Upland region.

(10) *Clethrionomys glareolus* (Schreber, 1780): a typical woodland species occurs in almost all fossil assemblages even during very cold periods. Only in LV phase and especially during Holocene, the bank vole becomes very abundant, being the dominant species in the majority of samples.

(11) *Arvicola terrestris* (Linnaeus, 1758): is a constant element of rodent communities during the last glaciation, although, especially in cooler breaks, its frequency was very low. The water vole from the Late Quaternary is taxonomically related to the small subspecies *A. t. exitus* (Nadachowski, 1982), which recently inhabits the Carpathians (Cais, 1974; Kowalski *et al.*, 1981). Holocene populations, especially, from the Cracow Upland, show a similarity to the big subspecies *A. t. terrestris*, which probably appeared as a post-glacial newcomer from the east, replacing the glacial relic form *A. t. exitus* in the lowlands.

(12) *Pitymys tatricus* Kratochvil, 1952: it was only mentioned from Holocene sediments of two caves in Tatra Mts. (Wołoszyn, 1970).

(13) *Pitymys subterraneus* (de Selys-Longchamps, 1836): its appearance in the territory north of the Carpathians is connected with a successive warming up of the climate during LV.

(14) *Microtus nivalis* (Martins, 1842): was previously reported from some localities in the Cracow Upland (Kowalski, 1961, Kowalski *et al.*, 1967, Nadachowski, 1976) as an accidental element of the rodent community. It appeared, however, that those findings concerned morphological variants of *M. oeconomus* (Nadachowski, 1982). It seems that the snow vole was limited to the Carpathians even during cooler periods, and occurred in some mountain regions (*e.g.* in Podhale) at least during V2/3 interstadial (Nadachowski & Wolsan, 1987).

(15) *Microtus oeconomus* (Pallas, 1776): a constant element of the fauna during both cool and mild phases, was especially frequent in V2/3 interstadial. It survived in the Cracow region probably up to the beginning of the Sub-Atlantic phase of the Holocene (Nadachowski *et al.*, 1989).

(16) *Microtus agrestis* (Linnaeus, 1761): is present as an accidental or accessorial element during the entire Late Quaternary including its climatic minima. Its frequency only increases during some phases of the Holocene, probably as a result of a wider expansion of forested areas.

(17) *Microtus arvalis* (Pallas, 1779): one of the most important species of rodents distinctly changing its frequency according to climatic fluctuations. Its absolute domination during V1/2 interstadial and codominance together with *M. oeconomus* in V2/3 period is the most characteristic feature of rodent community during the mild phases of the last glaciation. In cool periods the common vole is replaced, sometimes completely, by *M. gregalis*. During almost the whole Holocene it is rather rare; the distinct increase of its frequency is connected with the appearance of cultivated fields.

(18) *Microtus gregalis* (Pallas, 1779): is the most common species among rodents of the steppe-tundra assemblage. Its immigration at the end of the Eemian Interglacial (Koziarnia Cave, layers 20—18; Chmielewski *et al.*, 1967) indicates the probable first appearance of cooler conditions and open environments. This species dominates during the Vistulian in almost all communities with the exception of distinct warmings-up of the climate in V1/2 and V2/3 when it is replaced by *M. arvalis*. The narrow-skulled vole survived in the Cracow Upland probably longer than the lemming, until the Sub-Boreal phase of the Holocene (Nadachowski *et al.*, 1989).

(19) *Lagurus lagurus* (Pallas, 1773): a very rare member of the steppe-tundra rodent community, appears probably towards the end of V1/2

interstadial in connection with the development of steppe environments and survived in most of the assemblages up to the V3 glacial phase, always as an accidental element of the fauna.

(20) *Mus musculus* Linnaeus, 1758: its appearance only in historical times is connected with human activity, although we lack precise information.

(21) *Rattus norvegicus* (Berkenhout, 1769): another representative of synanthropic elements; it probably appeared much later than *M. musculus*, and is known only from Dużej Sowy Cave (Bocheński *et al.*, 1983).

(22) *Rattus rattus* (Linnaeus, 1758): has been recorded in subfossil state in Silesia from Early Iron and Medieval times (Chrzanowska, 1985; Wyrost & Chrzanowska, 1985), but data from Western Europe (Yalden, 1982) and the Carpathian Basin (Kordos, 1978) indicate its earlier introduction than by the previous species.

(23) *Micromys minutus* (Pallas, 1771): is absent in steppe-tundra communities in Poland and probably appears in warmer periods in the end of LV (*e.g.* Bramka; Nadachowski, 1982). Its wide expansion in the Neoholocene is probably connected with human activity.

(24) *Apodemus agrarius* (Pallas, 1771): seems to appear in Central Europe in post-glacial times in connection with the development of cultivated fields. It is probably present in northern Hungary already during the Atlantic episode (Kordos, 1982). In subfossil state in Poland it is only known from one locality (Bocheński *et al.*, 1983).

(25) *Apodemus (Sylvaemus)* group: the three species of this subgenus recorded from Poland (*Apodemus sylvaticus*, *A. flavicollis* and *A. microps*) are hardly distinguishable in their fossil state, they are treated together here. Remains of this taxon appear as accidental elements during V1/2 and at the beginning of V2 cold phase. *Apodemus (Sylvaemus)* is present again in the rodent community in mild periods of LV. During the Holocene it becomes a constant element of the fauna but its frequency fluctuates depending on local conditions.

(26) *Sicista betulina* (Pallas, 1778): this rare species first appears in the Cracow Upland during V3 glacial phase of Mamutowa Cave (Nadachowski, 1976, 1982), and is present in the region up to the Neoholocene (Nadachowski *et al.*, 1989).

(27) *Eliomys quercinus* (Linnaeus, 1766): appears as a very rare member of the woodland fauna, probably only during the Neoholocene.

(28) *Dryomys nitedula* (Pallas, 1779): lack of fossil evidence from Poland.

(29) *Glis glis* (Linnaeus, 1766): a typical representative of the woodland faunal complex joins the mentioned rodent community during the end

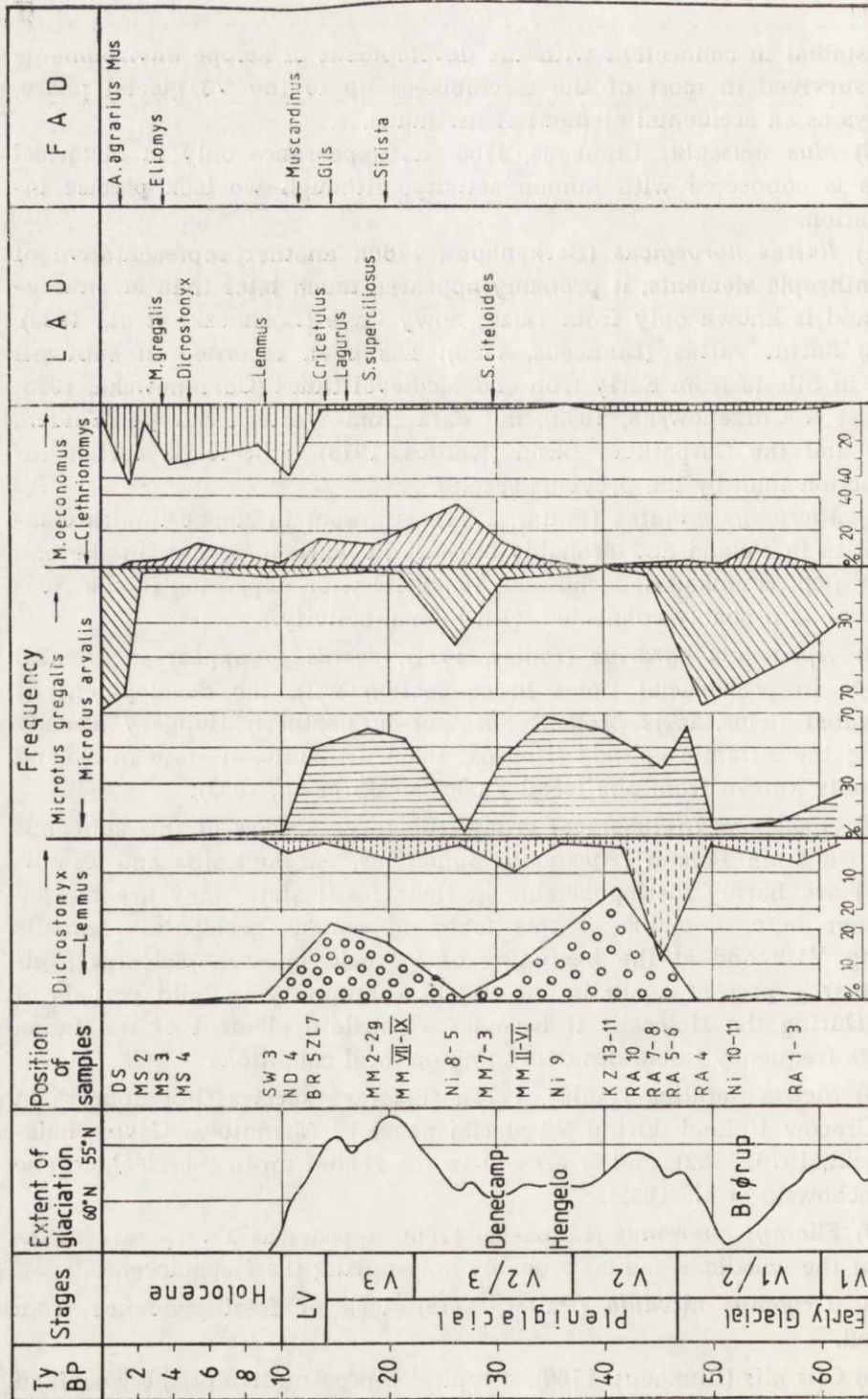


Fig. 1. Stratigraphy and succession of rodents during the Late Quaternary. LAD — last appearance dates, FAD — first appearance dates. For further explanation see Table 1 and the text.

of V3 and warm phases of LV. It is regularly present in most of the Holocene assemblages as accidental or accessorial element.

(30) *Muscardinus avellanarius* (Linnaeus, 1758): probably appears slightly later than the previous species (Nadachowski, 1982) and occurs in the majority of Holocene communities.

4. RECONSTRUCTION AND SUCCESSION OF LATE QUATERNARY RODENT COMMUNITIES

Investigation of community structure and changes of faunal diversity of particular samples (Table 1, Fig. 1) assignable to climatic phases of the last glacial cycle can be summarized as follows:

(1): Vistulian 1/2 (=Early Vistulian B and D=i.e. Amersfoort, Brørup and? Odderade Interstadials) — V1/2

A period of mild conditions represented by assemblages RA 1—3, NI 10—11 and RA 4 is characterized by a distinct predominance of *Microtus cf. arvalis*. Highly arctic species, such as lemmings, occur with low frequency while *Lemmus* dominates over *Dicrostonyx*; *Microtus gregalis* is also relatively scarce. Steppe elements are represented by accidental *Spermophilus citelloides* and *Lagurus*. Inhabitants of forests (*Castor fiber*, *Clethrionomys*, *Apodemus*) occur sporadically. Species connected with moist environments (*Microtus oeconomus* and *Arvicola terrestris*) are accessorial elements.

(2): Vistulian 2 (Older Pleni-Vistulian) — V2

The most important change in the community structure during the second very cold break of the last glaciation is the increase of *Microtus gregalis* frequency and decrease of *Microtus cf. arvalis* in the successive assemblages (cf. samples RA 5—6, RA 7—8, RA 10 and KZ 13—11). At the same time both lemmings become more frequent. At first, *Lemmus* plays more an important part while during climatic minima, *Dicrostonyx* becomes very abundant and *Lemmus* distinctly diminishes its frequency. Species connected with steppe conditions (*Spermophilus superciliosus*, *S. citelloides*, *Cricetus*, *Lagurus*) appear occasionally, and are very scarce. Eurytopic taxa (*Arvicola*, *Microtus cf. agrestis* and *Microtus oeconomus*) are accessorial elements; the only woodland species represented are accidental *Clethrionomys* and *Apodemus (Sylvaemus)*.

(3): Vistulian 2/3 (=Inter-Pleni-Vistulian=? Hengelo and Denecamp Interstadials) — V2/3

This period of slightly milder climate (represented by NI 9, MM 7—3, MM II—VI and NI 8—5 assemblages) is distinguishable by a gradual

disappearance of the tundra index species (*Dicrostonyx*, *Lemmus* and *Microtus gregalis*) in favour of *Microtus cf. arvalis* and *Microtus oeconomus*. Especially the latter one becomes more frequent and plays an important part in comparison with previous communities. Also, *Arvicola* markedly increases its frequency. Taxa of steppe environments have survived as accidental elements (both *Spermophilus* species, *Lagurus*, *Cricetulus*). Other elements, eurytopic or connected with woodland areas (e.g. *Clethrionomys*, *Microtus cf. agrestis*), are represented accessorially or sporadically, even in milder phases.

(4): Vistulian 3 (Younger Pleni-Vistulian) — V3

A period of maximum extent of continental glaciation during the Vistulian is characterized by a repeated increase of *Dicrostonyx* and *Lemmus*, and a distinct predominance of *Microtus gregalis*. (cf. MM 2—2g and MM VII—IX assemblages). This period is the last appearance date (LAD) of two steppe elements — *Lagurus lagurus* and *Spermophilus superciliosus*; while the other species of souslik (*S. citelloides*) has not survived. On the other hand, other open country species reappear (e.g. *Cricetulus*, *Cricetus*). Noteworthy is the presence of *Sicista* in some assemblages.

(5): Late Vistulian — LV

This relatively short period is characterized by distinct changes between rodent communities attributed to cool and mild phases. During cool periods (Older and Younger Dryas) represented in the present analysis by the ZL7 fossil assemblage, a recovery of steppe-tundra communities is observed with a distinct predominance of *Dicrostonyx* and *M. gregalis*. The other species of the lemming, *L. lemmus*, disappears or is very rare. Of the typical steppe forms, only *Cricetulus* is present, while both *Spermophilus* species and *Lagurus* have not survived, at least in the Cracow Upland. During periods of mild climate (e.g. Bøling, Allerød) a distinct increase of species diversity is observed (samples BR5, ND4, SW3) as indicated by the appearance of several inhabitants of forests (e.g. *Glis*, *Sciurus*, *Muscardinus*). *Clethrionomys* becomes the dominant element while *Pitymys subterraneus* occurs accidentally. In some assemblages *Cricetus*, *Arvicola* and *Apodemus* are also very abundant, which is probably connected with some local conditions.

(6): Holocene

During the last 10 thousand years, a continuous increase of the frequency of sylvan and eurytopic species, especially of *Clethrionomys* and *M. agrestis* is observed. Among the index taxa of the steppe-tundra community, only two species — *Dicrostonyx* and *M. gregalis* survived until the beginning of the Neoholocene at least in the Cracow Upland. The period under discussion is also characterized by the development of

human activity. The appearance of cultivated fields and urban ecosystems, especially in the Sub-Atlantic phase, is responsible for a rapid expansion of *Microtus arvalis* and *Apodemus agrarius* as well as several synanthropic species of rodents (e.g. *Rattus*, *Mus*).

5. DISCUSSION AND CONCLUSIONS

The history of rodent faunal succession in Poland during the last 60—70 thousand years can be generally divided into two periods: (1) the Pleni-Vistulian (V2-V2/V3), which is characterized by the development of steppe-tundra communities and (2) the Late Vistulian (LV) and the Holocene, distinguished by the successive remodelling of the community structure towards the recent species composition.

The faunal assemblages during the Pleni-Vistulian were relatively stable in species diversity. Noteworthy is the presence of both tundra (e.g. *Dicrostonyx*, *Lemmus*) and steppe (e.g. *Cricetulus*, *Spermophilus*, *Lagurus*) elements. Such a mixture of taxa is characterized for the majority of fossil assemblages within the broad zone of Europe, Northern Asia and Beringia of that time, which agrees with the concept of a steppe-tundra biome (Guthrie, 1982). The most characteristic features of this ecosystem were the development of extensive grassland vegetation with *Artemisia* and the coexistence, among invertebrates, birds, large and small mammals, of both arctic and steppe forms, which has no exact modern analogy (Hopkins *et al.*, 1982).

Pleni-Vistulian rodent communities from Poland are characterized by a very low frequency of steppe elements (up to 2.8%); while their age equivalents further to the east, e.g. in the Ukraine, show a distinct increase of these elements (up to 40—70% in some communities), belonging first of all to *Lagurus*, *Allactaga jaculus* (Pallas, 1778), *Marmota bobac* Müller, 1776 and *Eolagurus luteus* (Eversmann, 1840) (Rekovets, 1985). South of the Carpathians, in the territory of Czechoslovakia, the frequency of steppe forms (e.g. *Marmota bobac*, *Spermophilus species*, *Sicista subtilis* Pallas, 1773 and *Cricetulus*) is similar to that in Polish data (Horáček & Sánchez Marco, 1984).

Another important feature of the Pleni-Vistulian rodents communities is a change in proportions of index species due to minor climatic oscillations. In the course of both stadial phases (V2 and V3) first an increase of the representation of *M. gregalis* and *Lemmus* is noted and only during climatic minima does *Dicrostonyx* distinctly increase its frequency. By the beginning of interstadial V2/3, a reversed trend seems to occur i.e. a repeated increase of *Lemmus* and *M. arvalis* as well as a decrease of *Dicrostonyx* and *M. gregalis* frequency.

The steppe-tundra biome in the territory north of the Carpathians is also characterized by stable although accessorial additions of sylvan species in the community (*Clethrionomys*) striking in comparison with the Ukrainian assemblages, where the above mentioned taxa are totally absent (Rekovets, 1985).

During cool phases the species diversity is lower than in interstadials, while the index of equitability does not change essentially in the period under discussion (Table 1). It is clear that the species dominance is preserved on the same level, independently of climatic fluctuations, because predominant taxa *M. gregalis* and *M. arvalis* are always the major components of the communities, respectively in both cool and mild phases of the Pleni-Vistulian.

Fossil evidence from the last glacial cycle concerning the temporal and spatial distribution of rodents indicates that the present faunal communities have already been fully formed during the Late Vistulian and the Holocene. Rapid changes in climate and vegetational patterns of these periods are mainly responsible for distinct changes in distribution of particular rodent species. Especially, the raise in temperature at that time had a great effect on the vegetation and, in consequence, on the fauna. A wide expansion of coniferous and mixed forests with shrubby undergrowth in relatively humid climate influenced the expansion of several sylvan species (*Clethrionomys*, *Apodemus*, *Pitymys*, *Sciurus*, glirids) and a gradual disappearance of taxa connected with the steppe-tundra environments. Typical steppe forms (*Lagurus*, *Spermophilus*, *Cricetulus*) disappeared first, while tundra species, especially *Dicrostonyx*, *M. gregalis* and *M. oeconomus*, survived far into the Holocene as relic forms.

Generally, the Holocene assemblages are characterized by higher values of species diversity and equitability indices. Interpretation of the data is based on the fact that mild climatic conditions will increase directly and through effect on vegetation structure, both species richness and equitability within an animal community.

The last period of the Holocene (Sub-Atlantic episode), which covers the last 2000 years, is dissimilar to previous phases as far as the rodent community structure is concerned. Both indices of community structure show extremely low values and are rather comparable with Pleni-Vistulian rodent communities. This characteristic is connected with an absolute predominance of *M. arvalis* and the appearance of synanthropic species of rodents (including *Apodemus agrarius*). Those two new phenomena are due to the deforestation and/or urbanisation connected with human activity.

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POCHODZENIE I HISTORIA WSPÓŁCZESNEJ FAUNY GRYZONI POLSKI
NA PODSTAWIE MATERIAŁÓW KOPALNYCH

Streszczenie

W oparciu o analizę około 16 000 szczątków gryzoni z młodszego czwartorzędu, należących do 25 gatunków, odtworzono historię przemian fauny gryzoni w tym okresie na terenie Polski. Porównano 21 prób faunistycznych o znanym wieku geologicznym, pochodzących z różnych stanowisk kopalnych, głównie południowej części Wyżyny Krakowskiej. Zbadano strukturę gatunkową i zmiany liczebności w zespołach gryzoni z poszczególnych okresów późnego plejstocenu i holocenu stosując ekologiczne współczynniki różnorodności Shannona (H), struktury gatunkowej (d) i jednorodności zespołu faunistycznego (e). Zgrupowanie gryzoni z chłodnych faz ostatniego zlodowacenia (Vistulianu) wyróżnia się dominacją gatunków tundrowych (*Microtus gregalis*, *Lemmus lemmus* i *Dicrostonyx gulielmi*) oraz obecnością niezbyt licznych gatunków stepowych (*Spermophilus citelloides*, *S. superciliosus*, *Lagurus lagurus* i *Cricetulus migratorius*). Współwystępowanie wspomnianych gryzoni, obecnie oddzielonych od siebie olbrzymimi dysjunkcjami, jest charakterystyczne dla ekosystemu stepo-tundry plejstocenijskiej, który nie ma współczesnego odpowiednika. Zespół gryzoni tego okresu wykazuje zasadnicze zmiany liczebności pomiędzy parami gatunków dominujących (*M. gregalis* — *M. arvalis* i *Lemmus* — *Dicrostonyx*) w zależności od wahań klimatycznych i środowiskowych. Stepotundrowy zespół gryzoni z terenu Polski wyróżnia się ponadto stałą obecnością bardzo co prawda nielicznych gatunków leśnych i eurotypowych, takich jak *Clethrionomys glareolus* i *Microtus agrestis*. Współczesna fauna uformowała się w pełni dopiero w okresie późnego glacjału i holocenu. Zasadnicze zmiany klimatyczne pociągające za sobą rozwój ekosystemów leśnych, spowodowały stopniowy zanik gatunków żyjących w stepo-tundrze i ekspansję form typowo leśnych (*Clethrionomys*, *Apodemus (Sylvaemus)*, *Glis glis*, *Muscardinus avellanarius*) i łąkowych (*Pitymys subterraneus*). Niektóre relikty plejstocenijskie, takie jak *Dicrostonyx* i *M. gregalis*, przetrwały jednak aż do początku późnego holocenu, przynajmniej na Wyżynie Krakowskiej. Obecny okres (faza subatlantycka) charakteryzuje się silną ekspansją *M. arvalis* i *Apodemus agrarius* na skutek rozwoju pól uprawnych oraz pojawieniem się kilku gatunków synantropijnych.