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# The taxonomic status of leporid remains from Ördöglyuk Cave, Solymár (Hungary)*

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Abstract. The near complete fossil skull which is the holotype specimen of "*Lepus praetimidus*" KRETZOI in JÁNOSSY, 1969 from the Middle Pleistocene of Ördöglyuk Cave in Solymár (Hungary) was revised, redescribed and compared with two extant subspecies of *Lepus timidus* LINNAEUS, 1758. The subspecies were *L. t. varronis* MILLER, 1910 from the Alps and *L. t. timidus* from the European part of Russia, St. Petersburg Oblast. The accompanying postcranial material was studied and described for the first time. The fossil remains (skull, mandibles, and isolated teeth) express all characteristic features of *Lepus timidus*. The dimensions of the skull and postcranial material are within the known range of variability of *Lepus timidus*, being most similar to the population from Russia. Thus, it is proposed to refer the specimen from Solymár to the species *Lepus timidus* and hence as *Lepus t. praetimidus*. The associated fauna of Solymár with *Lagurus lagurus* (PALLAS, 1773) and *Arvicola mosbachensis* (SCHMIDTGEN, 1911) was recently established as late Middle Pleistocene in age.

Key words: Lagomorpha, *Lepus timidus praetimidus*, Pleistocene, Solymár, Hungary.

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## I. INTRODUCTION

The mountain hare, *Lepus timidus* LINNAEUS, 1758 is today a common inhabitant of tundra and taiga environments across the greater part of the Palearctic (ANGEBJÖRN & FLUX 1995). It was widely, and continuously, spread throughout Europe in the Late Pleistocene (KURTÉN 1968, THULIN 2003). *Lepus timidus* is known to hybridize easily with *Lepus europaeus* PALLAS, 1778 in the overlapping areas of their distributions (THULIN 2003). Moreover, judging from the mitochondrial DNA traits of *Lepus timidus* found in some Iberian hares, such as *Lepus granatensis* (ROSENHAUER,

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1856), *Lepus castroviejoi* PALACIOS, 1977, as well as the Spanish populations of *Lepus europaeus* (MELO-FERREIRA et al. 2005), the Western border of its distribution range could have reached Spain. After the Late Glacial, when the ice masses began to withdraw northward, *Lepus timidus* colonised Ireland, Scotland, and Scandinavia, where the species has survived up to now (THULIN 2003). In Central Europe relicts of the wider Late Pleistocene distribution were preserved as isolated populations of the small subspecies *Lepus timidus varronis* MILLER, 1901 inhabiting the Alps (ANGERBJÖRN & FLUX 1995).

The majority of fossil finds of *Lepus europaeus* and *Lepus timidus* in Central and Western Europe date from the Vistulian Glaciation (Weichselian). Finds from the Eemian and pre-Eemian period are rare and well-preserved material, with unbroken bones or complete skulls, allowing for more detailed morphological comparisons is rare. Moreover, given the general scarcity of the fossil record of the Middle Pleistocene, the timing of the first appearance of the mountain hare in the European mammal assemblages is not yet known. In this paper we describe some of the earliest and richest assemblages of *Lepus timidus* from Central Europe.

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## II. MATERIAL AND GEOLOGICAL SETTINGS

The Middle Pleistocene fossil site of Ördöglyuk Cave in Solymár is a complex and extended cave system formed in the Dachsteinian limestone of Zsíros Hill, about one km West of Solymár village, near Budapest (JÁNOSSY 1986). The palaeontological investigations started in the cave in 1939 and were conducted first by VÉRTES, and then by JÁNOSSY, TOPÁL, and KRETZOI. There are two faunal assemblages found in the Ördöglyuk Cave. The Late Pleistocene fauna was discovered in the "Kiskörut" corridor. The second, earlier faunal assemblage was found at the end of the "Kiskörut", in the shaft filled with red clay and its age was determined as upper Middle Pleistocene (JÁNOSSY 1986). The Ördöglyuk Cave in Solymár and its sediments (the red clay) were proposed as a stratotype of the Solymárian substage (KRETZOI 1953; JÁNOSSY 1986), correlated with Steinheim and Swanscombe (JÁNOSSY 1986).

The leporid fossil material, including a near complete skull, the type specimen of "*Lepus praetimidus*", and numerous postcranial material of *Lepus* sp. were excavated from the red clay accompanied by a rich fauna of small mammals (JÁNOSSY 1969, 1986). The nomenclature of the list of mammals from Solymár, as presented by JÁNOSSY (1986), is partly incorrect from a current point of view and needs further revision. JÁNOSSY (1986), following KRETZOI'S indications, added some new species and subspecies of uncertain taxonomic status. The faunal list given in the present work was reviewed in order to modernise the nomenclature and the actual names are given in parentheses. The new species and subspecies indicated by KRETZOI, and cited by JÁNOSSY (1986), were omitted with indications only of the genera present. This was because of the uncertain taxonomic status mentioned by JÁNOSSY (1969) in his earlier work on the mammals from Solymár. Thus, the revised list of mammals from Solymár is as follows:

*Talpa europaea* LINNAEUS, 1758, *Crocidura* sp., *Sorex araneus* LINNAEUS, 1758, *Rhinolopus ferrumequinum* (SCHREBER, 1774), *Rhinolopus* cf. *hipposideros*, *Myotis* sp., *Plecotus* sp., *Ursus* sp., *Vulpes* sp., *Mustela* cf. *nivalis*, *Mustela* cf. *erminea*, *Putorius furo* (LINNAEUS, 1758), *Ochotona pusilla* (PALLAS, 1769), "*Lepus praetimidus*", *Glis glis* (LINNAEUS, 1766), *Sicista loriger* (=*subtilis*) (PALLAS, 1773), *Spalax* sp., *Apodemus* (=*Sylvaemus*) *sylvaticus* (LINNAEUS, 1758), *Cricetus cricetus* LINNAEUS, 1758, *Mus* sp., *Clethrionomys* sp., *Myodes* (=*Clethrionomys*) *glareolus* (SCHREBER1780), *Lagurus lagurus* (PALLAS, 1773), "*Arvicola* sp. III", *Microtus arvalis* (PALLAS,

1778), *M. oeconomus* (PALLAS, 1776), *M. gregalis* (PALLAS,1779), *Pitymys* (=*Microtus* (*Stenocranius*)) *gregaloides* (SCHRANK, 1798), *P.* cf. *subterraneus–arvalidens* (=*Microtus* (*Terricola*) cf. *subterraneus–arvalidens*), *Alces brevirostris* (KRETZOI in JÁNOSSY, 1969) (an almost complete skeleton), *Cervus elaphus* (LINNAEUS,1758), *Dicerorhinus kirchbergensis* (JÄGER,1839) and *Equus* sp.

The remains of "*Arvicola* sp. III" mentioned by JÁNOSSY (1986), with thin and slightly anteriorly thickened enamel, most probably represent the transitional forms between "*Arvicola cantiana*" (HINTON, 1910) and *A. terrestris* (LINNAEUS, 1758). The revision of the type material of *A. cantiana* and *A. mosbachensis* (SCHMIDTGEN, 1911) by MAUL et al. (2000) restricted the name "*A. cantiana*" to the type material from Ingress Vale in Kent, England, while all other Middle Pleistocene *Arvicola* were referred to *A. mosbachensis*.

The age of the fauna from Solymár was determined as late Middle Pleistocene, at the boundary of *Arvicola mosbachensis – Lagurus lagurus* partial range zones (KORDOS 1994).

The fossil material of *Lepus* from Solymár described here is housed in the collection of Department of Geology and Paleontology in the Hungarian Natural History Museum, (GYN).

The comparative material of extant *Lepus timidus* came from: Senckenberg Museum, Frankfurt a. Main: *Lepus t. varronis* (SM 9619, 9637, 25896, 81671, 81721, 94092, 882, 16480, 16374); Zoological Institute RAN (St. Petersburg): *Lepus t. timidus* (ZIN 59294, 50726, 39495, 51396, 58020, 84660, 84653, 59293, 61718, 59588); Museum für Naturkunde, Berlin: *Lepus timidus* (ZMB 81668, 56829, 22421, 81691, 81692).

## III. SYSTEMATIC PART

Family: **Leporidae** FISCHER VON WALDHEIM, 1817

Genus ***Lepus*** LINNAEUS, 1758

***Lepus timidus*** LINNAEUS, 1758

***Lepus timidus praetimidus*** KRETZOI in JÁNOSSY, 1969

1969 *Lepus praetimidus* KRETZOI in litt. (1944). In: JÁNOSSY: p. 610–611, Pl. VI: 1–2.

1986 *Lepus praetimidus* KRETZOI in JÁNOSSY. In: JÁNOSSY: p. 112–113, 180.

Holotype: Skull without nasal bones (GYN/492, coll. Hungarian Natural History Museum, Department of Geology and Paleontology, Budapest), Solymár, Middle Pleistocene, Hungary.

D i a g n o s i s. Large subspecies of *Lepus timidus*; larger than *Lepus t. varronis* and equal or exceeding the large specimens of *Lepus t. timidus*. Mandible with a relatively heightened alveolar part, marked by a convex ventral margin of the body of the mandible. The upper incisors lack cement. The upper premolars and molars P3-M2 have a strongly crenulated hypostria on the anterior and posterior margins. The p3 has an extended crenulated protoflexid and crenulation on the distal margin of the hypoflexid.

Type locality and stratigraphy: Solymár near Budapest, Hungary; Middle Pleistocene, Saalian.

M a t e r i a l. 2 fragments of maxilla sin. juv.; 3 dex. and 2 sin. mandibles; 1 atlas; 1 epistropheus; 5 cervical; 13 thoracic, and 19 lumbar vertebrae; 1 proximal fragment of sacral bone; numerous fragments of ribs; 6 (including 4 juv.) dex., 5 (including 3 juv.) sin. fragments of scapulae; 1 dex., 1 sin. proximal fragments of humerus; 3 dex. juv., 4 sin. distal fragments of humerus; 4 dex., 9 sin. (including 5 juv.) fragments of ulna; 3 dex., 2 sin. juv. radii; 1 sin. metacarpal II bone (including 3 juv.) sin., 1 dex. metacarpal III bone; 3 dex., 3 sin. (including 2 juv.) metacarpal IV bone; 1 phalanx proximalis of hand juv.; 1 dex. pelvis; 4 (including 3 juv.), 7 (including 6 juv.) sin. fragments of ilium; 7 (including 5 juv.) dex., 5 sin. juv. femora; 1 dex., 1 sin. proximal part of femur; 2 distal parts of femur; 3 femora juv. damaged; 3 dex., 1 sin. tibiae; 11 fragments of tibiae juv.; 2 dex., 3 sin. (in-

cluding 2 juv.) calcanei; 1 talus dex.; 1 navicular bone; 2 dex. juv., 7 sin. (1 juv.) metatarsal II bone; 7 dex. (including 3 juv.), 1 sin. juv. metatarsal III bone; 4 dex. (including 3 juv.), 5 sin. metacarpal IV bone; 5 dex., 3 sin. metatarsal V bone; 5 phalanxes proximales of the foot; 1 p3 sin., 2 p3 dex. juv.; 1 P2 dex. juv.; 1 i1 sin.

Minimum number of individuals = 9.

Age structure: six juveniles, including five very young (less than 6 months old), one fully adult, and two subadult specimens.

D e s c r i p t i o n. The holotype (GYN/492) is an almost complete skull (Fig. 1A-E) of a relatively young, although fully grown, specimen. The sagittal suture is not fully obliterated; the suture within the *os frontale* is ossified along half its length; the nasal bones are missing, and the occipital region is loosely connected to the skull. These features indicate a young ontogenetic status, about early age class III, which is approximately 9-10 month old (CABOŃ-RACZYŃSKA 1964). The morphology of skull reveals all the specific characters of *Lepus timidus*. The roots of the upper incisors extend to the premaxilla-maxilla suture, the maxillary root of the zygomatic arch is, in ventral view, shorter, strongly rounded, and more prominently lateral than in *Lepus europaeus* (GUREEV 1964, KOBY 1959). The frontal spine, although damaged in the anterior part, was probably relatively short in the described specimen, judging from its narrow base. Regardless of the fact that the overall morphology of the frontal spine is strongly variable in both species, at least in some specimens of extant *Lepus timidus* it is narrow in the posterior part and relatively short. Moreover, in *Lepus timidus* it forms a triangular sharp-ended wedge, strongly tapering anteriorly, which differs from the wider and frequently blunt-ended one of *Lepus europaeus* (GUREEV 1936, 1964, KOBY 1959, 1960). The condition of the posterior part of frontal spine in the specimen from Solymár falls within the *Lepus timidus* morphotype.

The supraorbital processes of the frontal, although also damaged in lateral parts, shows stronger development of the posterior parts, being relatively wide at the base. The short but broad posterior supraorbital processes and poorly developed anterior ones are generally characteristic of *Lepus timidus* (GUREEV 1936, 1964, KOBY 1959, 1960). However, the shape and size of the processes change in ontogeny and cannot be used as diagnostic characters with certainty (CABOŃ-RACZYŃSKA 1964).

The upper incisors are square in cross-section and are not compressed mesio-distally as in *Lepus europaeus*, with both lobs equally thick (Fig. 1F). The thickness-to-width index of the upper incisors is 82% in the specimen from Solymár, being characteristic for *Lepus timidus* (KOBY 1959). The mesial groove is relatively deep and narrow, not filled with cement. The P2 is rather compact with a deeply incised lingual re-entrant (hypoflexus). The axes of the two lingual lobes are more parallel than in most *L. europaeus* specimens and are typical of *L. timidus* (KOBY 1959). The hypostriae of the cheek teeth (P3-M3) are strongly crenulated (Fig. 1G).

The specimen from Solymár is relatively large and the dimensions of skull are closer to those of *Lepus timidus* from the European part of Russia (St. Petersburg Oblast) than to the relict alpine populations of *Lepus t. varronis* (Table I).

The preserved mandibles are relatively high (Fig. 2, Table I). The condyloid and coronoid processes are damaged in all specimens; thus it is hard to determine the exact angle between the condyloid process and the body of the mandible, which is generally smaller in *Lepus timidus* than in *L. europaeus* (GUREEV 1936, 1964). In the specimens described the remnants of the condyloid processes are inclined more caudally, forming a slightly larger angle than typical for *L. timidus* (GUREEV 1936, 1964). However, some specimens of extant *Lepus timidus* are known to possess a slightly more posteriorly inclined condyloid process, than generally observed in the whole population and the feature shows some variability. The lower incisors do not differ in morphology from those of modern *L. timidus*. They are relatively thick and narrow, square in cross section (Fig. 2C) with thickness-to-width ratio about 90%. KOBY (1959) stated this index to be one of the most important features distinguishing *Lepus timidus* (84-95%) from *Lepus europaeus* (74%). The p3's are elongated mesio-distally and have a complicated enamel pattern with crenulation on the antero-

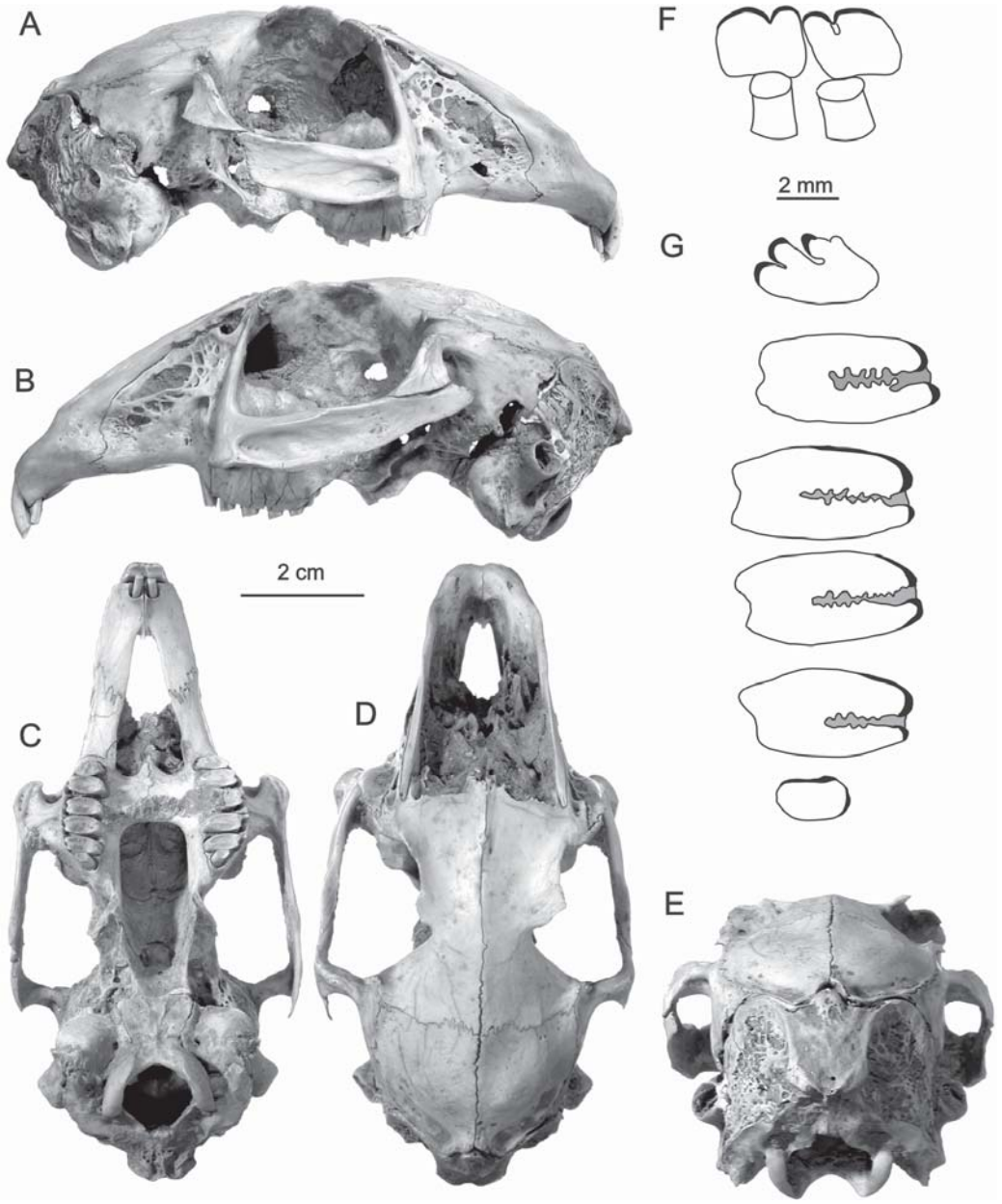


Fig. 1. Skull of *Lepus timidus praetimidus* (holotype, GYN/492) from Ördöglyuk Cave in Solymár, Middle Pleistocene, Hungary. A, B – lateral views, C – ventral view, D – dorsal view, E – aboral view at the occipital region, F – occlusal surface of upper incisors, G occlusal surface of upper cheek teeth.

Table I

Comparison of cranial measurements of *Lepus timidus praetimidus*, *Lepus timidus varronis* from the Alps, and *Lepus timidus timidus* from Russia (St. Petersburg Oblast). Measurements in mm; number of specimens in parentheses. O.R. – observed range

| Measurements | *Lepus timidus praetimidus* | *Lepus timidus varronis* | *Lepus timidus timidus* |
|---|---|---|---|
| Skull length | 99.8 | (8)<br>92.9 ± 4.3<br>O.R. 87.2–100.5 | (10)<br>98.3 ± 4.3<br>O.R. 91.3–104.7 |
| Width of muzzle at the anterior border of the P2 alveoli | 23.3 | (9)<br>20.7 ± 1.4<br>O.R. 18.0–23.2 | (10)<br>21.9 ± 1.8<br>O.R. 19.7–25.1 |
| Width of the skull measured at the lateral-most points of the alveolar processes of the maxilla | 29.3 | (9)<br>26.9 ± 1.2<br>O.R. 25.7–29.1 | (10)<br>28.8 ± 1.4<br>O.R. 26.5–31.2 |
| Width of the skull at the zygomatic arches | 45.8 | (9)<br>41.8 ± 1.9<br>O.R. 39.5–45.4 | (10)<br>45.84 ± 2.0<br>O.R. 41.5–48.3 |
| Minimal width of frontale, posterior to the supraorbital processes | 14.6 | (9)<br>15.8 ± 0.8<br>O.R. 14.9–17.1 | (10)<br>16.0 ± 0.8<br>O.R. 14.3–16.7 |
| Alveolar length of the upper tooth row | 19.9 | (9)<br>18.5 ± 1.3<br>O.R. 17.7–21.0 | (10)<br>19.7 ± 0.7<br>O.R. 18.5–20.7 |
| Length of the maxillar diastema | 28.6 | (9)<br>27.3 ± 1.5<br>O.R. 24.7–30.3 | (10)<br>26.8 ± 1.3<br>O.R. 24.6–29.1 |
| Width of choanae | 11.1 | (9)<br>10.3 ± 0.6<br>O.R. 9.9–11.7 | (10)<br>11.2 ± 0.8<br>O.R. 9.9–12.7 |
| Length of the mandibular diastema | 21.8 | (9)<br>19.9 ± 1.5<br>O.R. 17.5–22.0 | (10)<br>21.5 ± 1.0<br>O.R. 20.1–23.6 |
| Length of the lower tooth row | 19.9 | (9)<br>19.3 ± 1.2<br>O.R. 17.8–21.5 | (10)<br>20.5 ± 1.0<br>O.R. 18.6–21.7 |
| Height of the mandibular body at p4/m1 | 17.4 | (9)<br>15.3 ± 1.7<br>O.R. 14.1–19.3 | (10)<br>16.5 ± 1.1<br>O.R. 15.3–18.2 |
| Index maxillar 1: tooth row/diastema length | 70% | 68% | 73.5% |
| Index mandibular 1: tooth row/diastema length | 91% | 97% | 95% |
| Index mandibular 2: height of mandible body/tooth row length | 88% | 79% | 80% |

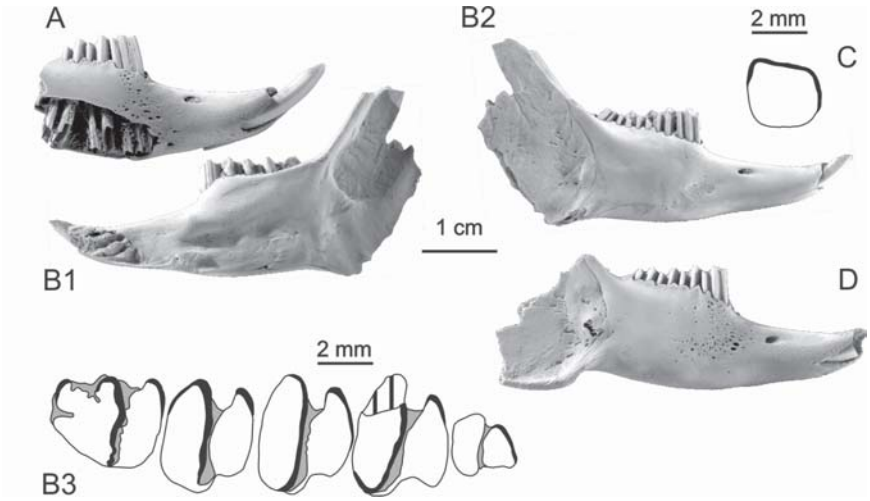


Fig. 2. Fragments of mandibles dex. of *Lepus timidus praetimidus* (GYN/491/1) from Ördöglyuk Cave in Solymár. A, B2, and D – buccal views, B1 – lingual view, B3 – occlusal view of the lower cheek teeth, C – outline of the i1 in cross-section.

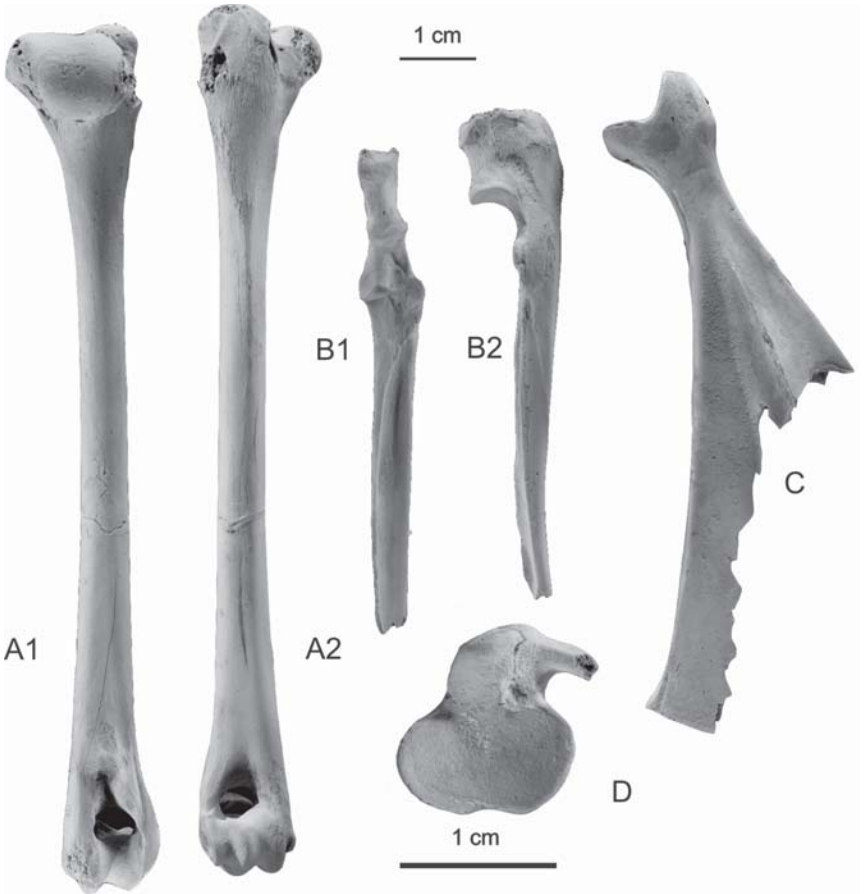


Fig. 3. Postcranial remains of the scapular girdle and forelimb of *Lepus timidus praetimidus* from Ördöglyuk Cave in Solymár. A – humerus sad. dex. (GYN/488/1), A1 – caudal view, A2 – cranial view; B – ulna dex. (GYN/493), B1 – cranial view, B2 – medial view; C – scapula sin. (GYN/488/2), lateral view, D – glenoid cavity of scapula dex.

Table II

Measurements of the forelimb bones and those of the scapular girdle of *Lepus timidus praetimidus* compared with extant specimens of typical *Lepus timidus* from Scandinavia. Measurements in mm; number of specimens in parentheses; standard deviation calculated for at least five specimens; O.R. – observed range

| Measurements | *Lepus timidus praetimidus* | extant *Lepus timidus timidus* |
|---|---|---|
| Scapula: | (4) | (5) |
| width of acetabulum | 11.8 | 10.9 ± 1.0, O.R. 9.2–11.9 |
| height of acetabulum | 7.7 | 7.2 ± 0.8, O.R. 5.8–8.1 |
| Humerus: | | |
| length | 108.8 | (4) 101.0, O.R. 88.3–106.9 |
| width of head | (2) 16.9–18.3 | (5) 17.0 ± 1.5, O.R. 14.7–18.5 |
| width of distal extremity | (4) 12.1, O.R. 11.6–12.4 | (4) 11.42, O.R. 9.9–12.2 |
| width of trochlea | (4) 5.1, O.R. 4.9–5.3 | (4) 5.0, O.R. 4.8–5.1 |
| Radius: | | |
| length | (3) 94.5, O.R. 89.9–103.6 | (4) 107.8, O.R. 93.0–118.9 |
| width of prox. extremity | (4) 8.5, O.R. 8.2–8.8 | (3) 5.6, O.R. 5.3–6.1 |
| width of dist. extremity | (2) 9.8–10.9 | (4) 10.1, O.R. 7.9–11.6 |
| Ulna: | | (4) |
| width of the olecranon | 12.3 | 10.9, O.R. 9.7–11.5 |
| height of olecranon | 11.5 | 10.9, O.R. 8.4–12.4 |
| Metacarpal II: | | (5) |
| length | 34.2 | 30.6 ± 3.6, O.R. 26.5–34.0 |
| Metacarpal III: | (2) | (4) |
| length | 36.1–35.2 | 32.4, O.R. 29.6–37.2 |
| Metacarpal IV: | | (5) |
| length | 24.4 | 26.0 ± 3.4, O.R. 22.5–30.4 |

external re-entrant (protoflexid) in some specimens (Fig. 2B3). However, the enamel pattern of the p3 is variable to some extent in both species of *Lepus*. The greater degree of elongation and the more complicated enamel pattern is very common in *Lepus timidus*, while in *L. europaeus* elongation is weaker and the antero-external re-entrants display a much simpler pattern.

The measurements of the postcranial skeleton (Figs 3, 4, Table II, III) taken from the adult and subadult specimens, in which the epiphyses were already well fused with diaphyses, indicate the large size of the individuals from Solymár. However, they generally lie within the observed modern range for the species *L. timidus*. The exceptions are a large humerus, an ulna, and a tibia (Fig. 3AB, 4A, Table II, III) that are slightly larger than usually observed in extant *Lepus timidus*.

## IV. DISCUSSION

The first and only contribution on leporid remains from Solymár was published by JÁNOSSY (1969), who referred to the unpublished manuscript by KRETZOI. The description of the skull (GYN/492) classified as "*Lepus praetimidus*" did not include a specific diagnosis or detailed meas-

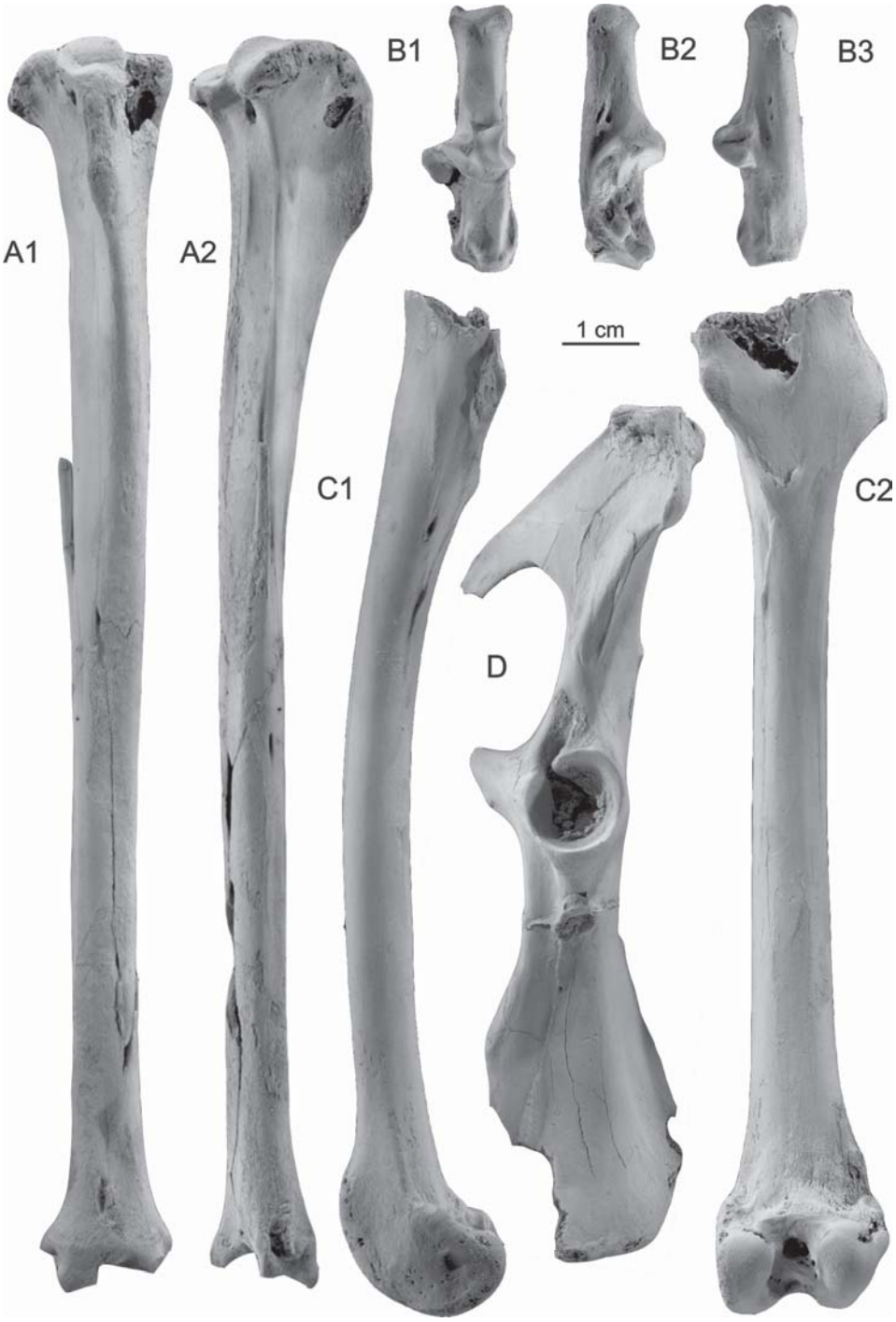


Fig. 4. Postcranial remains of pelvic girdle and hindlimb of *Lepus timidus praetimidus* from Ördöglyuk Cave in Solymár. A – tibia dex. (GYN/493/1), A1 – cranial view, A2 – medial view; B calcaneus sin. (GYN/493/2), B1 – dorsal view, B2 – medial view, B3 – lateral view; C – femur dex. (GYN/493/3), C1 – medial view, C2 – caudal view; D – pelvis dex. (GYN/493/4) in lateral view.

Table III

Measurements of hind limb bones and those of the pelvic girdle of *Lepus timidus praetimidus* compared with extant specimens of typical *Lepus timidus* from Scandinavia. Number of specimens in parentheses; O.R. – observed range

| Measurements | *Lepus timidus praetimidus* | *Lepus timidus timidus* |
|---|---|---|
| Pelvis: | | (4) |
| length | 101.1 | 95.0, O.R. 92.4–97.9 |
| length of acetabulum | 12.6 | 12.1, O.R. 11.8–12.2 |
| height of acetabulum | 11.6 | 11.2, O.R. 10.4–11.8 |
| Femur: | | |
| length | ±135.0 | (4) 129.4, O.R. 113.9–136.8 |
| width of prox. extremity | 29.4 | (4) 26.7, O.R. 22.4–28.5 |
| width of dist. extremity | 21.2 | (4) 19.4, O.R. 17.9–20.7 |
| Tibia: | | |
| length | 157.0 | (3) 146.4, O.R. 134.8–156.6 |
| width of prox. extremity | 21.5 | (4) 19.5, O.R. 16.6–21.0 |
| width of dist. extremity | 16.8 | (3) 14.9, O.R. 13.9–15.4 |
| Calcaneus: | (5) | |
| length | 31.1 ± 1.8, O.R. 28.7–32.9 | (4) 33.1, O.R. 28.4–35.3 |
| length of tuber calcanei | 13.5 ± 1.1, O.R. 11.8–14.6 | (3) 17.5, O.R. 16.8–18.1 |
| Metatarsal II: length | (4) 60.7, O.R. 56.90–63.3 | (4) 56.2, O.R. 48.4–65.1 |
| Metatarsal III: length | (4) 61.5, O.R. 58.35–64.57 | (4) 58.0, O.R. 51.7–64.5 |
| Metatarsal IV: length | 62.1 | (4) 56.6, O.R. 53.0–61.8 |
| Metatarsal V: length | (2) 55.2–55.7 | (4) 50.5, O.R. 46.2–57.4 |

urements and was a brief discussion with KRETZOI's description. The postcranial material was not mentioned.

JÁNOSSY (1969), after KRETZOI, emphasised the large size of the specimen, the shorter rostral part of the skull, and the lack of cement in the groove of the I1, which, in his opinion, distinguished the specimen from typical *Lepus timidus*. He stated that "*Lepus praetimidus*" differs clearly from *Lepus europaeus*. The difference between "*Lepus praetimidus*" and *Lepus timidus* were seen mainly in the stratigraphic position of the former (JÁNOSSY 1969).

The present revision of the morphology and measurements of the skull from Solymár, as well as the accompanying postcranial material, reveals that the remains belonged to relatively large individuals of *Lepus timidus* from the Middle Pleistocene. The leporid specimens from Solymár do not display any feature which could serve as a basis for separating it into a different species. The prominent and anteriorly extended zygomatical process of the maxilla, the ends of the I1 roots, at the praemaxilla-maxilla suture, as well as relatively thick and square, in cross-section, incisors are the most characteristic features that allow one to distinguish *Lepus timidus* from *Lepus europaeus* (GUREEV 1936, 1964, KOBY 1959, 1960, CABOŃ-RACZYŃSKA 1964). They are all present in specimens from Solymár (Figs 1, 2). The lack of cement in the anterior groove of the upper incisor stressed by JÁNOSSY (1969) can sometimes be observed in *Lepus timidus* (personal observation), although it is an atypical and rare feature in this species. One can also note the virtual absence of cement in the P2. It is probably related to the relatively young age of the specimen.

The postcranial skeleton generally bears no diagnostic characters. KOBY (1959) suggested that the radius-to-tibia length ratio for *Lepus t. varronis* (67-72%) is lower than for *Lepus europaeus* (73-78%). The ratio calculated for the two largest complete bones from Solymár (presumed to belong to one specimen) gave an index value of 66%, being comparable with that for *L. t. varronis*, and much lower than for *L. europaeus*.

It is known that mountain hares attain full size at the age of four months (ANGERBJÖRN & FLUX 1995), thus the measurements (Table I-III) of the skeleton and skull are regarded here as representative for the population from Solymár. The Solymár specimen (GYN/492) estimated as relatively young (9-10 months) exceeds in skull size that of *Lepus t. varronis*. The northern populations of extant *Lepus timidus* from Europe tend to be larger, supporting Bergmann's rule (ANGERBJÖRN & FLUX 1995). The data obtained from the study of fossil charcoals (*Taxus baccata*, *Larix* and *Pinus*) indicated a cooler and wetter climate than in Hungary today (JÁNOSSY 1986). Therefore, it cannot be excluded that the large size of the Solymár specimen could be attributed to the Bergmann's rule.

Considering all the discussed morphological features and the larger than average size, as well as the variability of extant mountain hares and the high adaptability of the species, as expressed by many distinct subspecific forms, it seems fully justified to include "*Lepus praetimidus*" in *Lepus timidus* at a subspecific level, *Lepus timidus praetimidus*. This subspecies could therefore include the Middle Pleistocene populations of *L. timidus* from Western and Central Europe characterised by large size and a relatively high alveolar part of the mandible. Although AVERIANOV (2001) suggested that all early populations of *Lepus timidus* inhabiting Europe in the Middle Pleistocene belonged to this subspecies, its stratigraphic and palaeogeographic distribution is still not well recognised. However, it seems to be related to the presence of *Arvicola mosbachensis*. A broader revision of *L. timidus* from the Middle Pleistocene will allow a determination of more the detailed characteristics of these early populations.

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