NKFI K 104506 project

Taxonomical, taphonomical, paleoecological and stratigraphical investigations of the most important Middle Pleistocene terrestrial site (Somssich-hegy 2, Villány) in Hungary

final report

Initially, a rich (including approximately 950,000 items) but mainly uncataloged bone material stored in the Department of Paleontology and Geology of the Hungarian Natural History Museum was available for our study, which was divided to 50 sampling units by Dénes Jánossy. Besides, samples 45-50 were unpicked and unsorted.

The first task was to organize the material and to sort out the bones that are suitable for further taxonomic determination. To speed up this process, five students from the Eötvös University were involved. Two of the students helped in the taphonomic analysis as well during 2014-2017. Twenty students of the Franciscan Secondary School in Szentendre helped to pick the shrew fossils from the sediment, to identify them, and to draw paleoecological conclusions as a part of the "Way to Science Grant Program" of the Ministry of Human Capacities (UT-2014/2015-0001 project), for which we were official contracting partners.

For taking new and appropriate samples for sedimentological, taphonomical, pollen and ESR analyses, we carried out two excavations during the summer of 2014 and 2015. During the first excavation, 15 samples of 1.0 kg were taken at depth intervals of 0.5 meters between 7.5–0.5 m in the entire section, which provided more than 4,000 additional remains. We also clarified, that there is no connection between Somssich Hill 1 and 2 sites, and we mapped the outline of the Somssich Hill 2 karst cavity.

The work was greatly hindered during the second excavation, because the covering of the site was intentionally broken up and the cavity was partially refilled by 3 cubic metres of constriction waste and communal trash. We had to clear out the cavity collaborating with the Duna-Dráva National Park. Despite of these difficulties, we were able to measure the background radiation values of the previous 15 sampling levels. This was necessary for the planned ESR dating. In addition, we also made detailed sedimentological observations for the entire section.

The dating was delayed by the relocation of the ESR Laboratory from the building of the MTA TTK Institute of Molecular Pharmacology into the building of the Budapest University of Technology and Economics. The analysis was also rescheduled because the host institution (the Hungarian Natural History Museum) was not able to pay in time for that, due to its liquidity problems. However, we were finally able to date the site during 2015, which allowed us to establish a very important, well-dated biostratigraphical reference point with an extremely rich revised fauna, around the Early–Middle Pleistocene Boundary. In addition, the ESR dating of 30 additional Pliocene–Pleistocene sites is currently in progress.

The taphonomical analysis was slightly delayed because the employment of A. Virág was rescheduled from 2013 to 2014 because of his other obligations. However, with the help of two university students, who worked under the supervision of A. Virág, the work was finished within the timeframe of the whole project.

The implementation of the whole research was hindered because the necessary equipment for taking and processing high resolution micrographs was not readily available in the host institution at the beginning of the project as it was promised. As a consequence, we had to obtain some previously unplanned items (a Canon EOS 700D camera, a tripod, three personal computers and an image processing software) and we had to ask for a one year prolongation for publication.

Overall, we managed to finish the planned research. The pollen analysis was the only subtopic that did not give any substantial results, because the samples unfortunetly proved to be sterile for pollen. Our major conclusions are discussed in detail below.

Taxonomical results

The reorganized and revised bone material is now stored in the Vertebrate Palaeontological Collection of the Hungarian Natural History Museum besides the newly collected remains. Our revision revealed a remarkably diverse vertebrate fauna with 109 identified taxa (Table 1). Considering the sheer number of bones, the material is dominated by herpetofaunal elements (around 910,000 remains), but the small mammals are the taxonomically most diverse group (with 45 species).

Regarding the herpetofauna, we have the following conclusions:

1. More than 100 000 amphibian bones were determined from the site, among which six anuran taxa (*Bombina variegata*, *Pelobates fuscus, Bufo bufo*, *B. viridis*, *Hyla arborea* and *Rana temporaria*) were identified. The investigations on the salamanders revealed the occurrence of three species (*Salamandra salamandra*, *Triturus cristatus* and *Lissotriton vulgaris*).
2. More than 800 000 reptile bones were determined from the site, among which two turtles (*Testudo lambrechti* and *Emys orbicularis*), three lizards (*Lacerta viridis*, *Pseudopus pannonicus* and *Ophisaurus pannonicus*), nine snakes (*Coluber hungaricus*, *C. viridiflavus*, *C. gemonensis*, *Coronella austriaca*, *Zamenis longissimus*, *Elaphe quatuorlineata*, *E. paralongissima*, *Natrix natrix* and *N. tesselata*) and two vipers (*Vipera ammodytes* and *V. berus*) were identified.

Regarding the shrew material, our general discoveries are listed in the following three points:

1. The bigger *Beremendia fissidens* and the smaller *B. minor* were distinguished by the previous researchers only on the basis of their size. The separation of the two species is now also supported by our morphometrical analysis that was based on their teeth. In addition, we found some details in the dental and mandibular morphology as new differential characters.
2. *Crocidura obtusa* was described by Kretzoi in 1938 as a new species from the Early Pleistocene locality of Gombasek (Slovakia). Since the holotype was lost in 1956, we designated and housed a neotype material (partly from the Somssich Hill 2 assemblage) in the collection of the Hungarian Natural History Museum, Budapest. Because of the incomplete original description given by Kretzoi, making of a new definition of the species was required as well, which was based on the detailed investigations on the *Crocidura* material of the Somssich Hill 2 site. Although these results are not published yet, we submitted a manuscript to the Journal of Vertebrate Paleontology.
3. *Sorex (Drepanosorex) savini* was described by Hinton (1911) from West Runton, England. In the Betfia (Romania) material, Kormos (1930) distinguished another species for a similar form as *S. margaritodon* based on its smaller size than *S.* (*D.*) *savini*. Further authors reported other findings of these shrews and tried to validate this distinction by morphological characters. However, the measurements of the Somssich Hill 2 specimens overlap those that were described as *S. (D.) margaritodon* and *S.* (*D.*) *savini* by several authors. Hence, on the basis of the results of the present project, we think that *S.* (*D.*) *margaritodon* Kormos, 1930 is a synonym of *S.* (*D.*) *savini* Hinton, 1911. The tiny differences between the two forms recognized by some authors may be the consequences

of intraspecific variability. It is supported by the fact that their areas do not separate from each other in time and space.

Regarding the voles and lemmings, we have the following results:

1. The intricately folded occlusal outline of the first lower vole molars is a key feature for taxonomy. With the successive infolding of the anterior part, the morphology changed in several lineages. However, this large variability causes complications if the aim is to develop a system, which can be used for comparing teeth that represent distinct evolutionary stages with different basic structures, such as the three different subgenera of genus *Microtus*. Thus, we developed a new landmark-based approach that can be applied to a wide variety of arvicoline rodents in order to map the intraspecific variability and track changes of teeth shape and size throughout a stratigraphic succession. This method can be applied for other taxa in the future.
2. Although Jánossy assigned the 'true' *Microtus* material from the Somssich Hill 2 site to four different species, our geometric morphometric results suggest that it should rather be referred to a single species, namely *Microtus nivaloides*. Furthermore, *M. nivaloides* have a morphology which is centrally positioned in a morphospace defined on the basis of the extant *Microtus* (*Microtus*) species in the region, and the morphology of its occlusal surface shows transitional features towards all of the recent taxa included in our study. Based on these observations, we think that *M. nivaloides* from Somssich Hill 2 (which is also the oldest dated 'true' *Microtus* in the Carpathian Basin) is the likely ancestor, from which the recent *Microtus* (*Microtus*) species evolved. From this species, two different evolutionary branches separated at the time of the Early–Middle Pleistocene transition. One of which lead to the recent *M*. (*M*.) *oeconomus* through *M*. (*M*.) *nivalinus*, whereas the other ended in the extant *M*. (*M*.) *arvalis-agrestis* group.
3. Besides the 'true' Microtus material, the other voles from the site can be referred to 'advanced' *Microtus* (*Allophaiomys*) *pliocaenicus*, *M*. (*Terricola*) *arvalidens* and *M*. (*T*.) *hintoni*, which makes Somssich Hill 2 the only locality in the region where species belonging to subgenera *Allophaiomys*, *Terricola*, and *Microtus* occur together in large numbers. It makes the site a preferable starting point for studies that aim to reveal the early radiation of genus *Microtus*. Using the Pleistocene to recent comparative material of the Hungarian Natural History Museum, we conducted a geometric morphometric study which revealed that *M*. (*A*.) *pliocaenicus* evolved from *M*. (*A*.) *deucalion* and it later gave rise to subgenera *Terricola* and *Microtus* during the late Early Pleistocene through *M*. (*A*.) *praehintoni* and 'advanced' *M*. (*A*.) *pliocaenicus*, respectively. A manuscript from these results is partially prepared, which will be soon submitted to a journal called Quaternary.
4. The new geometric morphometric methodology was also applicable in the case of the *Mimomys savini* material (457 specimens) from the site. In this case, our aim was to reconstruct the changes that take place during tooth wear. By mapping this kind of variability, we can provide a reliable dataset that can serve as a standard for future taxonomic works, and can help to unravel the evolutionary history of the *Mimomys-Arvicola* lineage. Another separate manuscript from these results is partially prepared, which will be soon submitted to a journal called Quaternary.
5. Approximately 300 lemming molars were studied from the site up to now. They can be assigned into *Prolagurus pannonicus* and *Lagurodon arankae*, amongst which the former predominates over the latter. The enamel thickness of both taxa shows positive differentiation, which is a modern trait in their lineage. There were a few isolated lower first molars in the record, which showed arankae-like pattern on their occlusal surface, but clearly *pannonicus*-like pattern on their base. This feature

can hold evolutionary importance, which can be studied in the future by a method similar to the one applied on the *Mimomys* material.

Regarding the dormice fauna, we got the following conclusions:

1. Four dormice species (*Glis sackdillingensis*, *G*. *minor*, *Muscardinus dacicus* and *Dryomimus eliomyoides*) were identified from the Somssich Hill 2 site.
2. Based on linear morphometric measurements made on the first lower and first upper molars of *Glis* species from six localities (including Somssich Hill 2), we proved that *G*. *minor* was part of the fauna of the Carpathian Basin until the end of the Middle Pleistocene (MIS 11).
3. Using morphotype analysis, we pointed out that the separation of the extant *Muscardinus avellanarius* and the extinct *M*. *dacicus* is not possible based on the first lower molars only. We think that the latter can be regarded as a junior synonym of the former.

Regarding the macromammal material, we can report the following results:

1. Compared to the extremely rich microvertebrate record, the only abundant macromammal species in the material is a hare (*Lepus terraerubrae*) with a few thousand remains.
2. The small carnivores are quite frequent within the assemblage, they are represented by 200-250 bones in total. Amongst them, mustelids are the most abundant with 6 taxa: *Mustela* cf. *palerminea*, *Mustela praenivalis*, *Pannonictis* sp., Mustelidae sp. (? *Putorius*), *Meles* cf. *atavus* and *Martes* cf. *intermedius*.
3. The remains of the sensu stricto large mammals are small fragmented postcranial elements and isolated and sometimes fragmented teeth, which makes the precise taxonomic identification problematic and rather dubious in most cases. The best preserved fossils are canids, which are represented by a smaller and a larger sized species: *Vulpes praecorsac* and *Canis mosbachensis*, respectively. In addition, ungulates are represented with some isolated teeth that can be assigned into *Cervus* cf. *acoronatus*.

ESR dating and biostratigraphical results

1. As a starting point for the stratigraphic interpretation, the 15 samples that were collected by us during the excavation in 2014 were correlated with the original sampling units of Jánossy based on their depth and faunal composition.
2. The calculated ESR ages of the samples varied between 2.0 and 0.5 Ma with a large error (from ± 10 kyr to 450 kyr). The mean was 1.15 Ma with a standard deviation of 0.45 Ma and the median was 1.0 Ma. The average age agrees well with the biostratigraphic interpretation for the bulk of the material. A linear regression was also fitted to the measurements, but due to the high variability of the data, the determination coefficient was extremely low. Thus, it was not possible to assess a reliable age difference between the lower and the upper part of the sequence.
3. Based on the ranges of the most abundant arvicolids in the material collected by Jánossy (*Mimomys savini*, *M. pusillus*, *Lagurodon arankae*, *Prolagurus pannonicus*, *Allophaiomys pliocaenicus*, *Microtus arvalidens*, *M. hintoni*, *M. nivaloides*), the fauna can be correlated with the *Mimomys savini*–*Mimomys pusillus* Biozone in the Biharian (MQ1).
4. The macromammal material from the Somssich Hill 2 site is rather fragmentary compared to the extremely rich microvertebrate record, but it shows some features which are characteristics of the so-called Epivillafranchian faunal turnover. The main indicators of this event are the size parameters

of *Mustela palerminea* and *Canis mosbachensis*, because the mandible size of the former is intermediate between the typical Villafranchian *M. palerminea* and the Middle Pleistocene (and recent) *M. erminea*, whereas the size of the isolated teeth of the latter are transitional between the Villafranchian *C. arnensis* (and *C. etruscus*) and the Middle Pleistocene *C. mosbachensis*. Considering the first appearance dates of *Crocidura obtusa*, *Cricetus runtonensis* and *Cervus elaphus acoronatus* and the last appearance dates of *Mustela palerminea* and *M. praenivalis*, the co-occurence of these taxa also supports the above mentioned age determination.

5. A few specimens mainly from the upper part of the section can be referred to taxa, which have ranges that suggest an older age than the bulk of the material, namely the *Mimomys pliocaenicus* Biozone in the late Villanyian (MN17). These taxa are the following: *Dryomimus eliomyoides*, *Villanyia exilis*, *Mimomys reidi*, *Pitymimomys pitymyoides*, *Borsodia newtoni*, *Asoriculus gibberodon*, *Beremendia minor*.

Sedimentological and taphonomical results

1. The Somssich Hill 2 site is an 8 m deep, vertical, downward tapering karst cavity with a surface diameter of 5 m in the Upper Jurassic (Oxfordian) Szársomlyó Limestone Formation. Above 3.8 m depth from the surface, the sediment is light yellowish brown, porous, carbonate-cemented silt, with scattered bones, gastropod shells and limestone fragments. Below 3.8 m, the infill is mostly breccia with brownish red silty clay matrix, in patches gravelly clay.
2. The sedimentological analysis showed that the red clay in the lower breccia is a weathering product, whereas the clasts and bone fragments within the matrix were most likely affected by short-distance water transport. The material of the upper yellowish brown silt could be interpreted as a result of at least partly aeolian transport. Thus, this could be one of the oldest dated loess-like sediment in the region.
3. The low proportion of abraded and weathered small mammal bones together with the fact that the relatively mobile elements are rare in the assemblage suggest that the remains were probably transported into the cavity from the close proximity of the site. Digestion marks are rare, and only light digestion was observed on the bones, which suggest that the material was at least partly accumulated as owl pellets. As a parautochtonous and relatively unaltered assemblage, the Somssich Hill 2 material can be considered as a reliable base for reconstructing the direct palaeoenvironment of the cavity.

Paleoecological results

1. We conducted a principal component analysis based on the relative abundances of small mammals and herpetofaunal elements in each of the 50 samples of Jánossy. According to our results, the section of Somssich Hill 2 site can be divided into five different palaeoecological units. Unit 1 was interpreted as a cold steppe with extreme dominance of *Prolagurus pannonicus*, *Cricetus runtonensis* and *Sorex runtonensis*, whereas Unit 2 was most likely a semi-closed environment with an open water surface in the close proximity of the site based on the molluscs and the vertebrate fauna. The temperature dropped, but the overall humidity increased at the beginning of Unit 3, which can be characterized with the most closed vegetation within the studied section (probably a karst shrubland). The moderate abundance peak of *P. pannonicus* together with the local minimum of *Microtus (Terricola) arvalidens* suggest these changes. Unit 4 was slightly more open, and the

abundance of *Apodemus sylvaticus* suggests a minor warming event at the end of this unit. Unit 5 was probably warm and dry grassland, based on the abundance peak of *Crocidura* and *M. (T.) arvalidens*.

2. The paleoecological importance of the shrew fauna was studied separately as well. We supposed warm climate with open grasslands where members of the genus *Crocidura* appeared, whereas colder climate was reconstructed for samples with abundant *Sorex* material. *S. minutus* most likely preferred bushy or wooded vegetation, whereas *S. runtonensis* lived in cold grasslands. The occurrence of *Neomys newtoni*, *Sorex (Drepanosorex) savini*, and perhaps *Beremendia* species indicate the appearance of open water surface in the surroundings of the site.
3. Within the fragmentary macromammal fauna, the relatively large number of the canids (and also a few *Homotherium* sp. remains) indicate open steppe conditions around the locality. However, the presence of *Meles* cf. *atavus*, cf. *Panthera onca gombaszogensis* and *Lynx* sp. in some parts of the sequence suggest that there were occasionally forested areas nearby. A few fragmentary remains of *Felis* cf. *chaus*, *Pannonictis* sp. and *Trogontherium* sp. indicate the appearance of open water surface or swampy conditions in the vicinity.

Outcomes

Taxonomic results were published in 13 articles. Besides we made a synthesizing paper for the Comptes Rendus Palevol about all of our taxonomical, sedimentological, taphonomical and paleoecological results. The extremely rich material allowed us to develop a new landmark based method, which we used to unravel evolutionary linages within the genus *Microtus*. Some of our results are already published in the Quaternary International and two manuscripts will be soon finished for a journal entitled Quaternary. Our main discoveries were also presented and discussed during eight national and eight international conferences in 19 oral and 10 poster presentations. We also published five popular science papers for a wide public.

Three of our university students (Dániel Botka, Levente Striczky and Kinga Gere) presented their results during the National Scientific Students' Associations Conferences in 2014 and 2016 under the supervision of P. Pazonyi, L. Mészáros, Z. Szentesi and A. Virág. Some of our mentorees from the the Franciscan Secondary School in Szentendre joined in the following academic competitions with their topic within the framework of the "Way to Science Grant Program" of the Ministry of Human Capacities (UT-2014/2015-0001 project): EU Contest for Young Scientists (2 students), Research Student Conference (2 students), National Research Student Essay Competition (2 students, 1st prize), Science Competition for Students (2 students, 2nd prize).

Some of our results and part of the studied material were presented in a temporary exhibition (Ice Age Riddles) of the Hungarian Natural History Museum during 2017. The material and the washing and sieving techniques that were used after the excavations were demonstrated to the public as a part of the program during the Researchers' Night in the HNHM in 2017.

National conferences

1. 16th Annual Meeting of Hungarian Paleontologists (2013)
2. 17th Annual Meeting of Hungarian Paleontologists (2014)
3. Scientific Students' Associations Conference of the Eötvös University (2014)
4. End of Year Meeting of the Hungarian Geological Society (2014)

5. 18th Annual Meeting of Hungarian Paleontologists (2015)
6. Meeting of the Paleontological and Stratigraphical Division of the Hungarian Geological Society (2015)
7. 19th Annual Meeting of the Hungarian Paleontologists (2016)
8. 20th Annual Meeting of the Hungarian Paleontologists (2017)

International conferences

1. 14th Congress of Regional Committee on Mediterranean Neogene Stratigraphy, Istanbul, Turkey (2013)
2. Russian conference with international participation "Systematics, phylogeny and paleontology of small mammals", dedicated to the anniversary of Professor Igor Mikhailovich Gromov (1913-2003), Saint Petersburg, Russia (2013)
3. 7th International Conference on Mammoths and their Relatives, Grevena, Greece (2014)
4. 5th International Students Geological Conference, Budapest, Hungary (2014)
5. European Geosciences Union General Assembly 2015, Vienna, Austria (2015)
6. XIV Annual Meeting of the European Association of Vertebrate Palaeontologists, Haarlem, The Netherlands (2016)
7. 1st International Meeting of Early-stage Researchers in Palaeontology, Alpuente, Spain (2016)
8. XV Annual Meeting of the European Association of Vertebrate Palaeontologists, Münich, Germany (2017)

Publications and abstracts

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Table 1. Revised taxonomical list of the Somssich Hill 2 site. Uppercase numbers indicate deviations from the original list published by Jánossy (1990). *Legend: 1 renamed taxon; 2 not present in the source list.*

Pisces

Carassius sp.
Osteichthyes indet.

Amphibia

Salamandra cf. *salamandra* (Linnaeus, 1758)[2]
Triturus cristatus (Laurenti, 1768)[2]
Lissotriton cf. *vulgaris* (Linnaeus, 1758)[2]
Bombina variegata (Linnaeus, 1758)[2]
Pelobates fuscus (Laurenti, 1768)[2]
Bufo bufo (Linnaeus, 1758)[2]
Bufotes viridis (Laurenti, 1768)[2]
Hyla arborea (Linnaeus, 1758)[2]
Rana temporaria (Linnaeus, 1758)[2]

Reptilia

Emys cf. *orbicularis* (Linnaeus, 1758)
Testudo lambrechti Szalai, 1934[2]
Lacerta cf. *viridis* (Laurenti, 1768)[2]
Anguis sp.[2]
Pseudopus cf. *pannonicus* Kormos, 1911[2]
Ophisaurus sp.
Hierophis cf. *viridiflavus* (Lacepède, 1789)[2]
Hierophis cf. *gemonensis* (Laurenti, 1768)[2]
Coronella austriaca Laurenti, 1768[2]
Elaphe cf. *paralongissima* Szyndlar, 1984[2]
Elaphe cf. *quatuorlineata* Lacepède, 1789[2]
Zamenis longissimus (Laurenti, 1768)[2]
Natrix natrix Linnaeus, 1758[2]
Natrix tessellata Laurenti, 1768[2]
Telescopus cf. *fallax* (Fleischmann, 1831)[2]
Vipera cf. *ammodytes* Linnaeus, 1758[2]
Vipera cf. *berus* Linnaeus, 1758[2]

Aves

Anser subanser Jánossy, 1983
Aythya sp. (large species)
Anatidae indet.
Tetrao partium (Kretzoi, 1962)[1]
Francolinus capeki Lambrecht, 1933
Coturnix cf. *coturnix* Linnaeus, 1758
Otis sp.
Surnia robusta Jánossy, 1977
Athene noctua cf. *lunellensis* Mourer-Chauviré, 1975
Aquila cf. *heliaca* Savigny, 1809
Falco tinnunculus atavus Jánossy, 1972
Falco cf. *vespertinus* Linnaeus, 1766
Picus cf. *viridis* Linnaeus, 1758
Dendrocopos submajor Jánossy, 1974
Galerida cf. *cristata* Linnaeus, 1758
Sitta europaea-group
Hirundo cf. *rustica* Linnaeus, 1758
Passeriformes indet.

Mammalia

Macaca sp.
Lepus terraerubrae Kretzoi, 1956
Ochotona sp.
Nannospalax cf. *advenus* (Kretzoi, 1977)[1]
Spermophilus primigenius (Kormos, 1934)[1]
Sciurus whitei hungaricus Jánossy, 1962[2]
Glis sackdillingensis Heller, 1930
Glis minor (Kowalski, 1956)[2]
Muscardinus dacicus Linnaeus, 1758[1]
Dryomimus eliomyoides Kretzoi, 1959
Sicista praeloriger Kormos, 1930
Apodemus sylvaticus (Linnaeus, 1758)
Allocricetus bursae Schaub, 1930
Allocricetus ehiki Schaub, 1930
Cricetus nanus (Schaub, 1930)
Cricetus runtonensis Newton, 1909
Villanyia exilis Kretzoi, 1956[2]
Mimomys savini Hinton, 1910
Mimomys pusillus (Méhely, 1914)[2]
Mimomys reidi Hinton, 1910[2]
Pitymimomys pitymyoides (Jánossy et Meulen, 1975)[2]
Borsodia newtoni (Forsyth Major, 1902)[2]
Pliomys episcopalis-hollitzeri group[1]
Myodes hintonianus-kretzoii group[1]
Lagurodon arankae (Kretzoi, 1954)[1]
Prolagurus pannonicus (Kormos, 1930)[1]
Allophaiomys pliocaenicus Kormos, 1932
Microtus (Terricola) arvalidens (Kretzoi, 1958)[1]
Microtus (Terricola) hintoni (Kretzoi, 1941)[1]
Microtus (Microtus) nivaloides Forsyth Major, 1902[1]
Talpa fossilis Petényi, 1864
Desmana thermalis Kormos, 1930
Crocidura kornfeldi Kormos, 1934
Crocidura obtusa Kretzoi, 1938
Sorex minutus Linnaeus, 1766
Sorex runtonensis Hinton, 1911
Sorex (Drepanosorex) savini Hinton, 1911[2]
Neomys newtoni Hinton, 1911[2]
Asoriculus gibberodon (Petényi, 1864)[2]
Beremendia fissidens (Petényi, 1864)
Beremendia minor Rzebik-Kowalska, 1976[2]
Erinaceus cf. *praeglacialis* Brunner, 1933
Rhinolophus ferrumequinum (Schreber, 1774)
Myotis cf. *nattereri* (Kuhl, 1817)
Myotis cf. *brandtii* (Eversmann, 1845)
Myotis dasycneme Boie, 1825
Plecotus cf. *auritus* Linnaeus, 1758
Miniopterus schreibersii (Kuhl, 1817)
Eptesicus nilssoni (Keyserling et Blasius, 1839)
Trogontherium cf. *cuvieri* (Laugel, 1862)[2]
Canis mosbachensis Soergel, 1925
Vulpes cf. *praecorsac* Kormos, 1932
Meles meles cf. *atavus* Kormos, 1914[1]
Mustela palerminea Petényi, 1864
Mustela praenivalis Kormos, 1934
Lutra sp.
Pannonictis sp.
Martes foina cf. *intermedia* (Severtzov, 1873)[1]
Felis cf. *chaus* Schreber, 1777
Lynx sp.
Panthera onca gombaszogensis (Kretzoi, 1938)[1]
Homotherium sp.
Equus sp.
Rhinocerotidae sp.
Capreolus sp.
Cervus cf. *elaphus acoronatus* Beninde, 1937[1]
? *Alces* sp.