Late Eemian (Late Pleistocene) vertebrate fauna from the Horváti-lik (Uppony, NE Hungary)

by
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Abstract — A Late Eemian (Marine Isotope Stage 5d) vertebrate fauna was excavated in Horváti-lik (Horváti Hole) at Uppony, NE Hungary, in 1977 and 1978. After the preliminary reports, the authors identified the whole fauna of the 25 layers of the small cave. Following the faunistical and cluster analysis, the 410 cm long profile is divided into three units: the uppermost layers 1–4 are Holocene, layers 5–6 are mixed, and layers 7–21 yielded similar faunal content of early Late Pleistocene age. The rodents are predominant; *Microtus arvalis* is the most abundant species. The steppe elements are present in high percentage (e. g. *Sicista*, *Ochotona*, *Citellus*, *Allocricetus*, *Spalax*, *Allactaga*, *Cricetus* and *Lagurus*), and *Dicrostonyx* also occurs.

Results of the ecotype analysis among the vertebrate fauna of the different Pleistocene layers (number of species, body size, trophic preferences and ecological units) are as follows. Layers 7–20 show similar ecotype, characterized by low diversity, dominance of the smallest body size category, and abundance of the granivores. Layer 21 is somewhat different, because it is containing more larger body size elements and more frequent browser/grazers and omnivores.

Using cluster analysis, biochronological methods and correlation with the Marine Isotope Stages and the continental stratigraphic units, the Pleistocene faunas of the Horváti-lik represent a significant steppe phase at the end of the Eemian, correlated with Marine Isotope Stage 5d, or Herning Stadial, dated as 120–110 kyr BP.

Keywords — Pleistocene, vertebrates, Eemian, steppe, Hungary.

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Introduction

The Horváti-lik (Horváti Hole) is located close the village of Uppony (NE Hungary), on the left side of the Uppony Gorge. The small cave lies at 270 metres above sea level and 70 meters above the bottom of the valley. The explored length of the cave is 17 m, and the largest vertical extension is 7.6 m. The Uppony Gorge contains several small caves, rock-shelters and holes. Most of them open in the south cliffs of the valley. VÉRTES found four caves in the area, and his excavation in the Uppony I. rock-shelter was succesful in 1949 (VÉRTES 1950). In 1963 JÁNOSSY (JÁNOSSY 1965; JÁNOSSY et al. 1968) continued VÉRTES' excavation and discovered an important late Middle Pleistocene vertebrate fauna, then established the "Uppony Phase" biochronologic unit.

On the northern side of the Uppony Gorge, there are also several unexcavated small caves, which are mentioned by VÉRTES (1950), and well known among the local people.

One of the small caves on the northern side of the Uppony Gorge is the Horváti-lik, where L. FŰKÖH and L. KORDOS collected fossils in 1977 and 1978 (FŰKÖH & KORDOS 1977, 1980). The total thickness of the excavated cave sediment, down to the bedrock, is 410 cm that is divided into 25 layers (Figure 1). Former sedimentological, micromineralogical, chemical investigations, and the results from malacological and vertebrate paleontological records divided the section into 3 or 4 depositional units: (1) layers 1–4, probably 1–2 are different, where the age of 1–2 layers is Late Holocene, and the 3–4 layers have Early Holocene age, (2) layers 5–6, Late Pleistocene without significant age and climatic markers, (3) layers 7–15 represent a continuous

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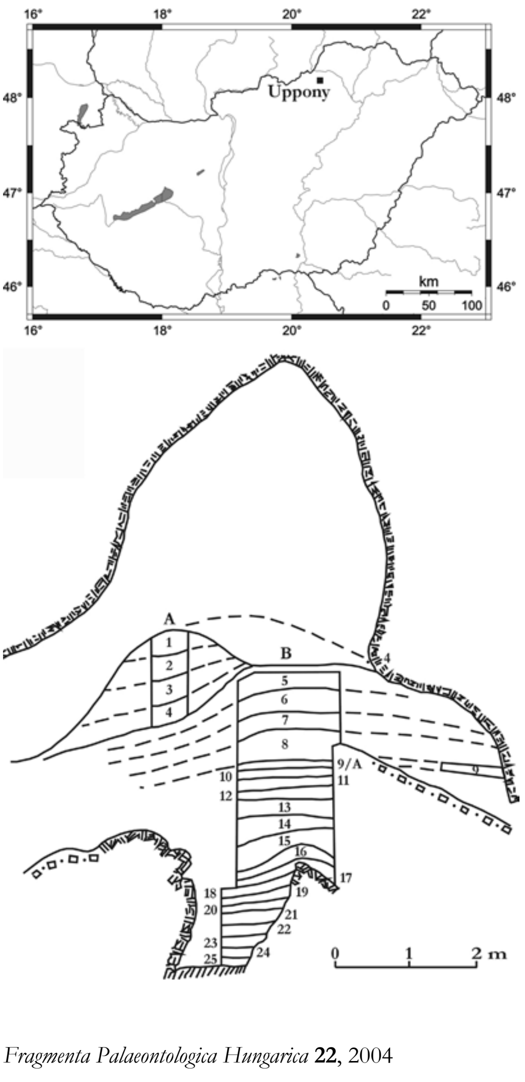

Figure 1 — Location of Uppony and the excavation sections of Horváti-lik (Horváti Hole). — **Section A**: Holocene deposits — **Section B**: Pleistocene deposits

depositional sequence, and these layers contain the most important succession of the vertebrate fauna of Late Eemian age, (4) layers 16–25 consist of yellow clay with limestone clasts, containing fewer vertebrate remains than the former unit but characterized by the same faunal assemblage.

While the molluscan fauna of the Horváti-lik and its paleoenvironment is thoroughly investigated (FŰKÖH 1980, 1983, 1993a, 1993b, 1995), few preliminary reports were published on the vertebrate fauna (FŰKÖH & KORDOS 1980; KORDOS 1990).

In this paper, the purposes of our investigation are (1) to determine the age of the Horváti-lik faunas, and (2) to describe the former environment by means of characterization of the mammalian faunas.

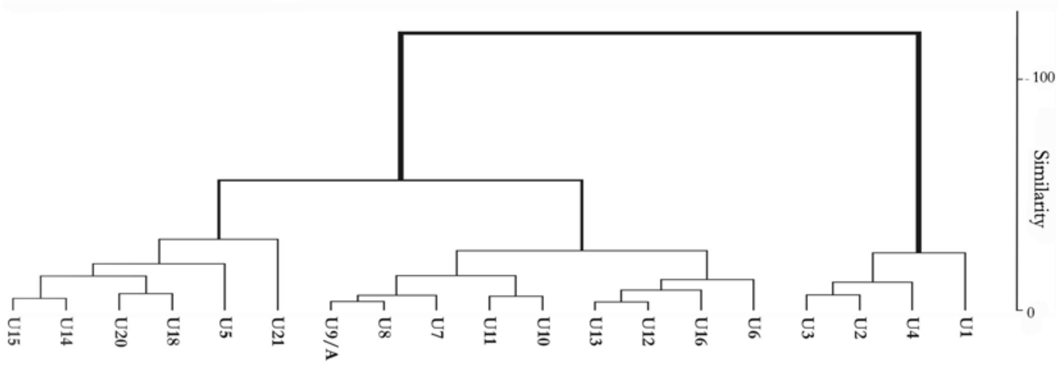

Figure 2 — Cluster analysis based on the small mammalian fauna of Horváti-lik. — The layers were divided into two large groups by this method. Layers U1–U4 are the first group (Holocene), and layers U7–U21 are the second group (Pleistocene).

Methods

The investigations were based on specimens of mammalian species. Materials of 6 layers (layers 17, 19, 22–25), due to their low species number, were left out from the faunistical and ecological analyses. Thus results were based on investigation of mammalian faunas of 19 layers.

The applied methods fall into two groups. Methods of the first type are based directly on species composition of mammalian faunas. The cluster analysis and the investigation of selected groups (arvicolids, steppe species) belong to this group. The other type consists of taxon-free methods, including the study of three ecological variables, trophic structure, body size distribution and diversity index. The cluster analysis and the investigation of selected groups allow determination of the age of layers. The application of taxon-free methods helps establish the ecological characteristics of these layers.

Cluster analysis — This method was applied to demonstrate changes in the species composition and dominance relations of mammalian faunas. Cluster analysis was based on small mammals (< 1 kg body weight) only. In the course of investigation two cluster analyses were made. The first time only the mammalian fauna of the Horváti-lik was studied. The percentage values were entered for each species in each layer. Thus, on the basis of species composition and dominance relations of small mammalian faunas, changes that occured in the layers, were demonstrated.

Database of the second cluster analysis contained all the Quaternary mammalian faunas from the Carpathian Basin that were suitable for faunistical and ecological investigations, including the Horváti-lik faunas. Using this method we could establish similarities between certain layers of Horváti-lik and other Quaternary localities. The cluster analyses were performed using the WARD's method on PAST software.

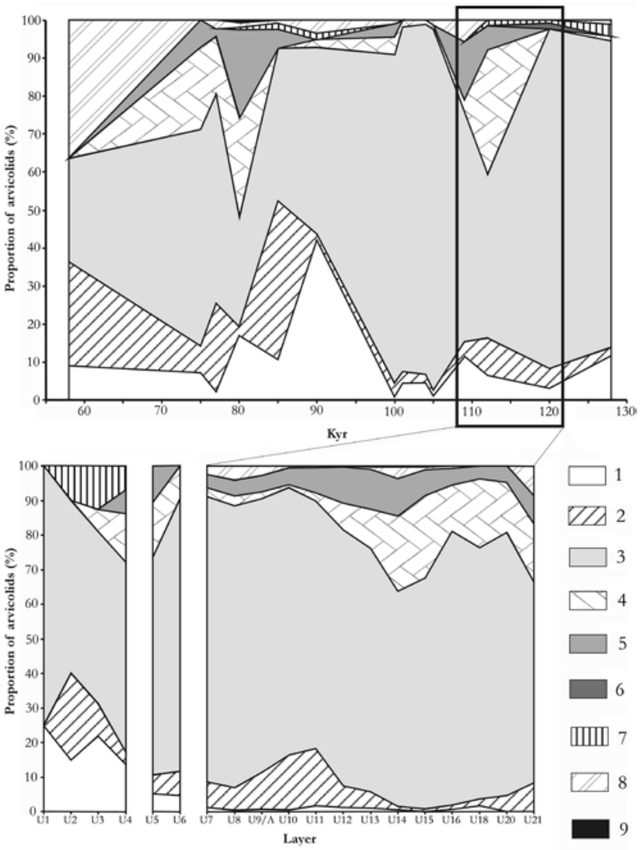

Figure 3 — Proportion of arvicolids between 130 and 55 kyr in all localities of the Carpathian Basin (above) and in layers of Horváti-lik (below). — Arvicolid fauna of the framed interval (about between 120 and 110 kyr) is most similar to layers U7–U21. — **1**: *Clethrionomys glareolus* — **2**: *Arvicola terrestris* — **3**: *Microtus arvalis* — **4**: *Microtus gregalis* — **5**: *Microtus oeconomus* — **6**: *Microtus nivalis* — **7**: *Pitymys subterraneus* — **8**: *Lagurus lagurus* — **9**: *Dicrostonyx torquatus.*

Investigation of selected groups — In addition to the cluster analyses, investigation of selected groups was also used for determination of age of Horváti-lik faunas. Two groups were investigated: the arvicolids and the steppe elements (*Spalax* sp., *Citellus* sp., *Ochotona* sp., *Cricetus cricetus*, *Allocricetus bursae*, *Allactaga* sp., *Sicista* sp., *Microtus gregalis*, *Lagurus lagurus*). In both cases the database contained the percentage values of arvicolids or steppe elements in each layer or locality. With the help of this method the age of layers was more precisely determined than by the cluster analysis.

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. 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 (PAZONYI 2004).

In case of extinct species, this model was 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.

Ecotypes — *Number of species* — The number of species is primarily determined by the environmental conditions and the vegetation. In adverse circumstances and less complex environment (such as in 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). Being one component of diversity, the number of species plays an important role in the interpretation of the diversity index values. Diversity is calculated using the Shannon-Weaver diversity index (SHANNON and WEAVER 1949).

Body size — Estimation of the body size can be made through a comparative method, by comparing the data of extant and fossil species. Through the comparative method, and using the body size categories of Andrews, we classified the species 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: >360 kg (ANDREWS et al. 1997). (Note that the original categories were determined in pounds, rather than in kilograms).

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

Ecological units — On the basis of the ecological variables of the given ecosystem, a temporal sequence of ecological units can be established, which characterize the changes in the mammalian fauna. Ecological units were characterized by ecological variables. 15 values were determined for each ecological unit (6 trophic preference categories, 8 body size categories and the diversity index). The interval of values was determined by cluster analysis in case of all ecotypes, thus three intervals were separated in all ecotypes: high, medium and low. These intervals are valid in the whole Quaternary, because the cluster analyses are based on values of the ecotypes of every Quaternary locality.

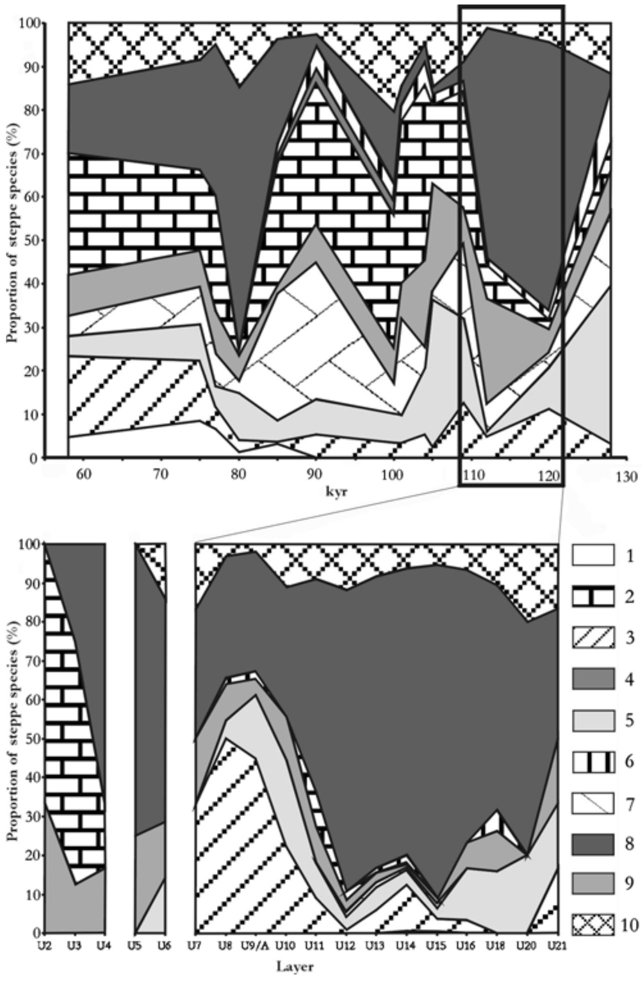

Figure 4 — Proportion of steppe species between 130 and 55 kyr in all localities of the Carpathian Basin (above) and in layers of Horváti-lik (below). — Distribution of steppe species in the framed interval (about between 120 and 110 kyr) is most similar to layers U7–U21. — **1**: *Allactaga* sp. — **2**: *Cricetus cricetus* — **3**: *Lagurus lagurus* — **4**: *Cricetulus* sp. — **5**: *Citellus* sp. — **6**: *Allocricetus bursae* — **7**: *Spalax* sp. — **8**: *Microtus gregalis* — **9**: *Sicista* sp. — **10**: *Ochotoma pusilla*.

Pleistocene vertebrate fauna of the Horváti-lik

The revised vertebrate fauna and the calculated number of the individuals of all layers of the Horváti-lik are listed in the Appendix as Table I, and II.

Cluster analysis of small mammalian fauna of Horváti-lik shows that the layers are divided into two large groups (Figure 2). Layers 1–4 fall within the first group. The second group is divided into two groups: layers 7–13 and layers 14–21. Position of layers 5–6 is not clear in the clusters; probably this method could not classify these mixed faunal layers. Because the fauna of the Holocene beds (1–4) was already discussed in detail (FŰKÖH & KORDOS 1980), and the layers 5–6 contain mixed faunas, we restrict our study to the Pleistocene layers.

Most of the Pleistocene layers contain a small amount of fish bones, frogs, lizards (*Anguis*, *Lacerta*), snakes and bird bones. Among the mammals the bats are rare, the *Talpa* and the soricids (*Sorex*, *Neomys*) are common. Rodents are dominant, especially the arvicolids.

Arvicolid fauna of all layers is characterized by dominance of *Microtus arvalis*. In layers 7–13, in addition to *M. arvalis,* mainly the proportions of *Arvicola terrestris* and *M. oeconomus* are significant, while in layers 14–21 the proportion of *M. gregalis* is higher. In layers 13–15, *Dicrostonyx* appeared, and greater proportions of *Lagurus* and *M. oeconomus* were observed. *Pitymys* is absent from all layers and the role of *Clethrionomys* is subordinate (Figure 3).

Based on investigation of steppe species in layers 7–11 the proportion of *Lagurus* is huge, in layer 8 it reaches 50% of all steppe species. Apart from *Lagurus*, *Microtus gregalis* is also well represented, whereas *Sicista*, *Ochotona*, *Citellus* and *Allocricetus* occur in smaller proportions. The lower layers are characterized by dominance of *M. gregalis*, with significant number of *Citellus* in layers 16–21. Layers 12–15 yielded the richest steppe fauna. In addition to the previously listed species, *Spalax*, *Cricetus* and *Allactaga* also appeared in these layers (Figure 4).

Remains of medium and larger size mammals are rare, due to the taphonomic situation of the small cave. In some layers *Mustela erminea*, *Mustela nivalis*, *Vulpes*, *Ursus*, bovids and ruminants are present.

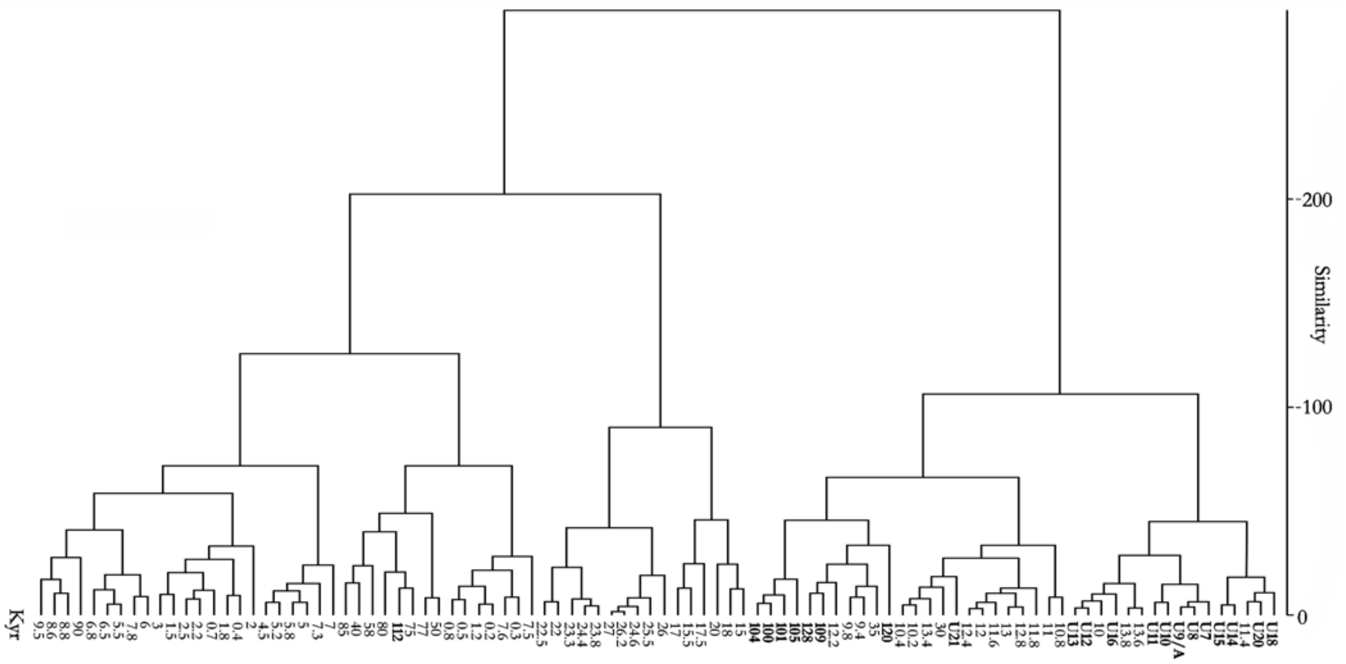

Figure 5 — Cluster analysis based on all the statistically suitable small mammalian faunas during the last 130 kyr and layers U7–U21 of Horváti-lik. — The layers and the faunas of probably similar age are shown in bold.

Results of ecological investigation

The taxon-free investigation showed only minimal differences among the layers. Except for layer 21, every layer is classified into the same ecological unit. This unit is characterized by low diversity index, dominance of the smallest mammals (body size category A) and granivores. The other body size and trophic preference categories are subordinate. The low diversity index suggest low environmental complexity. This is supported by distribution of body size and trophic preference categories, where proportion of the large carnivores, omnivores and grazers is insignificant comparised with the small granivores. Low proportion of insectivores suggest cold climate and open vegetation. Summarizing these findings, the ecological characters of the fauna indicate cold climate and open, probably steppe vegetation.

Fauna of layer 21 show different ecological characters from the above. Diversity index is also low, but the distribution of body size and trophic preference categories are more equalized. In addition to the smallest species (category A), proportion of the large mammals (category G and H) is considerable as well. Beside the granivores, proportion of browser/grazers and omnivores are important. These characters show a more complex environment than the previous one. Major proportion of browser/grazers and omnivores in the fauna indicate a more closed vegetation, presence of wooded areas. The low proportion of insectivores suggests small woodland patches only, and cold climate. In summary, ecological characters of the fauna indicate cold climate and more closed, probably forest steppe vegetation.

Stratigraphy and Chronology

Cluster analysis — The cluster analysis based on all the statistically suitable Quaternary small mammalian faunas demonstrated that layers 1–4 show relationship with Early Holocene faunas. The layers 5–6 are related to the Late Pleistocene, while the other layers show connection with localities dated between 100 and 250 kyr.

Because the cluster analysis revealed an age of layers 7–21 between 100 and 250 kyr, the layers were compared with the faunas of similar age. Faunas of the Eemian interglacial event (about 130 kyr B.P.) were precluded, because the fauna of Horváti-lik include cold climate and steppe vegetation.

Based on the two selected groups (arvicolids and steppe species), especially due to the proportion of *Lagurus* and *Clethrionomys* and the lack of *Pitymys*, the period before the Eemian (250–130 kyr) was also precluded, because in this period other arvicolids were also characteristic (*Microtus arvalinus*, *Arvicola cantiana-terrestris*) and the proportion of *Clethrionomys* and *Pitymys* was larger than in layers of Horváti-lik. It follows that the age of layers 7–21 is between 100 and 130 kyr (Figure 5).

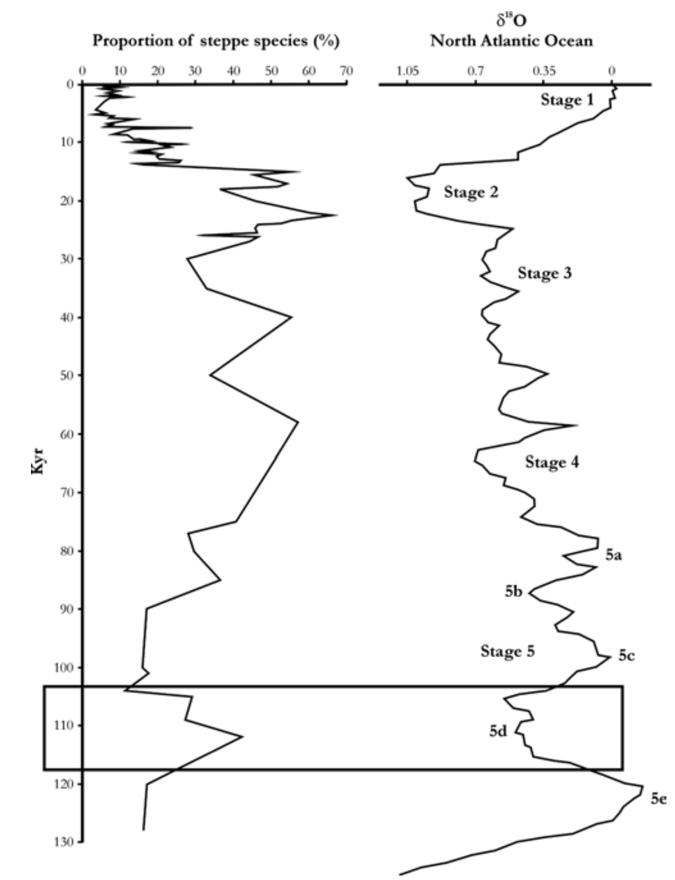

Figure 6 — Proportion of steppe species in the Carpathian Basin during the last 130 kyr (left) and an oxygene isotope curve from the North Atlantic Ocean (VOGELSANG 1990) (right). — High proportion of steppe species and high $\delta^{18}O$ value indicate cold climate and open vegetation, while low proportion of steppe species and low $\delta^{18}O$ value show warm climate and closed vegetation. Proportion of steppe species of the Horváti-lik layers 7–21 was mostly correlated with the framed interval (substage 5d, about 110–120 kyr).

Biochronology — In the latest classical vertebrate biochronologic classifications in the Late Pleistocene (KRETZOI 1953; KRETZOI & VÉRTES 1965; JÁNOSSY 1979), the following faunal phases are distinguished at the Eemian-Weichselian (or Riss-Wurm and Early Wurm) period: (1) Süttő Phase, correlated with the warm Eemian, (2) Varbó Phase, when the Mediterranean elements disappeared, and the fauna is of a „prewurm" mixed forest steppe type, (3) Subalyuk Phase, with increasing number of arctic-subartic steppe elements, as Early Wurm, (4) Tata Phase, etc.

Revision of the classical and studies of newly discovered vetrebrate faunas from the Carpathian Basin allowed the reconstruction of an almost complete succession from the Late Saalian to the Early Weichselian:

Late Saalian–Eemian transition — Type fauna Süttő 6, layers 1–10 (JÁNOSSY 1979; KORDOS 1990, 1991). The lowermost layer is contains *Dicrostonyx* and *Lagopus mutus* remains, while among the *Microtus gregalis* decreases and replaced by the predominance of *M. arvalis*. In the younger levels *Pitymys*, *Apodemus*, *Mus*, *Testudo graeca* and the lacertilians appeared. In the upper layers soricids, glirids and some steppe elements (*Citellus*, *Sicista*, *Spalax*, *Lagurus*) are present.

Eemian — The classic locality of the last interglacial is the karst fissure faunas of Süttő (KORMOS 1925; KRETZOI 1953; JÁNOSSY 1979). This fauna, which is probably mixed and selectively collected, is dominated by *Microtus arvalis* and *Apodemus*, and does not contain significant steppe and cool elements. Another locality from the Carpathian Basin is Por-lyuk at Jósvafő (JÁNOSSY et al. 1973) that has a similar faunal character with more forest elements (*Clethrionomys*, more murids and glirids), and sporadically some steppe taxa (*Citellus*, *Sicista*, *Spalax*, *Ochotona*).

Eemian–Weichselian trasition — This transition period is characterized by several newly discovered faunas, as Horváti-lik at Uppony (FŰKÖH & KORDOS 1977, 1980, and in this paper), Eger-Dobó-bástya (KORDOS & KROLOPP 1980), Süttő 9 (JÁNOSSY 1979), Tatabánya-Kálvária 4. (KORDOS 1994), Poros-lyuk at Répáshuta (JÁNOSSY 1979), and Bajót 3. rock-shelter 5a layer (KORDOS 1994). The faunas of these localities appear to fill the 25–30 kyr gap between the end of the Eemian Süttő Phase and the Early Weichselian Varbó Phase in Hungary.

Characteristic for these faunas is the greater abundance of *Microtus gregalis* (while *M. arvalis* remains predominant among the rodents), *Dicrostonyx* is sometimes present, the diversity of the eastern steppe taxa is increasing due to a characteristic steppe extension event (joint appearence of *Ochotona*, *Microtus gregalis*, *Allocricetus*, *Cricetus*, *Citellus*, *Sicista*, *Lagurus*, *Spalax* and *Allactaga*). The Eemian-Early Weichselian transition period is represented by a typical faunal event, where in the first phase the abundance of *M. gregalis* is increasing, later the second one is characterised by *Lagurus* becoming predominant among the steppe taxa, and finally the general dominance of the *Microtus arvalis* is declining.

Marine Isotope Stages and Continental Stratigraphic Units — Within the classical frame of the Oxigene Isotope Stages of the Quaternary (EMILIANI 1955), for the last interglacial SHACKLETON (1969) distinguished the 5a, b, c, d and 5e substages. During 5e substage a global temperature was warmer than today, the ice volume is decreased, the sea level is elevated. The substage 5e was dated between 130 and 116 kyr (KUKLA et al. 2002; SHACKLETON et al. 2003), and it is correlated with Eemian Stage (ZAGWIJN 1961; MANGERUD 1991).

In the stratotype (Amersfoort) and in the parastratotype (Amsterdam Terminal) sections of the Eemian, the basal lacustrine sediment with subarctic parkland vegetation is covered by the marine deposits containing mixed forest remains. The end of the warm Eemian (5e) is characterised by the increase of steppe elements, dropping sea level, and a global cooling event (5d substage). This period is named as Herning Stadial, or Melisey I. Stadial in France (MANGERUD 1991; RAVAZZI 2003). The age of 5d was between 115 and 103 kyr (TURNER 2002; MCMANUS et al. 2002).

The vertebrate remains of the Horváti-lik layers 7–21 is best correlated with the 5d MIS substage (Herning Stadial; cca between 120 and 110 kyr) (Figure 6).

Conclusions

In North Hungary, close to village of Uppony, the Late Pleistocene fossiliferous cave locality of Horváti-lik was excavated in 1977–78. Following previous, preliminary reports the present paper is based on a comprehensive study of the Pleistocene vertebrate fauna that permits ecological interpretations and determination of the stratigraphical position.

Layers 7 to 21 contain Late Pleistocene vertebrate faunas. On the basis of cluster analysis, these faunas represent a unit between the Eemian and the Early Weichselian faunas of the Carpathian Basin.

The taxon-free investigations showed only minimal differences among the faunas of different Pleistocene layers, except for layer 21. The entire unit is characterized by low diversity index, dominance of mammals of very small size, and granivores. The ecological characters of the fauna indicate cold climate and open, probably steppe vegetation.

Biochronologically these Pleistocene layers are filling a gap in the traditional system in the Carpathian Basin, between the Süttő and Varbó Phases. The Eemian–Early Weichselian transition period is represented by a distinctive faunal event. This fauna and cooling event is correlated with the Marine Isotope Stage 5d and the Herning Stadial, between 120 and 110 kyr.

Appendix

Table I. — Faunal lists with anatomical description of layers of Horváti-lik.

Uppony 1.

Pisces indet.	1 fr.
Rana sp.	11 div. fr.
Lacerta sp.	1 dentale
Ophidia indet.	4 vertebrae
Aves indet.	2 div. fr.
Crocidura leucodon	1 mand.
Talpa europaea	1 mand., 1 dent, 3 fr.
Chiroptera indet.	1 max., 2 mand., 3 dentes, 1 fr.
Sciurus vulgaris	1 M sup.
Clethrionomys glareolus	1 M_1, 1 M_2
Microtus arvalis	5 M_1
Apodemus sylvaticus-tauricus	3 max., 6 mand., 6 M_1, 13 div. M
Glis glis	1 mand.

Uppony 2.

Pisces indet.	2 vertebrae
Pelobates fuscus	1 vertebra, 2 ilium, 17 div. fr.
Lacerta sp.	5 dentale, 2 div. fr.
Anguis fragilis	1 squama
Ophidia indet.	7 vertebrae, 1 fr.
Aves div. sp. indet.	15 div. fr.
Talpa europaea	1 mand., 3 dentes, 3 phalanx, 9 div. fr.
Chiroptera div. sp. indet.	7 mand., 9 dentes, 6 div. fr.
Sciurus vulgaris	1 max. with 2 M
Cricetus cricetus	4 M fr. (2 specimens)
Clethrionomys glareolus	5 M_1, 13 div. M
Arvicola terrestris	9 M_1
Microtus arvalis	20 M_1
Pitymys subterraneus	4 M_1
Apodemus agrarius	9 M_1
Apodemus sylvaticus-tauricus	53 M_1
Apodemus sp.	7 max., 27 mand., 75 M
Glis glis	4 M and P (2 specimens)
Muscardinus avellanarius	3 M (2 specimens)
Sicista sp.	1 max., 1 M_1, 2 M

Uppony 3.

Pelobates fuscus	1 dentale, 1 vertebra, 3 ilium, 17 div. fr.
Lacerta sp.	13 max., intermax., dentale
Ophidia indet.	28 vertebrae, 4 div. fr.
Aves div. sp. indet.	23 div. fr.
Erinaceus europaeus	1 dent
Sorex araneus	1 M fr.
Sorex minutus	1 M
Crocidura leucodon	1 mand., 1 M
Crocidura suaveolens	2 mand., 1 M
Talpa europaea	1 mand., 6 dentes, 3 phalanx, 10 fr. (2 specimens)
Rhinolophus hipposideros	1 bulla
Miniopterus schreibersii	1 humerus
Chiroptera div. sp. indet.	1 max., 2 mand., 3 dentes, 1 fr.
Lepus europaeus	1 dent, 1 fr.
?*Sciurus vulgaris*	2 M
Cricetus cricetus	3 max., 5 M_1, 6 M, 3 div. fr. (5 specimens)
Clethrionomys glareolus	14 M_1
Arvicola terrestris	1 max., 5 M_1, 18 M
Microtus arvalis	31 M_1
Microtus gregalis	3 M_1
Pitymys subterraneus	7 M_1
?*Micromys minutus*	1 max., 1 mand. with M_1-M_2, 4 M_1, 1 M^1
Apodemus agrarius	8 M_1
Apodemus sylvaticus-tauricus	97 M_1
Apodemus sp.	26 max., 12 mand., 205 M, 3 div. fr.
Mus musculus	2 M_1
Glis glis	1 cranium, 12 M and P, 1 I (3 specimens)
Muscardinus avellanarius	3 M (1 specimen)
Dryomys nitedula	4 M (2 specimens)
Sicista sp.	1 M_2
Vulpes vulpes	1 M_1

Uppony 4.

Pisces indet.	2 div. fr.
Pelobates fuscus	2 div. fr.
Anura indet.	13 div. fr.
Lacerta sp.	5 max., dentale
Ophidia indet.	27 vertebrae, 2 costae
Aves indet.	21 div. fr.
Sorex araneus	1 I sup.
Crocidura leucodon	3 max., 3 mand., 1 I sup.

Crocidura suaveolens	4 mand.
Talpa europaea	8 div. fr. (1 specimen)
Chiroptera div. sp. indet.	25 div. fr.
Lepus europaeus	1 P^4
Sciurus vulgaris	1 M sup., 1 mand. fr.
Cricetus cricetus	2 max. fr., 1 mand. fr., 2 M_1, 1 M^1, 4 div. fr.
Clethrionomys glareolus	7 M_1
Arvicola terrestris	1 M_1
Microtus arvalis	32 M_1
Microtus gregalis	7 M_1
Microtus oeconomus	3 M_1
Pitymys subterraneus	4 M_1
Micromys minutus	2 M_1
Apodemus agrarius	10 M_1
Apodemus sylvaticus-tauricus	58 M_1
Mus sp.	1 M_1
Glis glis	12 M and P (2 specimens)
Muscardinus avellanarius	2 M (1 specimen)
Dryomys nitedula	1 M
Sicista sp.	1 M_1
?*Vulpes* sp.	1 juv. M
Ursus sp.	1 juv. C, 1 M germ

Uppony 5.

Anura indet.	1 fr.
Lacerta sp.	1 max., 3 dentale
Ophidia indet.	3 vertebrae
Aves indet.	3 div. fr.
Sorex araneus	1 mand., 1 M
Talpa europaea	1 phalanx
Chiroptera div. sp. indet.	4 max., 12 mand., 24 dentes, 44 div. fr.
Clethrionomys glareolus	1 M_1
Arvicola terrestris	1 M_1, 6 M
Microtus arvalis	24 M_1
Microtus gregalis	5 M_1
Microtus oeconomus	4 M_1
Apodemus sylvaticus	4 M^1
Eliomys quercinus	1 M_3
Sicista sp.	1 max. with P^4, M^1
Macromammalia indet.	1 fr.

Uppony 6.

Pisces indet.	2 vertebrae
Anura indet.	1 ilium
Lacerta sp.	4 max., 5 dentale
Ophidia indet.	12 vertebrae
Aves indet.	7 div. fr.
Sorex araneus	2 max., 2 mand., 1 M sup.
Sorex minutus	1 mand.
Talpa europaea	14 div. fr. (2 specimens)
Chiroptera div. sp. indet.	3 max., 42 mand., 75 dentes, 46 div. fr.
Ochotona sp.	1 M sup.
Citellus sp.	1 max. fr., 1 P sup.
Clethrionomys glareolus	3 M_1
Arvicola terrestris	5 M_1
Microtus arvalis	68 M_1
Microtus gregalis	7 M_1
Apodemus sylvaticus	1 M_1
Sicista sp.	1 M_1, 1 M
?*Vulpes* sp.	1 M inf.
Mustela nivalis	2 C
Bovidae indet.	1 enamel fr.

Uppony 7.

Pisces indet.	1 dent, 16 vertebrae
Anura indet.	11 div. fr.
Lacerta sp.	1 max., 5 dentale
Anguis fragilis	1 squama
Ophidia indet.	13 vertebrae
Aves div. sp. indet.	14 div. fr.
Sorex araneus	1 max., 5 mand., 1 I sup., 3 I inf., 1 humerus
Sorex minutus	3 mand.
Talpa europaea	17 div. fr. (3 specimens)
Chiroptera div. sp. indet.	8 mand., 24 dentes, 9 div. fr.
Ochotona sp.	1 mand.
Clethrionomys glareolus	1 M_1
Arvicola terrestris	12 M_1
Microtus arvalis	131 M_1
Microtus gregalis	3 M_1
Microtus oeconomus	5 M_1
Lagurus lagurus	4 M_1
Apodemus sp.	1 M_2
Glis glis	1 M inf.
Sicista sp.	2 M_1
Mustela nivalis	1 mand., 2 C
Bovidae indet.	1 enamel fr.

Uppony 8.

Pisces indet.	120 div. fr.
?*Bufo* sp.	15 ilium
?*Rana* sp.	2 ilium
Anura indet.	74 div. fr.
?Urodela indet.	1 vertebra
Lacerta sp.	4 dentale
Anguis fragilis	25 squama
Ophidia indet.	1 dentale, 40 vertebrae
Aves div. sp. indet.	79 div. fr.
Sorex araneus	11 max., 44 mand., 58 div. fr.
Sorex minutus	2 mand.
Neomys sp.	4 mand., 1 humerus
Talpa europaea	2 max., 5 mand., 4 humerus, 51 div. fr.
Chiroptera indet.	1 M, 2 humerus
Ochotona sp.	1 mand. fr., 4 I, 3M (2 specimens)
Citellus sp.	5 P_4, 55 div. M, max., mand.
Allocricetus bursae	1 mand. with M_3, 1 M_2
Clethrionomys glareolus	6 M_1
Arvicola terrestris	99 M_1
Microtus arvalis	1242 M_1
Microtus gregalis	39 M_1
Microtus oeconomus	67 M_1
Lagurus lagurus	64 M_1
Sicista sp.	4 max., 11 mand., 12 M
Mustela erminea	3 M (2 specimens)
Mustela nivalis	5 mand., 20 dentes, 1 humerus (5 specimens)
Bovidae indet.	1 fr.
Ruminantia indet.	6 enamel fr., 1 femur caput

Uppony 9/A.

Pisces indet.	76 div. fr.
Anura indet.	18 ilium, 115 div. fr.
Lacerta sp.	1 max., 2 intermax., 3 dentale
Anguis fragilis	1 squama
Ophidia indet.	14 vertebrae
Aves div. sp. indet.	99 div. fr.
Sorex araneus	9 max., 38 mand., 34 div. fr.
Sorex minutus	4 mand., 7 dentes
Neomys sp.	2 mand., 1 humerus
Talpa europaea	3 max., 15 mand., 31 humer., 11 radius, 79 div. fr.
Chiroptera indet.	1 M
Ochotona sp.	1 I, 1 M
Citellus sp.	15 max., 5 mand., 3 P_4, 22 M
Allocricetus bursae	1 max., 2 mand.
Clethrionomys glareolus	9 M_1
Arvicola terrestris	165 M_1
Microtus arvalis	1237 M_1
Microtus gregalis	29 M_1
Microtus oeconomus	74 M_1
Lagurus lagurus	43 M_1
Sicista sp.	1 max., 1 mand., 5 M (2 specimens)
Vulpes vulpes	1 M^3
Mustela erminea	2 mand., 1 M^3
Mustela nivalis	1 max., 16 mand., 12 div. fr.
Bovidae indet.	1 astrogalus
Ruminantia indet.	11 enamel fr.

Uppony 10.

Pisces indet.	61 div. fr.
Anura indet.	19 ilium, 35 div. fr.
Lacerta sp.	5 max., 3 dentale
Ophidia indet.	8 vertebrae
Aves div. sp. indet.	84 div. fr.
Sorex araneus	5 max., 24 mand., 24 div. fr.
Neomys sp.	2 mand.
Talpa europaea	1 max., 19 mand., 49 humerus, 68 div. fr.

Ochotona sp.	1 tibia
Citellus sp.	4 max., 2 mand., 1 P_4, 2 M (2 specimens)
Clethrionomys glareolus	4 M_1, 4 M
Arvicola terrestris	131 M_1
Microtus arvalis	641 M_1
Microtus gregalis	5 M_1
Microtus oeconomus	39 M_1
Lagurus lagurus	4 M_1
Sicista sp.	2 M
?*Vulpes* sp.	1 M
Mustela nivalis	1 max., 5 mand., 3 C, M
Bovidae indet.	2 enamel fr., 1 radius-ulna fr., 1 fr.
Ruminantia indet.	1 metacarpus fr., 1 M fr.

Uppony 11.

Pisces indet.	52 div. fr.
Anura indet.	12 ilium, 48 div. fr.
Lacerta sp.	6 max., 18 dentale
Ophidia indet.	8 vertebrae
Aves div. sp. indet.	22 div. fr.
Erinaceus europaeus	1 P
Sorex araneus	3 max., 36 mand., 32 div. fr.
Sorex minutus	1 M
Neomys sp.	1 mand.
Talpa europaea	1 max., 18 mand., 20 humerus, 90 div. fr.
Chiroptera indet.	4 mand., 8 M, 1 humerus
Ochotona sp.	1 max., 2 mand., 3 I, M
Citellus sp.	1 max., 1 mand., 2 M
Cricetus cricetus	1 M_2
Clethrionomys glareolus	10 M_1, 26 M
Arvicola terrestris	94 M_1
Microtus arvalis	407 M_1
Microtus gregalis	12 M_1
Microtus oeconomus	41 M_1
Lagurus lagurus	2 M_1
Apodemus sylvaticus	1 max., 1 M_1, 1 M_2
Sicista sp.	1 mand., 2 M
Mustela nivalis	10 mand., 11 I, P, M, 2 humerus
Mustela putorius	2 M (1 specimen)
Bovidae indet.	4 enamel fr.

Uppony 12.

Pisces indet.	54 vertebrae, 4 div. fr.
Anura indet.	19 ilium, 59 div. fr.
Lacerta sp.	9 max., 10 dentale
Anguis fragilis	3 squama
Ophidia indet.	32 vertebrae
Aves div. sp. indet.	76 div. fr.
Erinaceus europaeus	2 M
Sorex araneus	11 max., 57 mand., 88 div. fr.
Sorex minutus	3 mand.
Neomys sp.	1 max., 4 mand.
Talpa europaea	6 mand., 3 humerus, 3 radius, 2 ulna, 26 div. fr.
Chiroptera indet.	12 div. fr.
Lepus sp.	2 M
Ochotona sp.	2 max., 22 mand., 20 I, P, M
Citellus sp.	28 div. max., mand., M (3 specim.)
Cricetus cricetus	2 max., 3 mand., 6 M
Clethrionomys glareolus	23 M1, 33 M
Arvicola terrestris	117 M1
Microtus arvalis	1391 M1
Microtus gregalis	143 M1
Microtus oeconomus	200 M1
Lagurus lagurus	1 M1
Spalax sp.	1 max., 1 M, 1 ulna
Apodemus sylvaticus	1 mand.
Sicista sp.	1 max., 5 mand., 12 M
Vulpes vulpes	1 juv. M, 1 M3
Ursus sp.	1 I, 1 P4
Mustela erminea	2 max., 3 mand., 1 M
Mustela nivalis	3 max., 22 mand., 35 div. fr.
Ruminantia indet.	3 I, 6 enamel fr.

Uppony 13.

Pisces indet.	6 dentes, 12 vertebrae
Anura indet.	2 ilium, 27 div. fr.
Lacerta sp.	4 max., 2 dentale
Ophidia indet.	21 vertebrae
Aves indet.	11 div. fr.
Sorex araneus	8 max., 30 mand., 59 div. fr.
Sorex minutus	4 mand.
Neomys sp.	2 mand.
Talpa europaea	4 mand., 2 radius, 1 femur, 22 div. fr.
Chiroptera div. sp. indet.	2 mand., 1 humerus, 8 div. fr.
Lepus sp.	1 M
Ochotona sp.	12 max., 13 mand., 19 div. fr.
Citellus sp.	7 max., 7 mand., 3 P_4, 30 P, M (5 specimens)
Allocricetus bursae	1 mand.
Clethrionomys glareolus	11 M_1
Arvicola terrestris	52 M_1, 15 max., M
Microtus arvalis	798 M_1
Microtus gregalis	126 M_1
Microtus oeconomus	129 M_1
Lagurus lagurus	10 M_1
Dicrostonyx torquatus	2 mand.
Spalax sp.	2 M
Apodemus sp.	2 M^1
Sicista sp.	3 max., 3 mand., 12 M
Ursus sp.	1 I, 2 juv. C
Mustela erminea	1 mand.
Mustela nivalis	11 mand., 11 div. fr.
Martes sp.	1 C
Ruminantia indet.	5 enamel fr.

Uppony 14.

Pisces indet.	1 dent, 52 vertebrae
Anura indet.	24 ilium, 83 div. fr.
Lacerta sp.	3 dentale
Anguis fragilis	1 squama
Ophidia indet.	37 vertebrae
Aves div. sp. indet.	88 div. fr.
Sorex araneus	46 max., 86 mand., 207 div. fr.
Sorex minutus	9 mand.
Neomys sp.	2 mand.
Talpa europaea	1 mand., 8 div. fr.
Lepus sp. I. (small)	1 mand
Lepus sp. II.	3 M
Ochotona sp.	28 max., 25 mand., 25 I, P, M
Citellus sp.	17 max., 10 mand., 28 P and M
Cricetus cricetus	1 M_1
Allocricetus bursae	3 max., 8 mand.
Clethrionomys glareolus	8 M_1
Arvicola terrestris	15 M_1
Microtus arvalis	950 M_1
Microtus gregalis	331 M_1
Microtus oeconomus	164 M_1
Lagurus lagurus	53 M_1
Dicrostonyx torquatus	1 M_1
Spalax sp.	1 max., 3 I, 1 M^1
Allactaga sp.	1 M^2, 1 M_3
Sicista sp.	3 max., 3 mand., 18 M
?*Vulpes* sp.	1 M_1 fr.
Mustela erminea	1 mand, 1 C, 1 M
Mustela nivalis	4 max., 8 mand., 9 dentes
Ruminantia indet.	1 germ, 11 enamel fr., 1 scapula

Uppony 15.

Pisces indet.	4 dentes, 24 ertebrae, 43 squama
Anura indet.	7 ilium, 24 div. fr.
Anguis fragilis	2 squama
Ophidia indet.	13 vertebrae
Aves div. sp. indet.	40 div. fr.
Sorex araneus	21 max., 58 mand., 115 div. fr.
Sorex minutus	2 mand.
Talpa europaea	2 P
Lepus sp.	1 M sup.
Ochotona sp.	17 max., 18 mand., 9 I and M
Citellus sp.	10 max., 4 mand., 3 P_4, 34 P and M
Clethrionomys glareolus	2 M_1
Arvicola terrestris	5 M_1
Microtus arvalis	807 M_1
Microtus gregalis	287 M_1
Microtus oeconomus	90 M_1
Lagurus lagurus	10 M_1

Dicrostonyx torquatus	2 M_1
Spalax sp.	2 max., 3 mand., 3 I, 1 M^1
Allactaga sp.	1 M^3
Sicista sp.	3 max., 3 mand., 11 M
?*Vulpes* sp.	1 C
Mustela erminea	2 mand., 1 M
Mustela nivalis	1 max., 8 mand., 4 I and M
Bovidae indet.	4 juv. enamel fr., 1 radius fr.

Uppony 16.

Pisces indet.	2 dent, 18 vertebrae
Anura indet.	8 ilium, 16 div. fr.
Lacerta sp.	1 max., 2 dentale
Anguis fragilis	1 squama
Ophidia indet.	6 vertebrae
Aves div. sp. indet.	25 div. fr.
Sorex araneus	8 max., 30 mand., 30 div. fr.
Sorex minutus	2 mand., 1 humerus
Talpa europaea	1 phalanx
Chiroptera indet.	2 mand., 1 C, 2 M, 1 humerus
Ochotona sp.	1 max., 4 mand., 11 dentes, 1 femur fr.
Citellus sp.	2 max., 1 mand., 7 P_4, 51 P and M
Clethrionomys glareolus	1 M_1
Arvicola terrestris	3 M_1
Microtus arvalis	254 M_1
Microtus gregalis	41 M_1
Microtus oeconomus	16 M_1
Lagurus lagurus	1 M_1
Sicista sp.	4 M (2 specimens)
Ursus sp.	2 juv. C
Mustela nivalis	1 mand., 3 M

Uppony 17.

Aves indet.	2 div. fr.
Cricetus cricetus	1 mand.
Arvicola terrestris	2 M_1
Microtus arvalis	12 M_1
Microtus gregalis	2 M_1
Vulpes vulpes	1 M_1

Uppony 18.

Pisces indet.	2 dentes, 14 vertebrae, 1 squama
Anura indet.	12 div. fr.
Lacerta sp.	4 max., 3 dentale
Anguis fragilis	11 squama
Ophidia indet.	12 vertebrae
Aves indet.	4 div. fr.
Sorex araneus	2 max., 12 mand., 27 div. fr.
Neomys sp.	1 mand. fr.
Talpa europaea	2 div. fr.
Chiroptera indet.	1 C, 4 M
Ochotona sp.	7 I, M
Citellus sp.	24 P and M (3 specimens)
Allocricetus bursae	1 max.
Clethrionomys glareolus	2 M fr.
Arvicola terrestris	1 M_1, 7 M
Microtus arvalis	79 M_1
Microtus gregalis	21 M_1
Microtus oeconomus	4 M_1
Sicista sp.	6 M (2 specimens)
Ursus sp.	1 I
Mustela nivalis	2 C

Uppony 19.

Pisces indet.	1 squama
Anura indet.	1 fr.
Lacerta sp.	1 max., 1 dentale
Aves indet.	2 div. fr.
Sorex araneus	1 mand., 1 I inf.
Neomys sp.	1 mand.
Chiroptera indet.	1 C, 1 M
Arvicola terrestris	1 M_1
Microtus arvalis	8 M_1
Microtus gregalis	3 M_1

Uppony 20.

Pisces indet.	1 vertebra
Anura indet.	5 div. fr.
Anguis fragilis	3 squama
Ophidia indet.	2 vertebrae
Aves indet.	1 fr.
Sorex araneus	2 max., 2 mand., 2 fr.
Sorex minutus	1 mand.
Talpa europaea	2 M
Chiroptera indet.	1 mand., 1 radius
Ochotona sp.	1 M
Citellus sp.	4 div. fr.
Arvicola terrestris	1 M_1
Microtus arvalis	32 M_1
Microtus gregalis	6 M_1
Microtus oeconomus	2 M_1
Glis glis	1 P_4
Ursus sp.	1 I, 1 juv. P
Mustela nivalis	2 mand.

Uppony 21.

Pisces indet.	1 dent, 2 vertebrae, 1 squama
Anura indet.	1 ilium, 1 fr.
Lacerta sp.	1 dentale
Ophidia indet.	2 vertebrae
Aves indet.	2 div. fr.
Sorex araneus	1 max., 2 mand., 4 div. fr.
Talpa europaea	4 div. fr.
Chiroptera indet.	1 mand., 1 M, 1 C
Ochotona sp.	2 M
Citellus sp.	1 mand., 2 P and M
Arvicola terrestris	3 M
Microtus arvalis	14 M_1
Microtus gregalis	4 M_1
Microtus oeconomus	1 M_1
Lagurus lagurus	1 M_1
Sicista sp.	1 mand.
Ursus sp.	1 P^4
Mustela nivalis	1 mand., 1 M
Cervidae indet.	1 metacarpus fr.
Bovidae indet.	1 fr.

Uppony 22.

Ophidia indet.	2 vertebrae
Aves indet.	1 fr.
Talpa europaea	2 div. fr.
Chiroptera indet.	1 fr.
Clethrionomys glareolus	1 M^1
Microtus arvalis	4 M_1

Uppony 23.

Pisces indet.	16 squama
Lacerta sp.	4 dentale
Anguis fragilis	1 squama
Ophidia indet.	5 vertebrae
Sorex araneus	1 mand. fr.
Chiroptera indet.	1 C, 2 M
Citellus sp.	1 M
Clethrionomys glareolus	1 M_1
Microtus arvalis	2 M_1
Apodemus sylvaticus	1 M_1
Cervidae indet.	1 C
Macromammalia indet.	2 div. fr.

Uppony 24.

Pisces indet.	1 squama
Lacerta sp.	1 max.
Ophidia indet.	2 vertebrae
Ochotona sp.	1 I
Arvicola terrestris	1 M_1
Microtus arvalis	2 M_1, 10 M

Uppony 25.

Pisces indet.	1 squama
Anguis fragilis	1 squama
Ophidia indet.	1 vertebra
Microtus arvalis	2 M_1, 6 M
Glis glis	1 M^2

Table II. — Number of specimens of mammalian taxa in layers of Horváti-lik.

Species \ Layer	1	2	3	4	5	6	7	8	9/A	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Erinaceus europaeus			1								1	1													
Sorex araneus			1	1	1	1	3	22	19	12	18	29	15	43	29	15		6	1	1	1		1		
Sorex minutus			1			1	2	1	2		1	2	2	5	1	1				1					
Neomys sp.								2	1	1	1	2	1	1				1	1						
Crocidura leucodon	1		1	2																					
Crocidura suaveolens			1	2																					
Talpa europaea	1	1	2	1	1	2	3	3	16	25	10	3	2	1	1	1		1		1	1	1			
Lepus sp.			1	1								1	1	2	1										
Ochotona sp.						1	1	2	1	1	1	11	7	14	9	2		2		1	1			1	
Sciurus vulgaris	1	1	1	1																					
Citellus sp.						1		3	8	2	1	3	5	9	5	4		3		1	1		1		
Cricetus cricetus		2	5	1							1	2		1			1								
Allocricetus bursae								1	1				1	4				1							
Clethrionomys glareolus	1	3	7	4	1	2	1	3	5	2	5	12	6	4	1	1		1				1	1		
Arvicola terrestris		5	3	1	1	3	6	50	83	66	47	59	26	8	3	2	1	1	1	1	1			1	
Microtus arvalis	3	10	16	16	12	34	66	621	619	321	204	696	399	475	404	127	6	40	4	16	7	2	1	1	1
Microtus gregalis			2	4	3	4	2	20	15	3	6	72	63	166	144	21	1	11	2	3	2				
Microtus oeconomus				2	2		3	34	37	20	21	100	65	82	45	8		2		1	1				
Pitymys subterraneus		2	4	2																					
Lagurus lagurus							2	32	22	2	1	1	5	27	5	1					1				
Dicrostonyx torquatus													1	1	1										
Spalax sp.												1	1	1	2										
Allactaga sp.														1	1										
Micromys minutus			2	1																					
Apodemus agrarius		5	4	5																					
Apodemus sylvaticus	3	27	49	29	2	1	1				1	1	1										1		
Mus musculus			1	1																					
Glis glis	1	2	3	2			1													1					1
Muscardinus avellanarius		2	1	1																					
Eliomys quercinus					1																				
Dryomys nitedula			2	1																					
Sicista sp.		1	1	1	1	1	1	6	2	1	1	3	2	2	2	2		2			1				
Vulpes vulpes			1	1		1			1	1		1		1	1		1								
Ursus sp.				1								1	1			1		1		1	1				
Mustela erminea								2	1			2	1	1	1										
Mustela nivalis						1	1	5	8	3	5	11	6	4	4	1		1		1	1				
Mustela putorius											1														
Martes sp.													1												
Cervidae indet.																					1		1		
Bovidae indet.						1	1	1	1	1	1				1						1				
Ruminantia indet.								1	1	1		1	1	1											
Macromammalia indet.																							1		

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