

MIDDLE PLEISTOCENE VOLES AND LEMMINGS (RODENTIA: ARVICOLINAE) FROM ZA HÁJOVNOU CAVE (JAVOŘÍČKO KARST)

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Abstract. Remains of fossil voles and lemmings (Arvicolinae) in two profiles in Za Hájojnou Cave, ZH P-2 (Komín I) and ZH P-8b (Narozeninová chodba, Area A), were preliminarily investigated. The assemblages from ZH P-2 layers 7 and 6 indicate Q3 biozone. Layer 7 may have been deposited during the lower part of the Saalian stage (probably MIS 8 and MIS 7) whereas layer 6 is also of the Saalian age but it originated later (probably MIS 6). The assemblage composition reflects the climatic inconsistency within layers 7 and 6, with a significant increase in number of elements typical for open dry environments, e.g. *Microtus (Stenocranius) gregalis*; however some other taxa indicating humid or warmer habitats nearby e.g. *Microtus (Pallasiinus) oeconomus* and *Clethrionomys glareolus*, were also reported. Although the voles in ZH P-8b, layers 2a, 2b and 2a, 2b (0–20 cm), belong to extant representatives, remains of Middle Pleistocene *Ursus cf. deningeri* enable assignment to Q3 biozone. We presuppose that layer 2a, 2b was deposited most probably within the upper part of the Holsteinian s.l. (probably MIS 9a). This assumption is supported not only by ²³⁰Th/U dating of slightly younger (267 ± 3 ka) sinter from the upper part of the equivalent layer 2a within ZH P-5 but also by the finding that layer 2a, 2b was deposited under relatively warm and humid climatic conditions in an open woodland environment which was documented by the presence of *C. glareolus* (total absence of lemmings), *M. (Stenocranius) gregalis* and *M. (Pallasiinus) oeconomus*. Overlying layers 1c(a) and 1c(b) were deposited most probably during a relatively warm period between the Middle and Late Pleistocene (Q3 or Q4 biozone). A more precise estimate of the biostratigraphical position of the deposits is impossible because of both the limited amount of fossil material available and gravitational redeposition during the Holocene.

■ Rodentia, biostratigraphy, palaeoecology, Za Hájojnou Cave, Javoříčko Karst, Moravia.

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Introduction

Rodents (Rodentia) are the most diverse order of mammals and have a worldwide distribution. Alongside the undeniable biostratigraphic significance (e.g. Nadachowski 1982, Fejfar and Heinrich 1990, Maul and Markova 2007, Minwer-Barakat et al. 2011) of many species, they also serve as good ecological, climatic and geographic indicators (Chaline and Brochet 1989, Escudé et al. 2013). A number of studies have also incorporated knowledge obtained from publications on their evolution (e.g. Horáček and Ložek 2004, Tougard and Renvoisé 2008). This is particularly valid for the voles and lemmings (Arvicolinae), the most progressive clade of the family Cricetidae (Wilson and Reeder 2005). Remains of small mammals are often found in cave sediments, sometimes in large quantities (Kowalski 1990).

Za Hájojnou Cave

Za Hájojnou Cave is situated on the southern slope of the Paní Hora hill in the valley of the Javoříčka stream. The entrance to the cave is located 20 m above the aforementioned

stream. A detailed description of the interior of the cave and the first description of cave deposits was published by Musil (2005). The studied samples of small mammals come from the profiles ZH P-2 (Komín I [= Chimney I]) and ZH P-8b (Narozeninová chodba [= Birthday Corridor], Area A).

ZH P-2 (Komín I): The whole profile is divided into eight layers, which are numbered in descending order from the base. Layer 8 situated at the base of the profile contains gravels of Culmian age. In layers 7a–7f silty-clayey and primarily non-calcareous deposits prevail. Layer 6, which was deposited after a hiatus, contains silty-clayey slightly calcareous sediment. Layer 5 also contains calcareous deposits which represent the end of sedimentation (Lisá 2005).

ZH P-8b (Narozeninová chodba, Area A): The studied part of ZH P-8b profile includes two layers opened during removal of sediment in the cross cutting of the Birthday Corridor. Both layers, layer 2a, 2b and 2a, 2b (0–20 cm) and layer 1c are virtually the same and contain a brown soil deposit almost without detrital limestone (Musil 2005). Within layer 1c a thin sinter layer is developed dividing layer 1c into 1c(b) and overlying 1c(a).

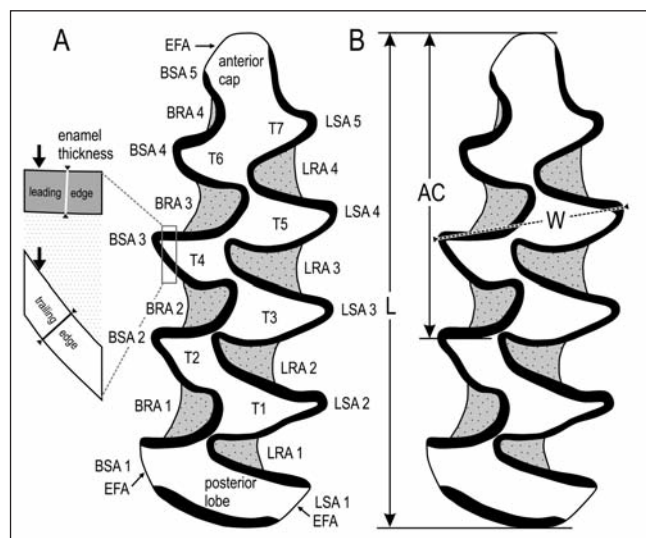
Material and methods

Samples of fossiliferous deposits were taken separately from each layer of section ZH P-2 (Komín I) and ZH P-8b (Narozeninová chodba, Area A). Water sieving on mesh (diameter 1 and 0.5 mm) was utilised with the assistance of a water pump (ROB II, 200W + pressure switch TR-1). Subsequently bones and teeth were separated out and put into self-sealing bags. Isolated molars, m1 and M3, were cleaned using an ultrasonic cleaner, UCC1, and their occlusal surfaces photographed using a Leica MZ16 with a digital camera, Leica DFC 480, 5 MP (Vöröš 2013).

The classification of higher taxonomical units is based on Wilson and Reeder (2005). Determination was essentially based on morphometric traits of the occlusal surfaces of m1 and M3 including e.g. shape of anteroconid complex (or posterior loop of M3), the presence/absence of cement in re-entrant angles (synclines), number of triangles (T1, T2, etc.) and enamel band thickness (Text-fig. 1A). For a detailed survey of these characters see Rabeder (1981), Boldrini (2008) and Cuenca-Bescós et al. (2010). Only m1 are discussed in detail in the systematic section.

Determination of fossil material was carried out using comparative material deposited in the Anthropos Institute, Moravian Museum, Brno as well as published sources (Nadachowski 1982, Musil 1988, Markova 1990, Maul et al. 2000, Anděra and Horáček 2005, Sesé and Villa 2008, Maul and Parfitt 2010).

Occlusal surfaces of molars of the most dominant taxa, i.e. *Microtus (Stenocranius) gregalis* (PALLAS, 1779) and *Microtus (Microtus) arvalis/agrestis* group (see Vöröš 2013), were measured according to a simplified version of Boldrini's method (2008). Molars were biometrically analysed using



Text-fig. 1. A – morphology of occlusal surface in *Microtus arvalis*: T1–7, triangle 1–7; BRA 1–4, buccal re-entrant angles (buccal synclines); BSA 1–5, buccal salient angle (buccal anticlines); LRA 1–4, lingual re-entrant angles (lingual synclines); LSA 1–5, lingual salient angle (lingual anticlines); EFA, enamel free area (modified according to Kalthoff et al. 2007, Cuenca-Bescós et al. 2010); B – measurements taken on the the occlusal surface of molar: L, total length; W, molar width (distance between apexes of T4 and T5); AC, anteroconid complex length + BRA 2 (Boldrini 2008, modified).

the tpsDig2 software and compared with published data (Nadachowski 1982, Maul et al. 1998, Kučera et al. 2009, Maul and Parfitt 2010).

The following biometric variables were measured on the molar occlusal surfaces (Text-fig. 1B): L tooth length; W – tooth width, i.e. distance between apexes of T4 and T5; AC – length of the anteroconid complex + BRA 2 (buccal re-entrant angle); AC/L index (relative length of the anteroconid complex + BRA 2). SDQ Index (quotient of enamel band differentiation) was calculated for m1 of *Arvicola* LACÉPÈDE, 1799 using Heinrich's method (1982, 1990). Measured values were processed in Microsoft Excel 2007 and STATISTICA version 9.1.

The biostratigraphic terminology used in this paper follows the terminology of Horáček and Ložek (1988).

All investigated material is deposited in the collections of the Anthropos Institute, Moravian Museum in Brno under collection numbers An 2/2013 and An 3/2013

Systematic palaeontology

Order **Rodentia** BODWICH, 1821

Family **Cricetidae** FISCHER, 1817

Subfamily **Arvicolinae** GRAY, 1821

Genus *Microtus* SCHRANK, 1798

Subgenus *Stenocranius* KASTSCHENKO, 1901

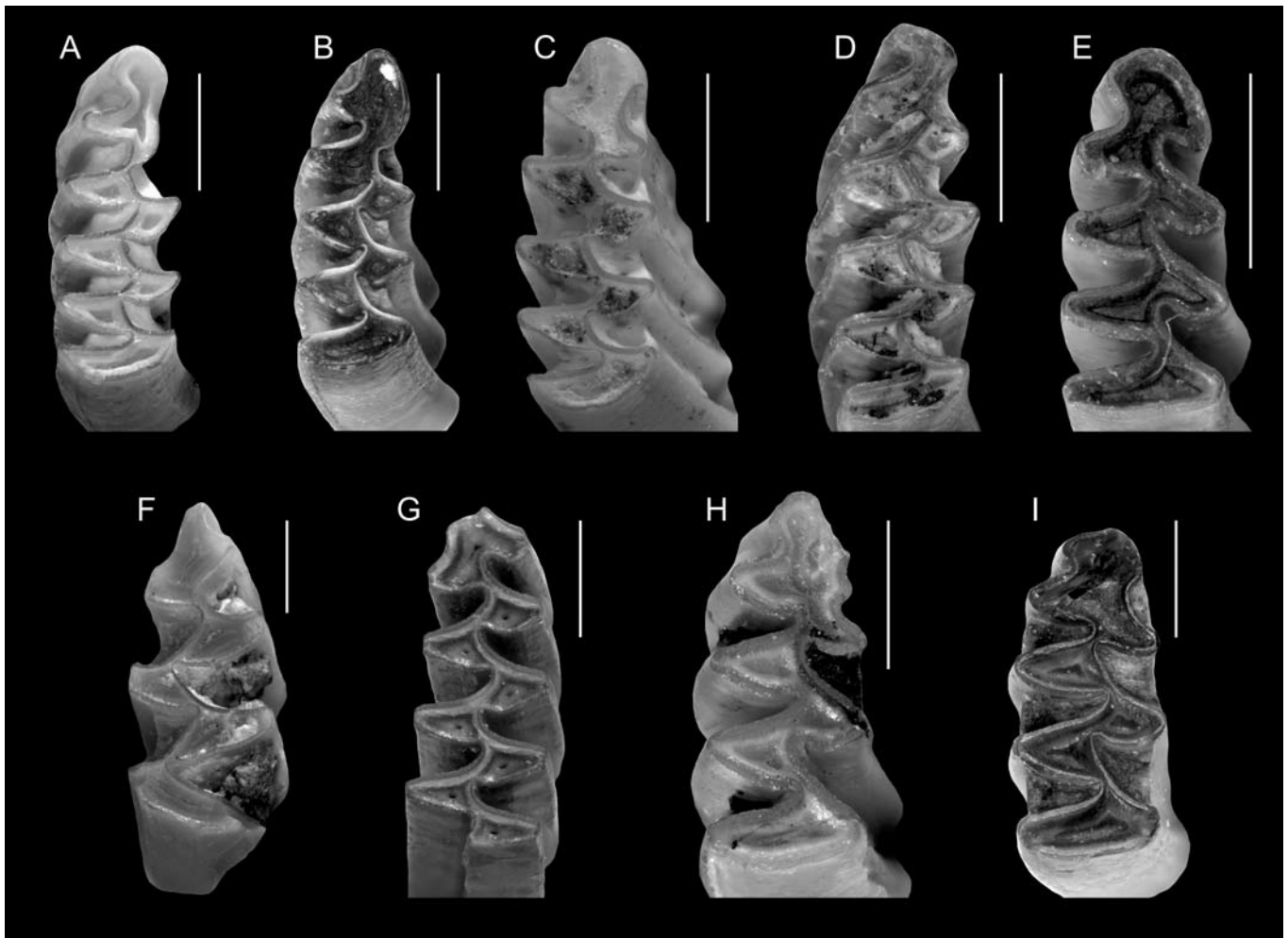
Microtus (Stenocranius) gregalis (PALLAS, 1779)

Material. Za Hájovnou Cave; ZH P-2 (Komín I): Layer 6a: 12× m1, 5× M3; layer 6ab: 15× m1, 5× M3; layer 6b: 4× m1, 1× M3; layer 7ab: 1× m1; layer 7cd: 6× m1; layer 7ef: 8× m1, 1× M3; ZH P-8b (Narozeninová chodba, Area A): Layer 1c(a): 5× m1, 2× M3; layer 1c(b): 1× m1, 1× M3; layer 2a, 2b (0–20 cm): 3× m1; layer 2a, 2b: 6× m1.

Description. m1 (Text-fig. 2A) – occlusal surface of rootless molar consists of five closed triangles (T1–T5) with cement in synclines. T2 and T4 are smaller in diameter than T1, T3 and T5. Apexes of T2 and T4 are pointed contrary to T1, T3 and T5. Enamel walls of the trailing edges are significantly thinner than leading edges. T6 is almost completely reduced but T7 is distinct and has a rounded apex producing a significant asymmetry in the anterior cap which is turned anteromedially.

Discussion. The prominent T7 together with reduced T6 produce a strong asymmetry of the anterior cap which is typical for m1 of modern *Microtus gregalis*. Moreover, no confluence between T4 and T5 (*Pitymys*-rhombus) was detected in the molars which is a typical character of the primitive *Microtus gregaloides* HINTON, 1923 (Kučera et al. 2009, Maul and Parfitt 2010).

The AC/L index was used to distinguish between modern and primitive phenotypes. The AC/L index value for the modern species *Microtus gregalis* is > 0.52 and for *M. gregaloides* ≤ 0.52 (Maul and Parfitt 2008). However, only in layer 2a, 2b (ZH P-8b) was the average value of the AC/L index lower (0.50; Vöröš 2013 – Appendix, Table 5), which



Text-fig. 2. m1 occlusal surfaces of arvicolines reported from Za Háčovnou Cave: A, *Microtus gregalis*, dext.; B, *Microtus oeconomus*, dext.; C, *Microtus arvalis/agrestis*, dext.; D, *Microtus* aff. “*coronensis*”, dext.; E, *Clethrionomys glareolus*, dext.; F, *Lemmus lemmus*, sin.; G, *Dicrostonyx* cf. *torquatus*, sin.; H, *Arvicola* cf. *cantiana*, dext.; I, *Arvicola terrestris*, dext. Scale bar equals 1 mm.

would not necessarily indicate a primitive phenotype *M. gregaloides*. Morphology of the m1 occlusal surfaces excluded an ancestral phenotype because BRA4 is not smooth and LRA4 is not greater than 90° which is typical for *M. gregaloides* (Maul and Parfitt 2010).

Fossil occurrences of the recent Palearctic species *Microtus gregalis* are known throughout a substantial part of Europe. In Central Europe this species appeared as early as the Middle Pleistocene (Toringian). According to Kowalski (2001) Biharian occurrences belong most probably to a more primitive phenotype *Microtus gregaloides* which probably evolved in eastern Europe from the ancestral form of the subgenus *Stenocranius*, i.e. *Microtus hintoni* KRETZOI, 1941.

Subgenus *Pallasinus* KRETZOI, 1964

Microtus (Pallasinus) oeconomus (PALLAS, 1776)

Material. Za Háčovnou Cave; ZH P-2 (Komin I): Layer 6a: 1× m1; layer 6ab: 3× m1, 2× M3; layer 7ab: 1× m1; layer 7cd: 1× m1; ZH P-8b (Narozeninová chodba, Area A): Layer 1c(a): 2× M3; layer 1c(b): 1× M3; layer 2a, 2b (0–20 cm): 2× m1, 1× M3; layer 2a, 2b: 2× m1, 2× M3.

Description. m1 (Text-fig. 2B) – occlusal surface of rootless molars have four closed triangles, larger T1 and T3 on the lingual side and smaller T2 and T4 on the buccal side, with the presence of cement in synclines. Syncline apexes (BRA 2, BRA 3) are pointed and inclined anteriorly. Apex of LSA2 is pointed and tips of all other anticlines are rounded. Enamel walls are well developed with leading edges slightly thicker than trailing edges. Only mesial margin of the anterior cap, a simple crescentic shape, is almost enamel free. T5 is strongly connected with the anterior cap and T6 is missing. LSA5 with a wide base reaches about half the height of other lingual anticlines.

Discussion. The typical m1 features of the subgenus *Pallasinus* are the presence of four closed triangles (T1–T4) and a broad conjunction of T5 with a simple crescentic anterior cap. The above mentioned features occur in *Microtus oeconomus*; however, the same pattern of occlusal surface was reported in the Early Pleistocene *Microtus eoratticeps* PAUNOVIC et RABEDER, 1996 morphotype from Deutsch Altenburg 2C1, Austria (Rabeder 1981) and *Microtus ‘ratticepoides’* HINTON, 1923 from several European early Middle Pleistocene localities (Maul et al. 1998, Maul and Parfitt 2010). The name *M. ‘ratticepoides’* is commonly used

for the primitive members of the *Pallasiinus* group (Maul and Parfitt 2010). The biometrical distinction between *M. oeconomus* and *M. 'ratticepoides'* is complicated because of much geographical variation. Although Recent *M. oeconomus* morphologically closely resemble early Middle Pleistocene *M. 'ratticepoides'* reported e.g. from the West Runton site, Norfolk, UK (possibly early part of MIS 17; Maul and Parfitt 2010), populations of the later species are characterised by m1 of distinctly smaller dimensions (m1 length: West Runton (n = 6): mean 2.34 mm, min. 2.17 mm, max. 2.57 mm; Přezletice (n = 4): mean 2.67 mm, min. 2.41 mm, max. 2.77 mm; Maul and Parfitt 2010) in contrast to Recent *M. oeconomus* (m1 length, Poland (n = 30): mean 2.98 mm, min. 2.74 mm, max. 3.37 mm; Nadachowski 1982). The m1 length of *M. oeconomus* from ZH P-2 and ZH P-8b (n = 3: mean 2.47 mm, min. 2.35 mm, max. 2.65 mm; Tab. 3) corresponds to that of the Middle Pleistocene populations reported from Boxgrove and Westbury-sub-Mendip, eastern England (Maul and Parfitt 2010) as well as from the Late Pleistocene (early Weichselian) locality of Burgtonna 2, Germany (n = 4: mean 2.47 mm, min. 2.27 mm, max. 2.74 mm; Nadachowski 1982, Maul et al. 1998).

Fossil representatives of extant *M. oeconomus* are largely known from the Middle and Late Pleistocene with the first Central European occurrence as early as MIS 16 or MIS 12 (Kučera et al. 2009). However, earlier occurrences concern most probably its generally smaller ancestor, *M. 'ratticepoides'* (= *Microtus (Pallasiinus) nivalinus* – sensu Nadachowski 1990) (Kowalski 2001, Maul and Markova 2007).

Subgenus *Microtus* SCHRANK, 1798

Microtus (Microtus) arvalis/agrestis species group

Material. Za Hájovnou Cave; ZH P-2 (Komín I): Layer 6a: 2× m1; layer 6ab: 3× m1, 1× M3; layer 6b: 1× m1, 1× M3; layer 7ab: 1× m1, 2× M3; layer 7cd: 3× m1, 3× M3; 7ef: 4× m1, 2× M3; ZH P-8b (Narozeninová chodba, Area A): Layer 1c(a): 12× m1, 11× M3; layer 1c(b): 3× M3; layer 2a, 2b (0–20 cm): 9× m1, 4× M3; layer 2a, 2b: 11× m1, 8× M3.

Description. **m1** (Text-fig. 2C) – occlusal surface of rootless molars consists of five closed triangles (T1, T3, T5 on lingual side and T2, T4 on buccal side) with a very slight confluence between T4 and T5. Buccal synclines are completely filled with the dentine while in lingual synclines cement reaches about 2/3 of their depth. Lingual triangles are slightly more elongated contrary to buccal triangles. Apexes of both anticlines and synclines are rounded. Enamel walls are well developed with leading edges distinctly thicker than trailing edges. The anterior cap is almost symmetrical, roughly bell-shaped, with well developed T6 and T7 which are situated opposite each other.

Discussion. It is very difficult to distinguish *Microtus arvalis* (PALLAS, 1778) from *M. agrestis* (LINNAEUS, 1761) in the fossil record on the basis of m1 or M3 because occlusal surfaces are morphologically very similar in both forms. The m1 of extant *M. arvalis* possesses rounded anticlines contrary to the usually sharp anticlines in *M.*

agrestis. However, this information is not sufficient for a more precise determination. Differentiation between the above mentioned two species can only be based on M2. These molars show a different number of triangles in the two species. *M. arvalis* has developed 4 triangles while 5 triangles are developed in *M. agrestis* (Anděra and Horáček 2005). Because M2 are absent in the fossil material we could only identify the present material as belonging to the *arvalis/agrestis* species group.

The m1 occlusal surface of the *arvalis/agrestis* group were biometrically analyzed. The AC/L index was used to distinguish between modern representatives of the *Microtus arvalis/agrestis* group from the more primitive *Microtus 'arvalinus'* HINTON, 1923. The value of the aforementioned index is < 0.52 for *Microtus 'arvalinus'* in contrast to the modern *Microtus arvalis/agrestis* species group where the AC/L index > 0.54 (Maul and Parfitt 2010). In all studied layers of ZH P-2 and ZH P-8b the average values of AC/L index were > 0.52 (Table 3). The forms corresponding to the diagnostic characteristics of '*arvalinus*', known e.g. in Dobrkovice 2 (Q3₁) or Stránská Skála (Q2) (Horáček, unpublished), exhibit on the occlusal surfaces more angular shaped synclines and differences in shape of the anterior cap from the above mentioned species. In Za Hájovnou Cave, the primitive form '*arvalinus*' was not recorded either according to morphological or biometrical criteria. As regards the first Central European occurrences of the *arvalis/agrestis* species group, the first *M. arvalis* is known from MIS 13 or 15 (Maul and Markova 2007) while the first distinct *M. agrestis* is of Saalian age (Kowalski 2001).

Genus *Microtus* SCHRANK, 1798

Microtus aff. '*coronensis*' KORMOS, 1933

Material. Za Hájovnou Cave; ZH P-8b (Narozeninová chodba, Area A): Layer 1c(a): 1× m1.

Description. **m1** (Text-fig. 2D) – a single rootless molar distinguished by a remarkable asymmetry of its anterior cap; it slightly resembles an inversed letter C with almost parallel branches of T7. The tooth bears six completely closed triangles (T1, T3, T5 on lingual side and T2, T4, T6 on buccal side). BRA 1 – BRA 3 are partially filled with cement but in the lingual synclines cement is present only on the apexes. The leading edges of the triangles are thicker than trailing edges. Buccal synclines are relatively shallow when compared to lingual synclines. Syncline apexes of BRA 1 – BRA 3 are strongly inclined anteriorly. All syncline apexes are in contact with the enamel walls of the opposite triangles.

Discussion. The very atypical shape of the anterior cap precludes identifying the form as any of the other species of *Microtus* appearing at the site. It either could represent an aberrant individual of *Microtus agrestis*, or more likely a separate species, possibly related to *Microtus coronensis* KORMOS, 1933, the form described from Q3 site Brassó and reported from several early Middle Pleistocene sites of Central Europe (Horáček in litt.).

Genus *Clethrionomys* TILESIIUS, 1850

Clethrionomys glareolus (SCHREBER, 1780)

Material. Za Hájovnou Cave; ZH P-2 (Komín I): Layer 6a: 1× m1; layer 7cd: 1× M3; 7ef: 1× m1; ZH P-8b (Narozeninová chodba, Area A): Layer 1c(a): 3× m1; layer 1c(b): 1× m1; layer 2a, 2b (0–20 cm): 1× m1, 2× M3; layer 2a, 2b: 1× m1.

Description. **m1** (Text-fig. 2E) – the examined teeth are rooted. The occlusal surfaces contain five triangles of which only two (T3, T4) are completely closed. Cement is present in the synclines only sporadically. The enamel walls are massively developed and there is no difference in enamel thickness between the leading and trailing edges. The only clearly visible reduction in the enamel wall thickness is seen on the mesial margin of the anterior cap. Axes of BSA 2 and BSA 3 are directed posterolaterally while all lingual anticlines are directed medially. The shape of the anterior cap is rounded with a distinct posterolaterally directed buccal projection.

M3 – cement is developed sporadically in the synclines. Triangles possess extremely thick enamel walls. The posterior loop is subcircular.

Discussion. Thick enamel walls, with weakly developed syncline cement and the typical shape of the anterior lobe together with moderate size of the teeth correspond relatively well to the conditions in *Clethrionomys glareolus*. This is valid also for one m1 (length: 2.15 mm) of a senile individual from layer 1c (b) in which the occlusal pattern is quite atypical (unusually waved, sometimes rectangular, syncline apices). *C. glareolus* is the dominant clade of the Pleistocene radiation, within which Kowalski (2001) also included the other medium-sized Early to Middle Pleistocene forms *C. hintonianus* KRETZOI, 1958, *C. acrorhiza* KORMOS, 1933 and *C. esperi* HELLER, 1930. Although it is difficult to distinguish between *C. hintonianus*, *C. acrorhiza*, and *C. glareolus* (Maul and Markova 2007), it is possible to distinguish between m1 of *C. hintonianus* from Recent and Late Pleistocene *C. glareolus* in that it has a very broad confluence between T4 and T5 (Maul and Parfitt 2010: 99, fig. 4a) if compared to *C. glareolus* (Bogičević et al. 2012: 89, fig. 8; Lenardić 2014).

Genus: *Lemmus* LINK, 1795

Lemmus lemmus (LINNEAUS, 1758)

Material. Za Hájovnou Cave; ZH P-2 (Komín I): Layer 6a: 1× m1; layer 6ab: 1× m1; layer 7ef: 1× m1.

Description. **m1** (Text-fig. 2F) – occlusal surface of rootless molar consists of three closed triangles with cement developed in synclines. T4 and T5 are largely confluent. Buccal triangles are smaller than lingual triangles. The thickness of the enamel walls is constant with the exception of enamel free areas in the trapezoidal anticline apices. Syncline apices are in contact with the bases of opposite triangles. The anterior cap is strongly reduced and forms only a small bump-like projection.

Discussion. The arrangement of triangles with EFA on the anticline apices and reduced bump-like anterior cap of m1 are typical for *Lemmus lemmus*. The first known European representatives of *Lemmus* were described as *Lemmus kowalskii* CARLS et RABEDER, 1988 from the Early Pleistocene of Schenfeld, Germany (Carls and Rabeder 1988, Kowalski 2001). This species was replaced in Central Europe by *Lemmus lemmus* during the early Middle Pleistocene with the last occurrence of *L. kowalskii* at Kozi Grzbiet ('Cromerian Interglacial II'). The first distinct *Lemmus lemmus* was reported from Kärlich G, Germany ('Cromerian Interglacial II') together with the oldest known *Arvicola* (Maul and Markova 2007).

Genus *Dicrostonyx* GLOGER, 1851

Dicrostonyx cf. torquatus (PALLAS, 1778)

Material. Za Hájovnou Cave; ZH P-2 (Komín I): Layer 6a: 1× m1; layer 6b: 1× m1; layer 7ab: 4× m1; layer 7cd: 1× m1.

Description. **m1** (Text-fig. 2G) – occlusal surface of rootless molar consists of 7 closed triangles with relatively narrow bases. No cement in the synclines. The buccal triangles are as large as the lingual triangles. Enamel walls are thinner on the anterior side of the triangles and thicker on the posterior sides. Enamel walls are reduced on the apices of anticlines. Anticline apices are trapezoidal in shape. Syncline apices are in contact with bases of the opposite triangles. The anterior cap is subtriangular and directed anterolaterally. The posterior loop was not preserved.

Discussion. The fragmentary m1 exhibits morphology which is typical for the genus *Dicrostonyx*: 1 – strongly reduced enamel walls on the apices of anticlines; 2 – absence of dental cement; 3 – subtriangular lobe. The oldest known species, *Dicrostonyx simplicior* FEJFAR, 1966 from the Late Biharian (Q2) of Koněprusy C718, the Czech Republic, is relatively typical due to the absence of bending of the mesial part of the anteroconid complex in m1 (Fejfar 1966, Kučera et al. 2009). The anteroconid complex is considerably more derived when compared to *D. simplicior* including forms from the Stránská skála-cave (Kučera et al. 2009). Nevertheless, triangle shape as well as differentiation of EFA in anticline apices indicates a distinctively more primitive condition in comparison with populations of Weichselian glaciation. As M2 have not been documented in the material from Za Hájovnou Cave, a more precise determination at the species level is indistinct and possible assignation to *D. gulielmi* (STANFORD, 1870) can not be excluded.

Genus *Arvicola* LACÉPÈDE, 1799

Arvicola cf. cantiana (HINTON, 1910)

Material. Za Hájovnou Cave; ZH P-2 (Komín I): Layer 6ab: 1× m1.

Description. **m1** (Text-fig. 2H) – the occlusal surface of the rootless molar is made up of three closed triangles, almost without syncline cement. The buccal

triangles are slightly smaller than the lingual triangles. The enamel wall is strongly developed with leading edges almost as thick as the trailing edges in each triangle. The anterior cap has developed a somewhat thinner enamel wall. Although the anterolateral margin of the anterior cap is damaged with an unpreserved enamel wall, the mesial margin can be recognised as rounded. The posterior loop possesses a thin enamel wand on the posterior edge of LSA1.

Discussion. The presence of a *Mimomys*-fold as well as relatively shallow BSA3 indicates rather primitive development of the anteroconid complex typical for *Arvicola cantiana* (= *A. mosbachensis* (SCHMIDTGEN, 1911) – sensu Rekovets et al. 2007, Maul et al. 2000). The enamel wall thickness of the only preserved m1 with SDQ index = 103.2 also corresponds to the extinct morphotype *Arvicola cantiana* (Heinrich 1990, Maul and Parfitt 2010) but this value falls within the m1 width variation of *Arvicola terrestris* (LINNAEUS, 1758) from the Late Pleistocene of Burgtonna 2, Germany (early Weichselian): SDQ (n = 64): mean 98.44, min. 76.0, max. 115.0 (Maul and Parfitt 2010). The use of SDQ index was recently questioned for specific determination of *Arvicola* populations (including biochronological framework) and it appears possible that all Pleistocene *Arvicola* populations may have belonged to a single species, *A. cantiana*, which shows great phenotypic variability (Escudé et al. 2008). Although the taxonomic status of the poorly preserved type material of *A. cantiana* is indistinct and some authors (Maul et al. 2000, Maul and Markova 2007, Minwer-Barakat et al. 2011) consider all described *A. cantiana*, with the only exception being the type material, as belonging to *A. mosbachensis*, we follow the detailed study of Escudé et al. (2008).

The first known *Arvicola*, probably derived from the *Mimomys* lineage (e.g. Fejfar and Heinrich 1990, Escudé et al. 2008), was reported from the beginning of the Toringian (Kowalski 2001). The earliest occurrence of *A. cantiana* (= *A. mosbachensis*), is known from German Kärlich G locality and dated as ‘Cromerian Interglacial III’ (Maul and Markova 2007).

Arvicola terrestris (LINNAEUS, 1758)

Material. Za Hájovnou Cave; ZH P-2 (Komín I): Layer 6ab: 2× M3; ZH P-8b (Narozeninová chodba, Area A): Layer 2a, 2b: 1× m1.

Description. **m1** (Text-fig. 2I) – occlusal surface of rootless molars consists of three closed triangles. Synclines are well filled with dental cement, almost reaching the anticline apices. Buccal triangles are somewhat smaller than lingual triangles. Apices of anticlines and synclines are rounded. Apices of BRA 1 and BRA 2 are inclined anteriorly. Trailing edges are thinner than leading edges. Mesial margin of the short anterior cap is rounded.

M3 – molar consists of two closed triangles with enamel wall of almost constant thickness. Synclines are filled with dental cement. The posterior loop is subcircular in shape.

Discussion. m1 has developed all the characters which in combination are typical for determination of this *Arvicola* species: 1 – short rounded anterior cap; 2 – number of triangles; 3 – absence of *Mimomys*-fold; 4 – very low SDQ index. Although the SDQ values show great

geographical, climatological and altitudinal variation (Escudé et al. 2008), the single measured m1 has a SDQ index (= 87.43) significantly below the typical values for *A. cantiana* (Cuenca-Bescós et al. 2010).

A. terrestris is one of the commonest Late Pleistocene (Eemian and Weichselian) rodents in Europe, with the earliest Central European occurrence in the early Weichselian (Kalthoff et al. 2007). In Eastern Europe *A. terrestris* appeared as early as the Eemian (Kowalski 2001, Maul and Markova 2007).

Biostratigraphy of studied sections in Za Hájovnou Cave

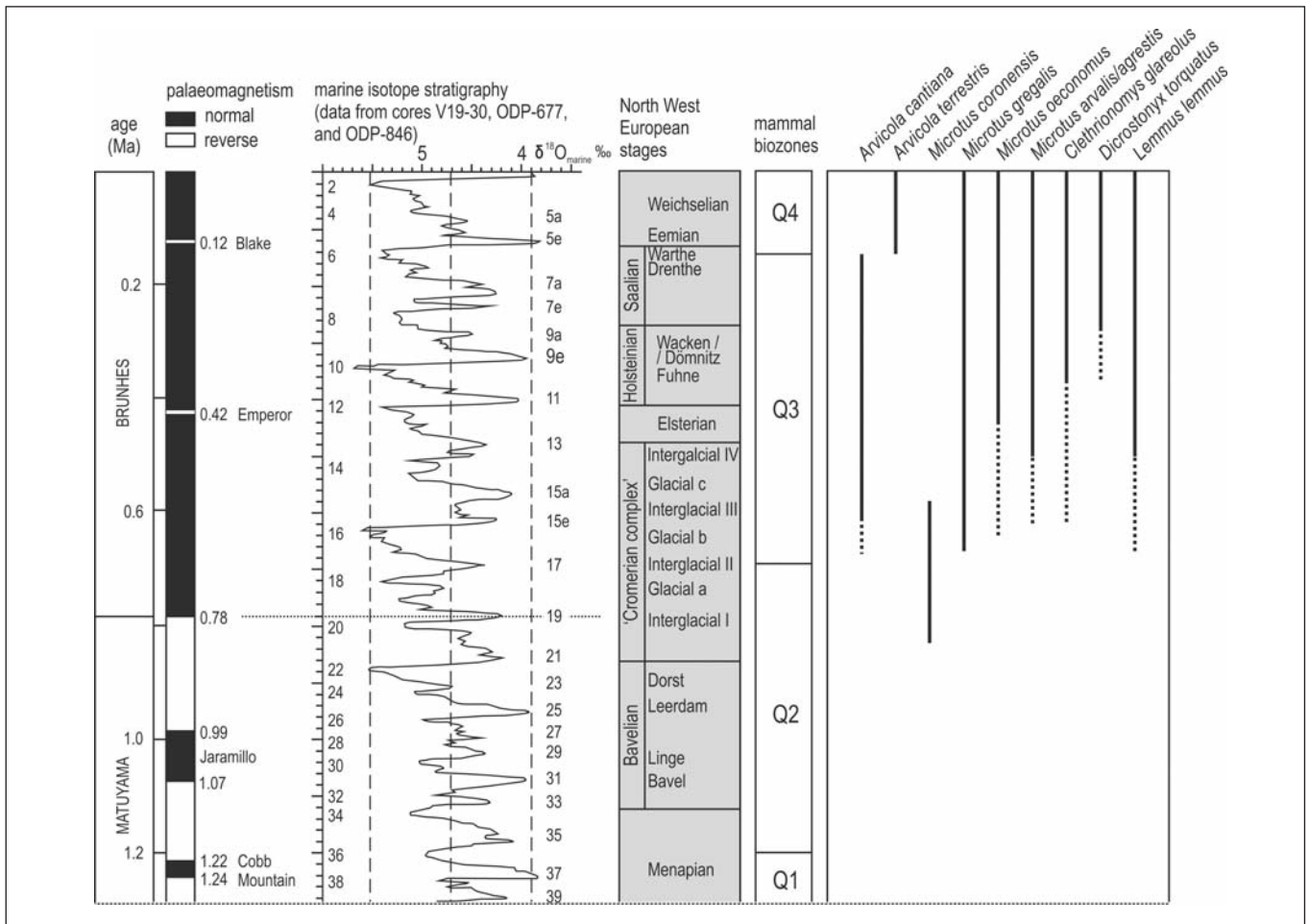
Arvicolinae assemblages reported from the ZH P-2 (Komín I) and ZH P-8b (Narozeninová chodba, Area A) are shown in Tables 1 and 2.

ZH P-2 (Komín I)

Layer 7ab: The following taxa have been reported from this layer occurring at the base of the gravels: *M. (Microtus) arvalis/agrestis*, *M. (Stenocranius) gregalis*, *M. (Pallasiinus) oeconomus* and *D. cf. torquatus*. The fossil record of the first three extant taxa dates back to the early Middle Pleistocene (Text-fig. 3). The earliest occurrence of *D. torquatus* (*D. gulielmi/torquatus* lineage – sensu Maul and Markova 2007) is presupposed to be in the Middle Pleistocene (MIS 10), with the first recorded occurrences in early Saalian MIS 8. Therefore, layer 7 deposits in ZH P-2 are most probably not of pre-Holstenian age (Text-fig. 3; Maul and Markova 2007). Although representatives of the *D. gulielmi/torquatus* lineage have been reported from numerous Central European localities until the Late Pleistocene, the m1 shows a distinctively more primitive condition in comparison with populations from Weichselian glaciation. Moreover, the layer undoubtedly corresponds with Q3 biozone (sensu Horáček and Ložek 1988) which is supported by the occurrence of the transitional form, *Arvicola cf. cantiana*, in the overlying layer 6ab. *A. cantiana* is only known from the Q3 biozone and this therefore excludes a Late Pleistocene age for the underlying layers. It is not possible to give a more precise age for layer 7ab but we presuppose that this layer could correspond to the cold Saalian MIS 8 rather than MIS 10.

Layer 7cd: Within this layer the assemblage composition is similar to the assemblage reported from the basal layer (Table 1). We presuppose this layer can be included in the Q3 biozone (Horáček and Ložek 1988).

Layer 7ef: also falls into the Q3 biozone because no taxa with different stratigraphical occurrence have been recorded. Although woodland *C. glareolus* appeared in Central Europe as far back as the early Holsteinian s.l. (= Holsteinian complex, MIS 9 and MIS 11 – sensu Dowling and Coxon 2001, Scourse 2006; see also Musil et al. 2014) with first presupposed occurrence in the “Cromerian Interglacial III” (Text-fig. 3; Maul and Markova 2007), we suggest that this layer could probably correspond to a warm period within Saalian MIS 7 rather than MIS 9. This assumption is partially supported by the presence of amphibians and reptiles (Ivanov



Text-fig. 3. Standard chronostratigraphy and biostratigraphical position of arvicolines reported from Za Hájovnou Cave. Standard chronostratigraphy modified according to Cohen and Gibbard 2011, Holsteinian s.l. sensu Dowling and Coxon (2001) and Scourse (2006). Stratigraphical range of voles and lemmings according to Kowalski (2001), Maul et al. (1998), Maul and Markova (2007) and Kučera et al. (2009).

Table 1. Voles and lemmings reported from ZH P-2 (Komín I). MNI – minimal number of individuals.

Taxon	ZH P-2 (Chimney I)						Total (MNI)
	6b	6ab	6a	7ef	7cd	7ab	
<i>Microtus (Stenocranius) gregalis</i>	3	10	9	5	4	1	32
<i>Microtus (Microtus) arvalis/agrestis</i>	2	1	2	3	3	1	12
<i>Microtus (Pallasinus) oeconomus</i>	0	2	1	0	1	1	5
<i>Clethrionomys glareolus</i>	0	0	1	1	0	0	2
<i>Lemmus lemmus</i>	0	1	1	0	0	0	2
<i>Dicrostonyx cf. torquatus</i>	1	0	1	0	0	3	5
<i>Arvicola cf. cantiana</i>	0	1	0	0	0	0	1

2005; see below) which are not as diverse as the abundant herpetofauna from nearby Mladeč 2 (MIS 9 according to Ivanov 2006), where typically interglacial representatives of *Elaphe longissima* (LAURENTI, 1768) were found in great number (Ivanov 2006, 2007).

Layer 6a: All reported taxa occurred from the Middle Pleistocene until the Holocene (Text-fig. 3). The presence of a sedimentary hiatus of unknown length between layer 7 and 6 (Musil 2005) and the occurrence of arctic *D. cf. torquatus* and *Lemmus lemmus* indicate possible deposition during one of the cold Saalian stages (probably MIS 6).

Layer 6ab: On the basis of the possible presence of *Arvicola cantiana*, which is restricted exclusively to the Middle Pleistocene (Maul et al. 2000), the layer was undoubtedly deposited within Q3 biozone and most probably during Q3₃ which corresponds to Saalian age.

Layer 6b: Although all three reported taxa *M. (Microtus) arvalis/agrestis*, *M. (Stenocranius) gregalis* and *D. cf. torquatus* occur in Q3–Q4 biozones, it is possible to consider layer 6b as corresponding to the Q3₃ biozone.

Earlier studies assumed that the age of layers 7 and 6 in ZH P-2 (Komín I) correspond with the Saalian up to the Weichselian glaciation (Musil 2005). On the basis of

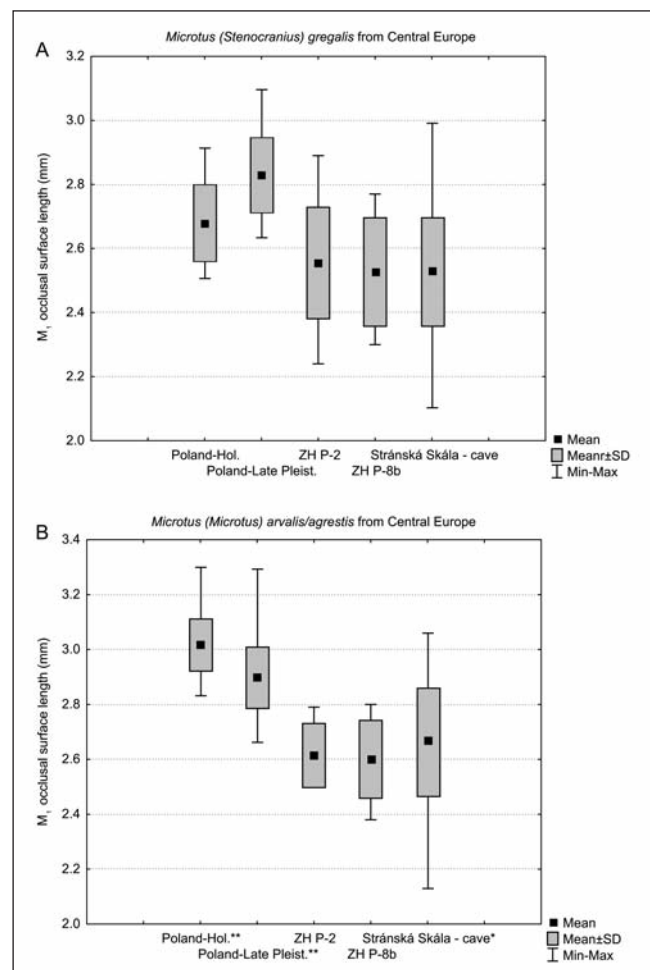
the vole and lemming assemblage composition we can confirm that layer 7 was deposited most probably within the Saalian complex (probably MIS 8 and MIS 7). Layer 6 also corresponds to Saalian age but is younger (probably MIS 6).

ZH P-8b (Narozeninová chodba, Area A)

Layer 2a, 2b and layer 2a, 2b (0–20 cm): Although most of representatives of rodent fauna reported from layer 2a, 2b including *M. (Microtus) arvalis/agrestis*, *M. (Microtus) gregalis*, *M. (Pallasiinus) oeconomus* and probably *C. glareolus* have been recorded in Central Europe from as early as the Cromerian complex (Maul and Markova 2007, Kučera et al. 2009), they are taxa which still inhabit the Central European region at the present time. *Arvicola terrestris*, known only from the Q4 biozone (Horáček and Ložek 1988) was also reported from the layer 2a, 2b. Although layer 2a, 2b in which remains of the Middle Pleistocene *Ursus cf. deningeri* REICHENAU, 1904 (Q2–3₂) were found is considered to be time analogous to layers 2a and 2b in Kostnice II (= Charnel-House II) (Musil 2005, Musil et al. 2014) we assume that layer 2a, 2b in ZH P-8b was contaminated by younger deposits. The earliest occurrence of *C. glareolus* postdates the earliest occurrence of *C. acrorhiza* and cannot be older than “Cromerian Interglacial III” (Maul and Markova 2007). Because the first distinct *C. glareolus* is known in Central Europe as early as MIS 10, the common occurrence with possible *U. cf. deningeri* (Musil et al. 2014) supports correlation with Holsteinian (s.l.) MIS 9 or early Saalian stage. ²³⁰Th/U dating (267 ± 3 ka) of the sinter from ZH P-5 developed in the upper part of the equivalent layer 2a in Kostnice II corresponds to MIS 8 (Lundberg et al. 2014). However, both the total absence of typically glacial arvicolid species (including lemmings) and pollen spectra indicating mild climate (with frequent tree elements including abundant *Carpinus*, *Tilia*, *Juglans* and *Quercus* and rare occurrence of *Pterocarya*) excludes cold climatic conditions typical for MIS 8 stage in layers 2a and 2b (Musil et al. 2014). Therefore, we consider the temperate climatic oscillation within layer 2a, 2b as most probably corresponding to MIS 9a substage of Holsteinian s.l.

Layer 1c(b) and 1c(a): The appearance of *M. (Microtus) arvalis/agrestis*, *M. (Stenocranius) gregalis* and *C. glareolus* indicates the Q3 or Q4 biozone. Although biometrical studies of the m1 occlusal surface of *M. (Stenocranius) gregalis* and *M. (Microtus) arvalis/agrestis* are in accordance with studies reported from the early Middle Pleistocene Stránská Skála-cave (probably MIS 16 or MIS 12; Kučera et al. 2009) we cannot distinguish a more precise age for layer 1c. The common occurrence of *Ursus spelaeus* in layer 1c, indicating Saalian or Late Pleistocene rather than Holsteinian age, together with unusual find of an ancient vole, *M. aff. ‘coronensis’*, known from late Q2 and early Q3 localities, is most probably a result of Holocene gravitational redeposition. Extensive gravitational redeposition of layer 1c was also documented by the character of the deposits (Lundberg et al. 2014).

Biometrical measurements: From the range of measurements of m1 occlusal surface length in *M. (Stenocranius)*



Text-fig. 4. Occlusal surface length (m1) of *Microtus* from Central European Pleistocene and Holocene: A, *Microtus (Stenocranius) gregalis*: Poland-Hol. (n = 20), Poland-Late Pleist. (Early Pleniglacial) (n = 30), ZH P-2 (n = 23), ZH P-8b (n = 9), Stránská Skála-cave (n = 179). B, *Microtus (Microtus) arvalis/agrestis*: Poland-Holocene (n = 20), Poland-Late Pleistocene (Early Pleniglacial) (n = 20), ZH P-2 (n = 5), ZH P-8b (n = 11), Stránská Skála-cave (n = 49). *, results based on *Microtus arvalis*; **, results based on *Microtus (Microtus) cf. agrestis*. Data from Poland according to Nadachowski (1982), data from Stránská skála- cave according to Kučera et al. (2009).

gregalis and *M. (Microtus) arvalis/agrestis* group (Table 3, Text-figs 4A, B), the average dimensions of molars of both taxa from the ZH P-2 (Komín I) and ZH P-8b (Narozeninová chodba, Area A) are generally less than for molars from the Polish Late Pleistocene and Holocene although the range of measurements for each dimension are at least partially overlapping (Fig. 4A, B). The length of the m1 occlusal surfaces from ZH P-2 and ZH P-8b correspond with molars from Stránská Skála-cave (early Middle Pleistocene, probably MIS 16 or MIS 12; Kučera et al. 2009). However, average values for the AC/L index are distinctly higher when compared to values from Stránská Skála-cave (Kučera et al. 2009, tab. 3 and 4).

The AC/L index for *M. (Stenocranius) gregalis* corresponds to values from the Late Pleistocene (Weichselian glaciation) populations reported from Javoříčko Karst (Kučera et al. 2009, tab. 7). Although biometrical measurements of m1

Table 2. Voles reported from ZH P-8b (Narozeninová chodba, Area A). MNI – minimal number of individuals.

Taxon	ZH P-8b (Birthday Corridor, area A)				Total (MNI)
	1c(a)	1c(b)	2a, 2b (0-20 cm)	2a, 2b	
<i>Microtus (Stenocranius) gregalis</i>	4	1	3	5	13
<i>Microtus (Pallasiinus) oeconomus</i>	0	0	2	1	3
<i>Microtus arvalis/agrestis</i>	6	0	5	9	20
<i>Microtus</i> aff. 'coronensis'	1	0	0	0	1
<i>Clethrionomys glareolus</i>	3	1	1	1	6
<i>Arvicola terrestris</i>	0	0	0	1	1

show a progressive increase in size over the period from the Middle to Late Pleistocene, and arvicoline molars from Za Hájovnou Cave correspond to a Middle Pleistocene rather than a Late Pleistocene age of deposits. This assumption cannot be supported without more detailed biometrical analysis of a larger sample of fossil material.

AC/L indexes (Table 3) of the two above mentioned taxa showed no trend in the development of this character within the different layers of the studied profiles (ZH P-2, ZH P-8b). Morphotypes *M. gregaloides*, *arvaloides* and 'arvalinus', from the beginning of the early Middle Pleistocene, cannot be distinguished either morphologically or by the AC/L index.

Palaeoecological evaluation of arvicolid assemblages from the Za Hájovnou Cave

ZH P-2 (Komín I)

The observed fauna of voles and lemmings from the different layers, 7ab, 7cd, 7ef and 6a, 6ab, 6b in ZH P-2 (Komín I) profile is of a variable composition (Table 1). In all layers of the Komín I profile, the most dominant species is *M. (Stenocranius) gregalis* whose appearance in glacial communities correlates positively with the occurrence of glacial species *D. cf. torquatus* and *L. lemmus* (Horáček and Ložek 1988).

As reflected by the abundance (MNI) of climatically significant taxa, the occurrence of *D. cf. torquatus*, inhabiting mainly polar and subarctic tundra (Hokr 1951, Anděra 1999), is not accompanied by any thermophilic species in layer 7ab (Table 1). This layer (7ab) probably deposited during the outgoing cold climatic cycle, and the occurrence of *M. (Pallasiinus) oeconomus* indicates the nearby presence of humid habitats (Hokr 1951, Pelikán et al. 1979).

In layer 7cd the absence of *D. cf. torquatus* is accompanied by a significant increase in the number of *M. (Stenocranius) gregalis* individuals (Table 1), the presence of which indicates an open steppe environment (Hokr 1951). The presence of *M. (Pallasiinus) oeconomus* indicates isolated marshy habitats in the close vicinity. In the overlying layer 7ef, the increasing influence of a dry steppe environment is documented by the higher number of *M. (Stenocranius) gregalis* individuals. This environment was not as cold as in layer 7ab which is reflected in the absence of arctic species and presence of *C. glareolus* which occupied isolated forested habitats (Anděra 1999). This assumption supports the finding of

an amphibian and reptile assemblage including *Bufo viridis* LAURENTI, 1768, *Lacerta* cf. *agilis* LINNAEUS, 1758, *Coronella austriaca* LAURENTI, 1768 and numerous *Vipera berus* (LINNAEUS, 1758) in the surroundings of layer 7 (Ivanov 2005) which could be a time equivalent of the upper part of layer 7 (probably 7ef).

Layer 6, which was deposited after a sedimentary hiatus (Musil 2005, 2014) is typical with remarkable increase in relatively cold steppe environment. This trend culminated during the deposition of layer 6ab but the presence of *M. (Pallasiinus) oeconomus* also indicates open damp biotopes. The upper part of the studied section (layer 6b) is marked by a sharp decline in the proportion of *M. (Stenocranius) gregalis* and the absence of thermophilic elements as well as elements indicating wet habitats. It is also supported by the presence of *D. cf. torquatus*. No remains of amphibians or reptiles have been reported from this layer.

ZH P-8b (Narozeninová chodba, Area A)

In both studied layers (2a, 2b and 1c(a)) representatives (MNI) of the *M. (Microtus) arvalis/agrestis* group, which prevail especially in the temperate interstadial sections of glacial period (Horáček and Ložek 1988), are the most widely represented taxon.

Although *C. glareolus* is present in layers 2a, 2b and 1c(a), 1c(b) the relatively high number of *M. (Stenocranius) gregalis* indicates the presence of open biotopes. Occurrences of *C. glareolus* and *M. (Microtus) arvalis/agrestis* group in both layers are not accompanied by glacial species typical for tundra environment such as *D. torquatus* or *Chionomys nivalis* (MARTINS, 1842) (Table 2). Moreover, remains of several bones of the eurythermic viper *V. berus* have been reported from layer 2a, 2b (Ivanov 2005). Therefore, we can assume that the layers 2a, 2b and 1c(a), 1c(b) did not originate under cold glacial conditions. The occurrence of *M. (Pallasiinus) oeconomus* and *A. terrestris* in the layer 2a, 2b (Table 2) document damp biotopes in the vicinity (Hokr 1951, Pelikán et al. 1979). Taxa typical for a damp environment are completely absent in layer 1c(a) and 1c(b) but palaeoecological conclusions will be affected by Holocene gravitational shifting of layer 1c.

Palynological study indicates that layer 2a, 2b was deposited during a relatively warm period. This statement is supported by the composition of palynospectra within layer 2a, 2b (Doláková 2014). Besides pollen of pine (*Pinus*) and spruce (*Picea*) also the presence of hazel (*Corylus*), linden (*Tilia*), hornbeam (*Carpinus*), maple

Table 3. Biometric characteristics of m1 (in mm) of *Microtus (Stenocranius) gregalis*, *Microtus (Microtus) arvalis/agrestis* and *Microtus (Pallasiiinus) oeconomus* from ZH P-2 (Komín I) and ZH P-8b (Narozeninová chodba, Area A). Abbreviations: AVG, mean; min, max, range; VAR, variance; SD, standard deviation; CV, coefficient of variance; skew, skewness; kurt, kurtosis. For variable abbreviations see Text-fig. 1.

Microtus (Stenocranius) gregalis

ZH P-2	n	AVG	min	max	VAR	SD	CV	skew	kurt
L	23	2.55	2.24	2.89	0.0303	0.174	0.068	0.390	-0.641
W	23	0.87	0.81	1.01	0.0030	0.055	0.063	0.892	0.365
AC	23	1.20	1.00	1.42	0.0089	0.094	0.079	0.577	0.793
AC/L	23	0.53	0.46	0.56	0.0005	0.022	0.042	-1.628	4.448

ZH P-8b	n	AVG	min	max	VAR	SD	CV	skew	kurt
L	9	2.53	2.30	2.77	0.0287	0.169	0.067	0.020	-1.426
W	9	0.81	0.77	0.86	0.0010	0.032	0.039	-0.100	-1.113
AC	9	1.21	1.09	1.48	0.0152	0.123	0.101	1.349	1.941
AC/L	9	0.52	0.44	0.54	0.0010	0.032	0.062	-2.529	6.832

Microtus (Microtus) arvalis/agrestis

ZH P-2	n	AVG	min	max	VAR	SD	CV	skew	kurt
L	5	2.61	2.50	2.79	0.0136	0.117	0.045	0.957	-0.114
W	5	0.87	0.77	0.94	0.0045	0.067	0.077	-1.025	0.579
AC	5	1.20	1.15	1.27	0.0020	0.044	0.037	0.552	0.868
AC/L	5	0.54	0.52	0.59	0.0008	0.028	0.051	2.196	4.855

ZH P-8b	n	AVG	min	max	VAR	SD	CV	skew	kurt
L	11	2.60	2.38	2.80	0.0202	0.142	0.055	0.001	-1.254
W	11	0.88	0.83	0.93	0.0009	0.031	0.035	0.550	-0.412
AC	11	1.22	1.09	1.43	0.0108	0.104	0.085	0.883	0.372
AC/L	11	0.53	0.49	0.55	0.0005	0.022	0.041	-1.281	0.631

Microtus (Pallasiiinus) oeconomus

	ZH P-2			ZH P-8b		
L	2.4			2.65	2.35	
W	0.98	0.87	0.87	0.92	0.82	0.98
AC	1.22			1.34	1.26	
AC/L	0.492			0.494	0.464	

(*Acer*) and occasionally ivy (*Hedera*) was reported. A rare finding of pollen grains of the genus *Pterocarya* confirmed the deposition of sediments within the Holsteinian s.l. (Doláková 2005). In this context the very limited composition of the herpetofaunal assemblage with no thermophilic taxa is interesting.

Conclusions

Fossil assemblages of voles and lemmings (Arvicolinae) in two profiles in the Za Hájojnou Cave including ZH P-2 (Komín I) and ZH P-8b (Narozeninová chodba, Area A) were preliminarily investigated. The study of dental material enabled us to precise both the biostratigraphical position of selected layers in ZH P-2 and ZH P-8b and palaeoenvironmental conditions of the studied localities:

1) The biostratigraphical position of layers 7 and 6 (ZH P-2, Komín I) corresponds to the Q3 biozone. Deposits of layer 7 correspond to the lower part of the Saalian stage (probably MIS 8 and MIS 7) whereas layer 6 is younger. The Middle Pleistocene age of layers 7 and 6 is partially supported by the biometrical analysis of m1 in *M. (Stenocranius) gregalis* and *M. (Microtus) arvalis/agrestis* species group.

2) The assemblage composition within the ZH P-2 profile reflects the climatic inconsistency within layers 7 and 6, with a significant increase in elements typical for open dry environments, *M. (Stenocranius) gregalis*, and also the presence of elements indicating nearby humid or warmer habitats including *M. (Pallasiiinus) oeconomus* and *C. glareolus*.

3) Although all voles within layers 2a, 2b and 2a, 2b (0–20 cm) in ZH P-8b belong to extant representatives, the assignment to Q3 biozone is supported by the numerous remains of Middle Pleistocene *Ursus cf. deningeri*. It can be assumed that layer 2a, 2b was deposited during MIS 9 (most probably MIS 9a) within the upper part of the Holsteinian s.l. This assumption is supported not only by ²³⁰Th/U dating of slightly younger (267 ± 3 ka) sinter from the upper part of the equivalent layer 2a within ZH P-5 but also by the finding that layer 2a, 2b was deposited under relatively warm and humid climatic conditions in an open woodland environment. This environment was documented by the presence of *C. glareolus* (absence of lemmings) and the presence of *M. (Stenocranius) gregalis* and *M. (Pallasiiinus) oeconomus*. The unusual occurrence of *A. terrestris* (known only from the Q4 biozone) may represent partial contamination by younger deposits.

4) The overlying layer 1c, in which a thin sinter layer occurs between layer 1c(a) and 1c(b), most probably originated during a warm period between the Middle and Late Pleistocene (Q3 or Q4 biozone). However, a more precise biostratigraphic position as well as palaeoecological evaluation of the vole assemblage is uncertain because of both the limited amount of fossil material and gravitational redeposition during the Holocene.

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