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A Late Pleistocene to Holocene succession of leporid species in the southern Vienna Basin (Austria)

Une succession d'espèces de léporidés du Pléistocène supérieur à l'Holocène dans la partie méridionale du bassin de Vienne (Autriche)

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ABSTRACT

The new archaeological and palaeontological site of Smrcka Lorenz-Abris yielded three different leporid species in stratigraphical sequence, mirroring the effect of environmental changes and the influence of humans in this area. *Lepus timidus* is a species with a wide Late Pleistocene distribution, but disappeared in the Vienna Basin at the end of the Pleistocene. *Lepus europaeus* appeared in the Holocene and became dominant in lower altitudes in Austria. Interspecific competition as well as anthropogenic and natural environmental changes are the main factors that caused this replacement. At Smrcka Lorenz-Abris, *L. europaeus* became dominant around 7000 a BP. This site yielded the last evidence of a mountain hare in the Vienna Basin, with a preserved lower jaw that was dated to be from around 14,000 a BP. The most recent immigrant is *Oryctolagus cuniculus*, which was introduced to Austria, and only found in the upper parts of the section.

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RÉSUMÉ

Le nouveau site archéologique et paléontologique de Smrcka Lorenz-Abris a fourni trois espèces différentes de léporidés dans la colonne stratigraphique, reflétant l'effet des changements environnementaux et l'influence de l'Homme dans cette région. *Lepus timidus* est une espèce à vaste distribution au Pléistocène supérieur, mais qui a disparu dans le bassin de Vienne à la fin du Pléistocène. *Lepus europaeus* est apparu à l'Holocène et est devenu dominant aux basses altitudes en Autriche. Une compétition interspécifique, ainsi que les changements environnementaux naturels ou dus à l'Homme, sont les principaux facteurs de ce remplacement. À Smercka Lorenz-Abris, *L. europaeus* est devenu dominant autour de 7000 a BP. Le site a produit la denière évidence d'un lièvre de montagne dans le bassin de Vienne, avec une mâchoire inférieure conservée, qui a été datée d'environ 14,000 a BP. Le plus récent immigrant est *Oryctolagus cuniculus*, qui a été introduit en Autriche et que l'on trouve seulement dans les parties hautes de la coupe.

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1. Introduction

1.1. The fossil record of leporids in Austria

Before the Pliocene, only ochotonids such as *Eurolagus*, *Amphilagus*, or *Prolagus* are known from Austria (Angelone and Veitschegger, 2015; Prieto et al., 2012 and references therein; Prieto et al., 2014). The first appearance of modern leporids in Europe was in the Late Miocene (Flynn et al., 2014 and references therein), and the first known leporid from Austria is *Hypolagus petenyii* ("*H. beremendensis beremendensis*") from Middle Pliocene fissure fillings (Deutsch-Altenburg 9, 20, 21; MN 16; ca. 3.0–2.5 Ma old) (Čermák, 2009; Döppes and Rabeder, 1997; Fladerer and Reiner, 1996a). This species evolved into, or was replaced by, the Early Pleistocene *Hypolagus brachygnathus*, which survived until the beginning of the Middle Pleistocene (Čermák, 2009; Fladerer and Reiner, 1996a). The first species of the genus *Lepus* may have appeared in the Middle Pleistocene in Austria. A *Lepus* sp. ("*L. terraerubrae*") inhabited the Early to Middle Pleistocene steppes of eastern Austria. This species, however, has not yet been properly described (Döppes and Rabeder, 1997; Fladerer, 1984).

Finds of *Lepus timidus* occur rather frequently in Late Pleistocene sediments in eastern Austria (Fig. 1) and the oldest dated evidence of this species are from the Salzofenhöhle (Styria), about 54,000–31,200 a BP, and from the Peggauerwandhöhle (Styria), about 42,400–22,600 a BP (Döppes and Rabeder, 1997; Fladerer, 1994; Pittioni, 1980). So far, the oldest occurrence of *L. timidus* in Lower Austria around the Vienna Basin is from the Late Palaeolithic locality Alberndorf 1 with radiocarbon dates of around 28,500 and 26,900 a BP (Jöris et al., 2010). The most recent evidences for fossil mountain hares in Austria so far are from the Merkensteinhöhle (Lower Austria), with an age of 13,000–10,000 a BP, and from the Teufelslucke near Eggenburg (Lower Austria), with an age of 13,000–7,000 a BP. The relative age of both caves, however, is based on the micromammal assemblages (e.g., *Dicrostonyx*) (Fig. 1) (Döppes and Rabeder, 1997).

So far the most reliable oldest evidence of the European hare, *Lepus europaeus*, in Austria is from the Knochenhöhle near Kapellen (Styria), where one specimen of *L. europaeus* was found among several hundred of *L. timidus*. A ^{14}C age of a mountain hare from the same layer dated back to about 14,000 a BP (Fladerer and Reiner, 1996b).

Oryctolagus cuniculus is endemic on the Iberian Peninsula, as well as southern France, and was introduced to Austria in the late Middle Ages around the 15th century (Spitzenberger, 2001). Newer evidence from eastern Austria (canabae legionis, Vindobona) suggests an earlier introduction, within the Roman period, but the temporal origin of these specimens still needs to be verified (Czeika, 2005).

1.2. The Smrcka Lorenz-Abris

The archaeological and palaeontological site of Smrcka Lorenz-Abris (about 380 m above sea level) is located in the Höllgraben, a small valley close to the village Enzesfeld-Lindabrunn in the southern part of the Vienna Basin (47°54′43″N, 16°10′10″E). This village is at the western margin of the southern Vienna Basin, about 35 km southwest from Vienna (Fig. 1). The Smrcka Lorenz-Abris is a single cliff in an artificial *Pinus nigra* forest on the southern hillside of the Höllgraben (Neitz, 2013). The cliff is built by cemented coarse grained gravels which were deposited by rivers during the Late Miocene (Pannonian), 11.6–10.5 Ma, and mainly consists of transported Alpine rubble (Wessely, 2006). The sediments under the Smrcka Lorenz-Abris and the surrounding talus were formed during Late Pleistocene and modern times. This sediment mainly consists of the eroded rubble from the cliff. Archaeological evidence, based on the recovery of stone tools (Neitz, 2013),

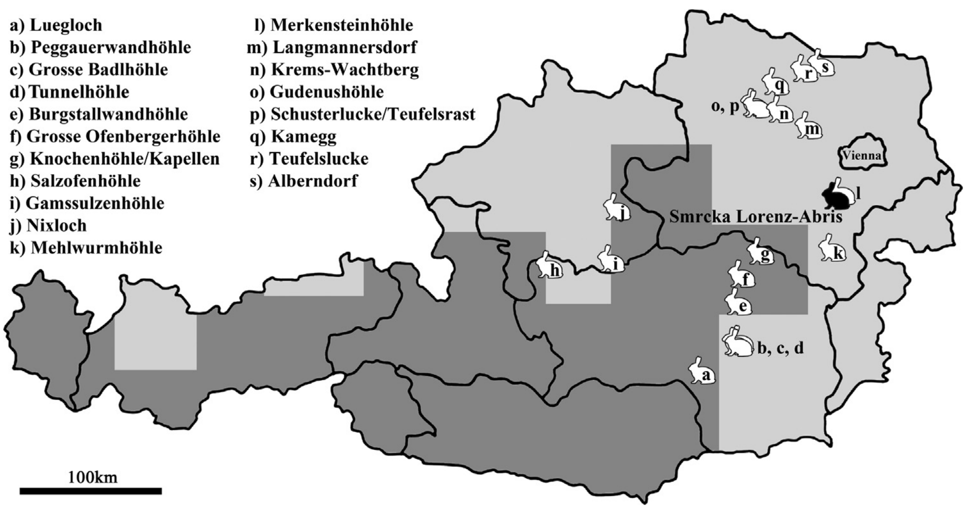

Fig. 1. Late Pleistocene findings of *Lepus timidus* in Austria (after Döppes and Rabeder, 1997). The dark grey area represents the modern distribution of the mountain hare in Austria (IUCN, 2008). The black hare icon indicates the position of the Smrcka Lorenz-Abris.

Fig. 1. Découvertes de *Lepus timidus* du Pléistocène supérieur en Autriche (d'après Döppes et Rabeder, 1997). La zone en gris foncé correspond à la distribution moderne du lièvre de montagne en Autriche (IUCN, 2008). L'icône représentant un léporidé noir indique la position de Smrcka Lorenz-Abris.

Table 1
List of the ^{14}C dated bones from the Smrcka Lorenz-Abris.
Tableau 1
Liste des os datés au ^{14}C en provenance de Smrcka Lorenz Abris.

ID	Cat. No.	Species	Layer	Age in cal a BP	Age in a BP
VERA-5724*	7000/LB-880	*Homo sapiens*	Bottom of Layer A	6,220–6,000	10,960 ± 50
VERA-5512**	7000/LB-810	*Capreolus capreolus*	Bottom of Layer A	6,400–6,270	5,505 ± 40
VERA-5722***	7000/LB-786	*Capreolus capreolus*	Bottom of Layer A	7,180–6,940	6,175 ± 40
VERA-5511****	7000/LB-846	*Alces alces*	Middle of Layer B	12,980–12,650	12,160 ± 50
VERA-5723*****	7000/LB-41b	*Lepus timidus*	Middle of Layer B	14,180–13,830	5,350 ± 40

dates this site from modern times back to the Neolithic age. Besides artefacts, several thousand remains of different Holocene and Pleistocene mammal and mollusc species were found. Some species belong to the extant wild fauna of the Vienna Basin, such as *Capreolus capreolus*, *Mustela nivalis*, *Cricetus cricetus*, and *Glis glis*; and other species are known from Late Pleistocene sites inside and around the Vienna Basin, such as of *Lepus timidus*, *Rangifer tarandus*, *Marmota marmota*, *Chionomys nivalis*, and *Dicrostonyx* sp. (Döppes and Rabeder, 1997; Neitz, 2013; Spitzenberger, 2001).

Three main layers have been distinguished within the profiles, at the top is Layer A, with findings of human artefacts, fire places, and one human bone. This layer dates from modern times back to the Neolithic Age, and is marked by findings of human artefacts as well as Holocene mammal species such as *Lepus europaeus, Cricetus cricetus*, and *Glis glis*. The second layer, Layer B, dates to the Late Pleistocene and is characterized by the occurrence of *Lepus timidus*, *Rangifer tarandus*, *Marmota marmota*, *Chionomys nivalis*, and *Dicrostonyx* sp., as well as the absence of human artefacts. The third and last layer, Layer C is characterized by numerous opercula of the round-mouthed snail, *Pomatias elegans* (Müller 1774), and the absence of vertebrate remains. The oldest findings in Layer A are dated at around 7,000 a BP (Table 1). Leporid specimens were found in Layers A and B (Fig. 6).

To our knowledge, this is the first time that *L. europaeus*, *L. timidus*, and *O. cuniculus* were found in succession in the same locality in Austria. Here, we present the findings of leporids from Smrcka Lorenz-Abris and discuss their significance for the palaeontological record of Austria.

2. Material and methods

The faunal material was excavated between 2004 and 2011 by members of the Paläontologischer Forschungsverein Lindabrunn (J. and M. Neitz, J. and M. Zierhofer), under the direction of Gerhard Trnka, Institute of Prehistoric and Historical Archaeology of the University of Vienna, and Michael Brandl, Austrian Academy of Sciences, Institute of Oriental and European Archaeology.

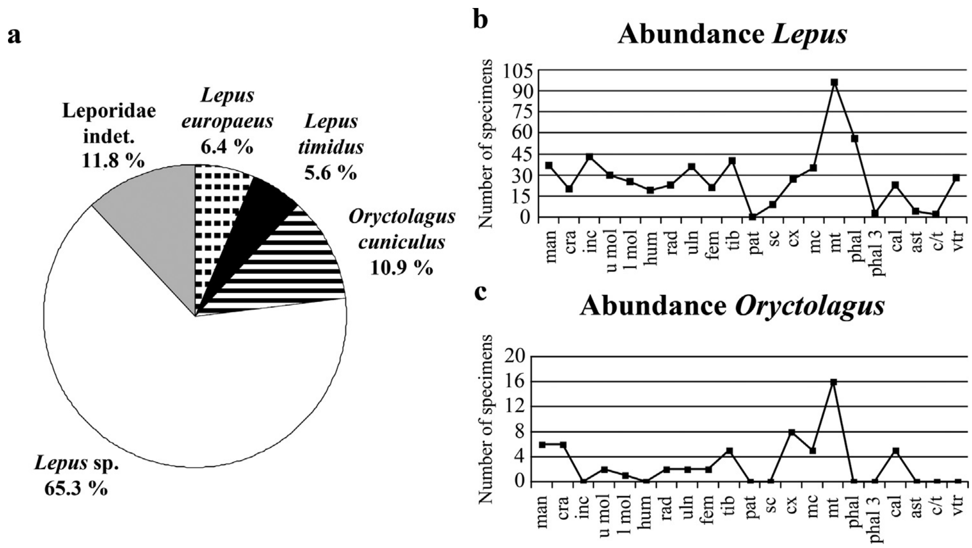

Fig. 2. Abundance of the different leporid species from the Smrcka Lorenz-Abris: a, pie chart with the taxonomic distribution of the leporid species; b, body part abundance of genus *Lepus*; c, body part abundance of genus *Oryctolagus*. Abbreviations: ast, astragalus; cal, calcaneus; cra, cranium; c/t, carpals/tarsals; cx, coxa; fem, femur; hum, humerus; inc, incisor; l mol, lower pre-/molar; man, mandible; mc, metacarpus; mt metatarsus; pat, patella; phal, phalange 1 & 2; phal 3, phalange 3; rad, radius; sc, scapula; tib, tibia; uln, ulna; u mol, upper pre-/molars; vtr, vertebra.

Fig. 2. Abondance des différentes espèces de léporidés en provenance de Smrcka Lorenz-Abris : a, camembert de distribution taxonomique des espèces de léporidés ; b, abondance de parties du corps du genre *Lepus* ; c, abondance de parties du corps du genre *Oryctolagus*. Abréviations : ast, astragale ; cal, calcaneus ; cra, crâne ; c/t, carpiens/tarsiens ; cx, coxa ; fem, femur ; hum, humérus ; inc ; incisive ; 1 mol, pré-/molaire inférieures ; man, mandibule ; me, métcarpe ; mt, métatarse ; pat, patella ; phal, phalanges 1 et 2 ; phal 3, phalange 3 ; rad, radius ; sc, scapula ; tib, tibia ; uln, ulna ; u mol, pré-/molaire supérieures ; vtr, vertèbre.

The leporid teeth were measured using the method of von den Driesch (1976), using a digital calliper to the closest 0.1 mm. Measurements of the upper and lower incisors from different localities (F.A. Fladerer, personal database) were added for species distinction. The excavations at the Smrcka Lorenz-Abris yielded 577 remains of leporids (Fig. 2). The majority of the material could not be identified to species level and therefore 386 remains are attributed to *Lepus* sp. and 65 to Leporidae indet. The remaining 126 remains belong to one of the three preserved leporid species: *Lepus europaeus*, *L. timidus* and *Oryctolagus cuniculus*.

Five bones from the total faunal sample (four large mammals, one leporid) were selected for ^{14}C dating by the VERA-laboratory at the Faculty of Physics, University of Vienna (Tab. 1). The faunal material is stored in the Department of Palaeontology at the University of Vienna (PIUW) under the collective inventory number 7000/LB. The archaeological material is stored in the Institute of Prehistoric and Historical Archaeology of the University of Vienna (IUHA).

3. Systematic part

Order LAGOMORPHA BRANDT, 1855
Family LEPORIDAE FISCHER, 1817
Genus *Lepus* LINNÉ, 1758
Lepus europaeus PALLAS, 1778

Material: thirty-five bones and teeth are preserved. Among the 16 teeth are lower incisors (four left, seven right), upper incisors (three left, one right), and a lower third premolar (one right). Furthermore, a premaxillary bone with incisor (one right), lower jaws (five left, five right), and ulnae (three left, five right) are preserved. Seven right lower incisors are represented, which shows that at least seven individuals are represented.

Lepus timidus LINNÉ, 1758

Material: thirty-one bones and teeth of the leporid assemblage could be assigned to the mountain hare: lower incisors (three left, nine right), upper incisors (three left, two right), lower third premolars (eight left, three right), one complete lower jaw and ulnae (two left).

Taxonomy:

The measurements of the incisor teeth (Figs. 3 and 4) show a rather clear distinction between *Lepus timidus* and *L. europaeus*. The mountain hare has generally more quadratic incisors than the European hare (e.g., Koby, 1959; Morel and Müller, 1997). Additionally, the lower third premolar can be used to separate these two species. The lower third premolars of both species share the same basic morphology with, for example, two different sized anteroconids (Callou, 1997). In *L. timidus*, however, this tooth is more elongated and rectangular compared to the more roundish outline the one of *L. europaeus* (Koby, 1959). Hauser (1921) also presented diagnostic features to distinguish between postcranial elements of *L. timidus* and *L. europaeus*. These characters, however, have proven to be not feasible and therefore dental characters are used for species distinction (Koby, 1959). Nonetheless, in the present study, we found that the olecranon of the ulna was useful for species distinction. They represent two morphotypes that were only found in layers with the one or the other species. In the mountain hare, the olecranon of the ulna is more slender and smaller than in the European hare (Fig. 5).

Genus *Oryctolagus* LILLJEBORG, 1873
Oryctolagus cuniculus (LINNÉ, 1758)

Material: sixty specimens of bones and teeth could be identified: one skull, two fragments of the skull, pre-/molars (two left, one right), upper jaws (three left), lower jaws (two left, four right), radii (two right), ulnae (two left), coxae (four left, four right), femora (two right), tibiae (two left, three right), calcanei (two left, three right), metacarpals (five left), and metatarsals (six left, ten right).

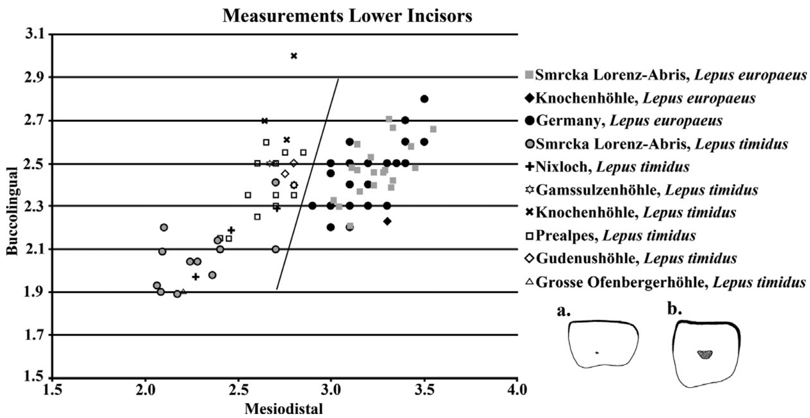

Fig. 3. Scatter-Plot of the measurements (in mm) from the lower incisors from *Lepus timidus* and *Lepus europaeus* from different localities: a, generalised cross section of a lower incisor of *Lepus europaeus*; b, generalised cross section of a lower incisor of *Lepus timidus*. (Redrawn after Koby, 1959).

Fig. 3. Diagramme de dispersion des mesures (en millimètres) sur les incisives inférieures de *Lepus timidus* et *Lepus europaeus* de différentes localités : a, coupe généralisée d'une incisive inférieure de *Lepus europaeus* ; b, coupe généralisée d'une incisive inférieure de *Lepus timidus*. (Redessiné d'après Koby, 1959).

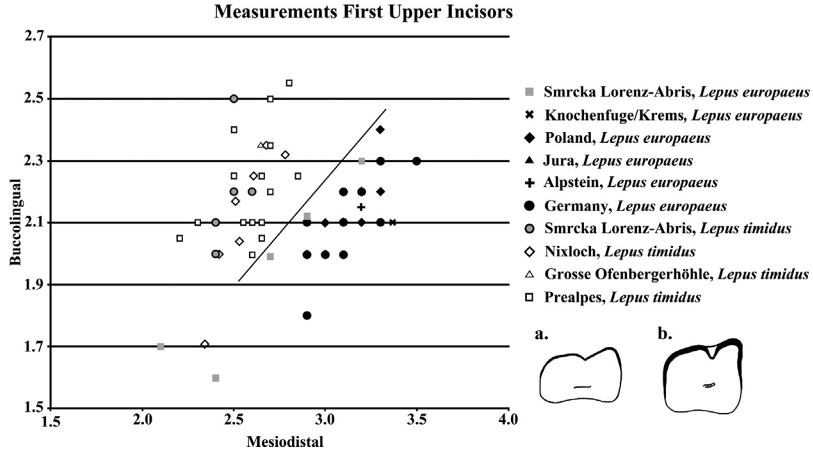

Fig. 4. Scatter-Plot of the measurements (in mm) from the first upper incisors from *Lepus timidus* and *Lepus europaeus* from different localities. The three specimens on the lower left part of the scatter-plot are from juvenile individuals: a, generalised cross section of an upper first incisor of *Lepus europaeus*; b, generalised cross section of an upper first incisor of *Lepus timidus*. (Redrawn after Koby, 1959).

Fig. 4. Diagramme de dispersion des mesures (en millimètres) sur des incisives supérieures de *Lepus timidus* et *Lepus europaeus* de différentes localités. Les trois spécimens de la partie inférieure gauche du diagramme de dispersion proviennent d'individus juvéniles : a, coupe généralisée d'une première incisive supérieure de *Lepus europaeus* ; b, coupe généralisée d'une première incisive supérieure de *Lepus timidus*. (Redessiné d'après Koby, 1959).

Inferred from the right mandibles, a minimum number of four individuals could be identified.

Taxonomy:

There are several diagnostic characters known to distinguish *Oryctolagus* from *Lepus*, apart from a generally smaller size. These have been extensively described by Callou (1997) and are only briefly presented here. Among other features, the skull of the European rabbit has, in general, a small sized choana, an os interparietale, a reduced protuberance occipital externa, a concave medio-caudal boarder of the parietal bone, a sphenoid crest, a slender and long maxillary palatine processus, a long processus temporalis. The foramen mentale in the lower jaw is rather big and the diastema is longer than in the hare. The upper incisors have a more roundish mesial lobe and, in the lower third premolar, the two anteroconids are about the same size and shape. There is a long processus hamatus on the acromion of the scapula and the tuberositas deltoidea of the humerus has an abrupt end. The radius is curved and the diaphysis of the ulna is continuous in thickness in cranial view. The foramen nutricium on the ilium is small. Also, the collum ossis femoralis is quite short in cranial view and the two tubercles which are forming the eminentia intercondylaris of the tibia are blunt.

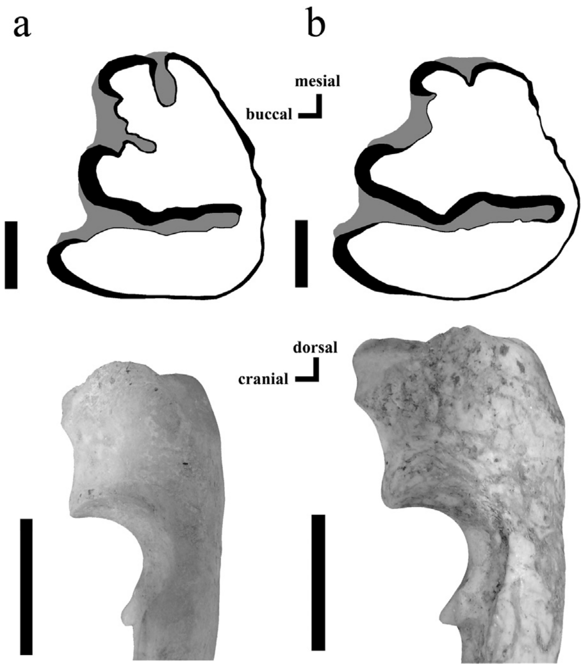

Fig. 5. Differences between the lower third molar and the ulna of *Lepus timidus* (a) and *Lepus europaeus* (b). a = cat. No. 7000/LB-41 (p3), cat. No. 7000/LB-131 (ulna); b = cat. No. 7000/LB-18 (p3), cat. No. 7000-LB-125 (both mirrored).

Fig. 5. Différences entre la troisième molaire inférieure et l'ulna de *Lepus timidus* (a) et *Lepus europaeus* (b). a = cat. n° 7000/LB-41 (p3), cat. n° 7000-LB-125 (les deux en miroir).

4. Discussion

4.1. The Smrcka Lorenz-Abris record

The archaeological site of Smrcka Lorenz-Abris yielded all three extant leporid species in succession, covering a time-span of about 14,000 years (Fig. 5). Radiocarbon dated bones at the bottom of Layer A allow us to propose a date for the replacement of the mountain hare by the spread of the European hare in the Alpine foreland. Findings of the European rabbit *O. cuniculus*, however, were uninformative. The stratigraphy of Layer A was partly disturbed and remains of the European rabbit were found in layers with stone tools (Neitz, 2013). This is likely an intrusion due to the behaviour of this animal. The European rabbit digs into the soil (e.g., Aulagnier et al., 2009) and, therefore, it is very probable that rabbit specimens are intrusive

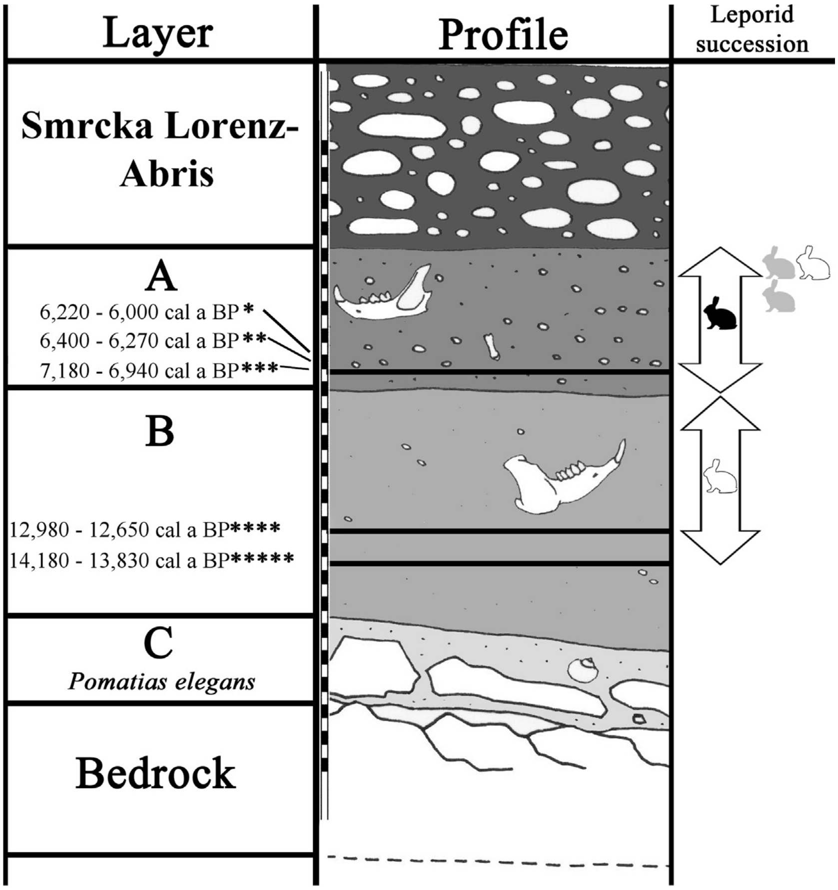

Fig. 6. Schematic profile of the Smrcka Lorenz-Abris with the dated bones shown. Horizontal bars are the depth in which the dated bones were found. The first three bars overlap in profile. The leporid succession is depicted on the right part of the figure. The white hare symbolizes *Lepus timidus*, the black one *Lepus europaeus* and the grey one *Oryctolagus cuniculus*. In Layer C a mass occurrence of *Pomatias elegans* (gastropod) was observed. Scale interval: 10 cm. *VERA-5724, **VERA-5512, ***VERA-5722, ****VERA-5511, *****VERA-5723.

Fig. 6. Profil schématique de Smrcka Lorenz-Abris montrant la situation des os datés. Les barres horizontales correspondent aux profondeurs auxquelles les os datés ont été trouvés. Les trois premières barres se recouvrent dans le profil. La succession des léporidés est figurée sur la partie droite de la figure. Le léporidé blanc symbolise *Lepus timidus*, le noir *Lepus europaeus* et le gris *Oryctolagus cuniculus*. Dans le niveau C, la présence en masse de *Pomalis elegans* (gastéropode) a été observée. Échelle d'intervalle : 10 cm. *VERA-5724, **VERA-5512, ***VERA-5722, ****VERA-5511, *****VERA-5723.

in older sediments and also caused disturbance of the sediments. Nevertheless, specimens of *O. cuniculus* were only found in the top half part of Layer A.

The European hare has been a natural member of the faunal community of Austria since the end of the Pleistocene (Spitzenberger, 2001). It is represented over the whole area of Layer A, which is also the artefact bearing layer. With the several dated bones from the bottom of Layer A, the establishment of *L. europaeus* as dominant species in this area very likely occurred around 7,000 a BP. In Austria in general, the European hare became widespread in the Late Atlantic (6,000–4,500 a BP) (Spitzenberger, 2001).

In Layer B, only one leporid species could be identified. This species is *Lepus timidus*, an animal which today lives in Austria only in the alpine regions (Fig. 1) (e.g., Alves and Hackländer, 2008; Spitzenberger, 2001). One lower jaw (7000/LB-41) of *L. timidus* was dated by radiocarbon (VERA-5723) to 14,180–13,830 cal a BP. This dated lower jaw is the youngest absolute age of *L. timidus* in the Vienna Basin at the end of the Pleistocene. The findings (two lower third premolars and one incisor) of *L. timidus* in the top part of Layer A can be a result of transport by humans, predators, or due to the activity of digging animals, thus indicating an allochthonous origin. In Austria, dated bones from sites in areas closer to or within the Alps, such as the Grosse Ofenbergerhöhle or the Knochenhöhle near Kapellen, show younger ages for *L. timidus* (Fladerer and Reiner, 1996b). These sites, however, are within the modern range of distribution of the mountain hare in Austria (IUCN, 2008) (Fig. 1).

The lowermost layer of the profile is Layer C, with 342 opercula of *Pomatias elegans* (Fig. 6). This layer is not dated and therefore every interpretation of the age of the remains of *P. elegans* is speculative. This snail, however, occurs only in warmer climates (Kerney et al., 1983) and has been found in undated fossil and subfossil sites in Austria (Edlinger, 1995; Klemm, 1974; Reischütz, 1993). Nowadays, this species is known only from one population in Austria, which has been introduced in modern times (Edlinger, 1995).

4.2. Environmental dynamics

During the end of the Pleistocene to the beginning of the Holocene, the temperatures began to rise to today's level (e.g. deMenocal, 2001). Within the Holocene, *Lepus europaeus* became dominant in the lower regions of Austria and *L. timidus* was pushed back to harsher refugia (Spitzenberger, 2001; Thulin, 2003). This species replacement event reflects the dynamics between concurring species. There are several reasons why the European hare could be so successful. In contrast to the mountain hare, this species is better adapted to the "artificial steppe" caused by agriculture. Therefore, the landscape change by Neolithic humans would favour the European hare (Spitzenberger, 2001; Thulin, 2003). Furthermore, competitive exclusion is also a reason why *L. europaeus* is more successful. In his review, Thulin (2003) shows how the European hare spreads while the distribution of the mountain hare declines in southern Sweden over a period of about 180 years. *L. europaeus* spread constantly from south to north after its introduction. In the beginning, a sympatric area where both species occurred could be identified, but after 1977, a strict separation in habitat was observed. This study was based on data from different authors (Gerell, 1977; Lönnberg, 1908; Nilsson, 1820; Thulin, 2000). Besides direct competition on the same food resource, other factors such as diseases and hybridisation could also have a more severe effect on the mountain hare than on the European hare (Thulin, 2003). The dominance of *L. timidus* throughout the cold periods of the Pleistocene can be attributed to the colder and harsher conditions of this time, since *L. europaeus* prefers more temperate conditions (Fig. 6) (Spitzenberger, 2001). During these cold periods *L. europaeus* survived in refugia in southern Europe (Fickel et al., 2008). The replacement of *L. timidus* at the end of the Pleistocene and the beginning of the Holocene is due to several different factors such as interspecific dynamics and climate change. No single cause, but rather a combination of different factors, has lead to the regional extinction of the mountain hare in areas such as the Vienna Basin.

5. Conclusion

The well-documented stratigraphy of the excavation at the Smrcka Lorenz-Abris as well as the well-preserved remains reflect the dynamics between concurring species at the end of the Pleistocene and within the Holocene. The European rabbit, the mountain hare, as well as the European hare are preserved in one locality and in a stratigraphic order. *Lepus europaeus* and *L. timidus* do not overlap in their stratigraphic range. This site has yielded the most recent fossil record so far of the mountain hare in the Vienna Basin, with an age of 14,180–13,830 cal a BP. The European hare became the dominant species in this area around 7,000 a BP. The record of *Oryctolagus cuniculus*, however, is not well resolved. Still, it is only found in the uppermost parts of the profile.

It seems that in warmer conditions, *L. timidus* is more likely to vanish from areas where *L. europaeus* is present due to interspecific competition, disease, hybridisation, and due to the impact of humans (Spitzenberger, 2001; Thulin, 2003). In general, the Austrian fossil and historical record of its three extant leporid species is patchy. The succession found during the excavation at Smrcka Lorenz-Abris is an important contribution to fill in the gaps in the record. Only further excavations will increase our understanding and knowledge of the complex picture of extinction and habitat occupation at the end of the Pleistocene and within the Holocene.

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