

Cricetinae in the Quaternary fossil record of the Czech Republic and Slovakia (Rodentia: Cricetidae)

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Abstract. The paper surveys the Quaternary (MN17–Q4) fossil record of Cricetinae in the Czech Republic and Slovakia with particular attention to the current glacial cycle (Q4: Vistulian–Holocene) and immediate history of extant taxa. Vast majority of records were reexamined using standardized techniques of morphometric analysis (in total 625 molars of *Cricetus*, 805 molars of small hamsters). *Cricetus cricetus*, recorded in 130 Q4 fossil communities, exhibits almost continuous appearance since the beginning of Vistulian, possibly with considerable range regressions during LGM and middle Holocene. It was recorded also in 27 Early Pleistocene (MN17–Q2) and 6 Middle Pleistocene (Q3) assemblages, with a small-sized form (*Cricetus cricetus nanus*) in MN17–Q1 stage and a mosaic of Q2–Q3 records exhibiting mostly excessively large size (*C. c. runtonensis*), similarly as the Vistulian items which are clearly larger than those of the post-LGM and early Holocene age. The appearance of hamster in fossil record shows a mosaic character suggesting temporal spatial and abundance fluctuations: in most sites it absents and in general, it appears as a rather rare sub-recedent element (in Q4 communities with overall dominance of mere 0.55% and this is valid also for its appearance in Early and Middle Pleistocene assemblages). Small hamsters arranged here in the genus *Cricetulus* (incl. *Allocricetus*) represent a constant element of the Early and Middle Pleistocene assemblages (43 sites in the Czech Republic and Slovakia). The items of Q4 record (21 communities) clearly differ from the Early to Middle Pleistocene form *Cricetulus bursae* by a consistently smaller size corresponding to extant species *Cricetulus migratorius*. The gap is quite distinct conforming even to the possible extinction of *C. bursae* during the Eemian interglacial followed by early Vistulian expansion of the extant species from its Asiatic range suggested by molecular phylogeography. We examined a question of possible appearance of *Phodopus* among the Q4 record of small hamsters, yet in our material, we did not succeed to confirm it.

Key words. Hamsters, phylogeny, biogeography, Pleistocene, Holocene.

INTRODUCTION

The dramatic rearrangements in setting of diverse biotic and abiotic factors accompanying the periodic alternation of glacial and interglacial periods of the Quaternary past represent key factors modulating the history of all taxa composing fauna of Central Europe. Thus the fossil record from diverse stages of the Quaternary can become an essential source for understanding the past of individual species of the present-day Central European fauna and the historical causes of their range dynamics and adaptive strategies (VON KOENIGSWALD 2003). Such information can

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be of essential importance also in conservation regards, particularly in the case of rare elements with discontinuous islet-like distribution and fluctuating range dynamics. The common hamster (*Cricetus cricetus*, one of the most popular European mammals, can serve as a pertinent example.

The common hamster (*Cricetus cricetus*) is the largest and currently the only Central European representative of the subfamily Cricetinae covering 18 species of seven genera distributed throughout most of the Palearctic region (WILSON & REEDER 2005). To some extent, it is also one of the best-studied mammals in Europe (cf. KRYŠTUFEK et al. 2020), and is now receiving concentrated attention, especially in Western Europe, where, due to its relict occurrence, it is considered one of the rarest and most endangered mammals in Europe.

However, this characteristic does not apply to most of the species range. A recent summary of the knowledge on this species (KRYŠTUFEK et al. 2020) shows that the hamster inhabits a large range extending from western Europe to central Siberia, ranging from 42 to 55° N latitude. It is a typical inhabitant of steppe open formations but also penetrates semi-open warmer habitats, including habitats of purely anthropogenic origin (fields, outskirts of human settlements). To survive the pronounced seasonality of the continental climate, it possesses a highly developed ability to hibernate. The average population density in a continuously populated area is 8.5–16.8 individuals/ha (i.e. an order of magnitude lower than that of the dominant forms of small land mammals). Periodically, however, once every 2–11 years there are significant abundance cycles, synchronized over areas of thousands of km², during which population densities can reach values of up to 880 burrows/ha (i.e. more than 1000 individuals/ha). Similar characteristics were pertinent also for the Czech Republic and Slovakia, where in the long term perspective the hamster was distributed almost continuously in most areas of the lowland and hilly stage (GRULICH 1975, VOHRALÍK & ANDĚRA 1976). However, at present, a more continuous occurrence is limited only to the Polabí and Poohří lowland basins and the Moravian lowlands, with insular occurrences in several other areas, especially in southern Bohemia – recent occurrence was confirmed only in 19% of the Czech Republic area (ANDĚRA & GAISLER 2012).

The genetic structure and history of the current hamster range have been the subject of a series of molecular phylogeographic analyses taking into account both the western part of the range (NEUMANN et al. 2005, 2006) and conditions in the eastern European part, including complex palaeobiogeographic scenarios (FEOKTISTOVA et al. 2017). The phylogeographic analyses show a compact cluster of interrelated populations in the eastern part of the range (referred to as the eastern lineage – E) and a specific situation in the European part of the range: a deeply separated group of Pannonian populations with two distinct haplotypes, P1 and P2, and a group of northwestern populations and lineage C widespread in northern Germany and lineage W, which includes insular occurrences in western Germany, France, Belgium, and the Netherlands. The Slovakian population and the population from Bohemia belong to the Pannonian lineage P1. The boundaries of this haplotype and barriers to its spread were the mountain ranges of the Western Carpathians and the peripheral mountains of the Bohemian Massif. The northwestern populations (C-W), which have a significantly reduced level of genetic diversity compared to the Pannonian lineage and Eastern European populations, show clear relationships with E1 populations. Divergence of the northwestern lineage and E1 is dated by molecular clock techniques to the range of 37–64 ka, and divergence between the Pannonian P1 and P2 groups to 25–44 ka. The northwestern and Pannonian lineages are separated by a relatively deep divergence dated at 85–147 ka (Eemian interglacial). The study by FEOKTISTOVA et al. (2017) confirms these conclusions, emphasizing the basal position of the Pannonian lineage and the divergence of the western populations of the eastern lineage (E1: Poland-Ukraine) and the specific situation at

the southern margins of the eastern European range. It is also reminiscent of the fossil records in southern France, Italy, and Croatia dated to the beginning of the Last Glacial (MIS5–4) indicating the extension of the range into the northern Mediterranean in that section.

A comprehensive overview of the European rodent fossil record by KOWALSKI (2001) reports the genus *Cricetus* from a total of 223 Quaternary sites in most European countries (11 MN17, 38 Q1, 27 Q2, 63 Q3, 84 Q4), of which 84 records come from the present cycle (mostly the late glacial-early Holocene). Further, it suggests that all European Quaternary records are part of a monotypic evolutionary lineage currently represented by the extant species *Cricetus cricetus*. Yet, such a concept conforming to the neontological point of view is quite exceptional in palaeontological literature. The search for stratigraphically defined chronotaxa leads here to recurrent debates about the substantive validity of individual fossil taxa formally described within the genus, which make the issue of the history of the genus and the stratigraphic distribution of the clade extremely opaque (KRYŠTUFEK et al. 2020).

The first formally distinguished fossil form is *Cricetus frumentarius major* Woldřich, 1880, described in the first volume of WOLDŘICH's (1880) monograph on the glacial fauna of Sudslavice by reference to an extremely large skull (greatest skull length 53 mm, length of M₁–M₃ 10.1 and 9.8 mm) from the Výpustek Cave in the Moravian Karst in a reference by LIEBE (1879). Another form with analogous size differences to the Recent species is described 29 years later as *Cricetus vulgaris Runtonensis* Newton, 1909 from the classic site of the Cromerian fauna "Upper Freshwater Bed of the Norfolk Forest Bed series at West Runton", based on the maxilla (length of M¹–M³ 9.3 mm). NEWTON (1909) points to differences in the mesial part of M¹ (constricted at the *major*), but the main argument for the distinctiveness of the two forms is the different stratigraphic ages: "If the 'Forest Bed' specimens were of the same age as those described by Dr. WOLDŘICH, one would have little hesitation in referring them provisionally to the same subspecies; but the evidence in favor of these Norfolk deposits being of Pliocene age is becoming stronger." (NEWTON 1909).

The key survey of the topics by SCHAUB (1930) confirmed the differences of the above-mentioned forms from the Recent populations of *Cricetus cricetus*, but at the same time emphasized the homogeneity in the basic morphological characters and classifies these forms as fossil subspecies of the Recent species. SCHAUB (1930) paid special attention to the earliest Pleistocene records from the classical locality Q1 Somlyóberg bei Püspekfördö (= Betfia 2), where he demonstrated the simultaneous presence of two forms – a small one, falling under the variation range of Recent populations (= *nanus*) and a form roughly corresponding to the size of the Recent species but differing in the more complicated structure of the molars with the regular presence of a mesolophid on the M₃, etc. Thus according to SCHAUB (1930), the fossil record of the genus *Cricetus* includes the following taxa: *Cricetus cricetus nanus* Schaub, 1930, T: Q1 Betfia 2, *Cricetus cricetus praeglacialis* Schaub, 1930, T: Q1 Betfia 2, *Cricetus cricetus runtonensis* Newton, 1909, T: Q2 UFB West Runton, and *Cricetus cricetus major* Woldřich, 1880, T: Q4 Výpustek.

A number of authors have commented on the validity of these taxa, the question of their separate species status, and possible relationships to Recent species. Worth mentioning is e.g. a study by HELLER (1972) who comprehensively surveyed the available Early and Middle Pleistocene fossil record of the genus stressing its fragmentarity: in most instances, just single isolated teeth are available, larger assemblages allowing population comparisons are quite unique. Among the latter the material from the early Middle Pleistocene site of Petersbuch analyzed in detail by FAHLBUSCH (1976) is particularly worthy of mention. A biometric comparison of 145 molars

from that locality with a sample of 59 Recent specimens from the Rhine population shows no overlap between the two assemblages suggesting their separate species statuses. The Petersbuch population stands stratigraphically between the Early Pleistocene (Q2) taxon *C. runtonensis* and the Late Pleistocene (Q4) *C. major*, with which it shares similarities in metric and non-metric characters. Logically, then, FAHLBUSCH (1976) concluded that all three taxa represent a single species unit, whose prior name is *Cricetus major* Woldřich, 1880, while the extant species is to be considered as an apochoric element appearing in Europe only in the latest Pleistocene past.

Consistent attention to the Quaternary fossil record of hamsters has been devoted by HÍR (1992, 1993b, 1997a, b, c, etc.) based on extraordinarily abundant evidence from the Pannonian region. In his studies on *C. cricetus nanus*, comparing morphometric variation in the type series from Q1 of the Betfia locality with that in Q1 samples from the Ostramos 14 and 8 sites, he argues that robustly pronounced size difference between the early Pleistocene form and hamster from later Pleistocene stages clearly substantiates considering them as a separate species *C. nanus* (HÍR 1992, 1997b). A subsequent series of papers (HÍR 1997a, b, c, 1998a, b) summarized corresponding data from other Hungarian localities and addressed the questions of the taxonomic status of other nominate fossil taxa. The most extensive study (HÍR 1998a) provides a comprehensive morphometric analysis of particularly rich material (1070 teeth) from the Q2 locality of Somssich-hégy 2 fully corresponding to the diagnostic specificities of *C. runtonensis*. For a population from the Middle Pleistocene site Solymár, corresponding to *C. runtonensis* in metrical characters, HÍR (1997a) reports the frequent presence of additive structures on the occlusal surface of M², M³, M₂, and M₃ and a tendency to duplicate mesolophid on M₂ and M₃ based on which he described it as a separate subspecies of *Cricetus runtonensis solymarensis*. As a summary of his studies, he proposed the following scenario of the Quaternary history of the genus *Cricetus*: (i) the oldest element was the species *C. nanus* accompanying the MN17 and Q1 communities with *Microtus (Allophaiomys) deucalion* and *M. (A.) pliocaenicus* (Koliňany 3, Betfia 2, 9, Osztramos 8, 2, 14, Deutsch-Altenburg 2C1). At the beginning of the Q2 biozone, it becomes extinct. (ii) *C. praeglacialis* from Villány 8 is considered to be the ancestral form of the Recent species *C. cricetus*, the clade recorded also in several Middle Pleistocene Hungarian sites (Tarkő, Várhegy, Söttő) and continuously occurring from the early Vistulian glacial. (iii) *C. runtonensis*, a large form metrically between *C. praeglacialis* and *C. major*, appearing in most localities of the late Early Pleistocene (Q2) and early Middle Pleistocene (Q3). Regarding to *C. runtonensis solymarensis*, the morphocline of this clade was characterized by a gradual increase in size and an increase in molar occlusal surface complexity, i.e. an inverse trend compared to size change in the *C. praeglacialis* – *C. cricetus* lineage. This argument is considered by HÍR (1997c) as evidence of the independent evolutionary history of the two lineages and the separate species status of these forms. (iv) *C. major*, the largest form of the genus, represents, according to HÍR (1997c), an independent group of gigantic forms sporadically distributed during the Middle and Late Pleistocene.

However, with possible doubts on the real taxonomic significance of differences in mean tooth size and minute rearrangements of the occlusal surface of the molars (additive cusplets, mesolophid) and with regards to a large span of phenotype variation of *Cricetus* both in within-population and between-population respects, either in stratigraphic and geographic terms, the above conclusions are far of being generally accepted. On contrary, KOWALSKI (2001) recalling the poorly justified assumptions of the separate species status of individual taxa and essential homogeneity of dental pattern in all of them proposed a view evaluating the entire Quaternary record of the genus as a single clade characterized by a pronounced capacity for temporal mor-

phometric variation. A similarly radical view is foreshadowed by KOWALSKI's (2001) assessment of other hamster species continuously represented in the European Quaternary record. This is a group of small hamsters arising from the rich Miocene and Pliocene radiation of the group (*Democricetodon*, *Neocricetodon*, *Kowalskia*, etc.). Following the comprehensive revision of the group by SCHAUB (1930), in its European Quaternary record, the three taxa are traditionally distinguished: *Allocricetus bursae* Schaub, 1930 – type locality MN 15 Csárnóta, *Allocricetus ehiki* Schaub, 1930 – type locality MN17 Vilány 3, *Cricetulus migratorius* (Pallas, 1773) – extant clade with numerous Late Pleistocene records. According to KOWALSKI (2001), the European Quaternary record of the group comes from 211 sites (19 MN17, 44 Q1, 35 Q2, 64 Q3, 48 Q4).

The form *Allocricetus ehiki*, distinctly different from the other forms by its larger size, is reported from several localities of biozones MN17 and Q1 (KURTÉN 1968, JÁNOSY 1986, PRADEL 1988). The distinctly smaller form *Allocricetus bursae* is a typical part of a large part of the European communities of the Late Pliocene, Early and middle Pleistocene (PRADEL 1988, MAUL 1990). The distinctness of the two forms has been repeatedly documented on material from Polish and Hungarian localities (FAHLBUSCH 1969, PRADEL 1988, HÍR 1992, 1995) and the separate species status of the two forms have been also accepted by KOWALSKI (2001). The Late Pleistocene (MIS 5–2) records characterized by very small size is traditionally assigned to the species *Cricetulus migratorius* whose Recent range covers a zone of dry forest-free land from the eastern Mediterranean (Jordan, Israel, Turkey, the eastern regions of Bulgaria and Romania) to the southern Urals, Central Asia, Kashmir, Mongolia, and western China (KRYŠTUFEK & VOHRALÍK 2009). Outside this range, from central and western Europe, it is known from a number of localities, especially from the early and middle stages of the Vistulian (JÁNOSY 1976, KOWALSKI 2001). The Late Pleistocene specimens identified as *Cricetulus migratorius* differ only in a smaller size from the Middle and Early Pleistocene specimens identified generally as *Allocricetus bursae*. For this reason, KOWALSKI (2001) considers them members of a single evolutionary lineage, which he refers to as *Cricetulus* spp.

However, the question of the real affiliation of all the Late Pleistocene records is far from clear. STORCH (1974) has pointed out that some of the specimens show very small dimensions corresponding rather to representatives of the Central Asian hamsters of the genus *Phodopus*. This possibility, as a more likely interpretation of such fossil populations, has been highlighted in recent years, e.g. by the analysis of a relatively large assemblage (n=31) from the beginning of the MIS3 zone at the Sesselfelsgrötte (VAN KOLFSCHOTEN 2014), which show clearly smaller dimensions than other European records and correspond in size to the extant *Phodopus sungorus*.

In this context, it should be emphasized that the tribus Cricetini, which includes all the genera mentioned in this paper (i.e. *Cricetus*, *Cricetulus*, *Allocricetus*, *Mesocricetus*, and *Phodopus*), is characterized by quite a uniform tooth design. Thus, intergeneric differences in tooth morphology usually do not exceed the level of differences between fossil populations of the same lineage, so the basic diagnostic criterion in this group remains the size or length and width dimensions of the dentition and individual teeth. In that respect, the European taxa of the small-sized hamsters differ clearly from *Cricetus* on the one hand, and the smallest forms of the tribe classified in the genus *Phodopus* on the other. Actually, it holds true for the species *Phodopus roborovskii* (Satunin, 1903) while the other species of the genus, *P. sungorus* (Pallas, 1773) including *P. campbelli* (Thomas, 1905), show somewhat larger dimensions and a possible overlap of metrical characters with *Cricetulus migratorius* cannot be excluded. Yet, the comparisons encountered in the palaeontological literature (cf. VON KOLFSCHOTEN 2014) are as a rule considerably restricted in sample size both as the fossil record and extant compa-

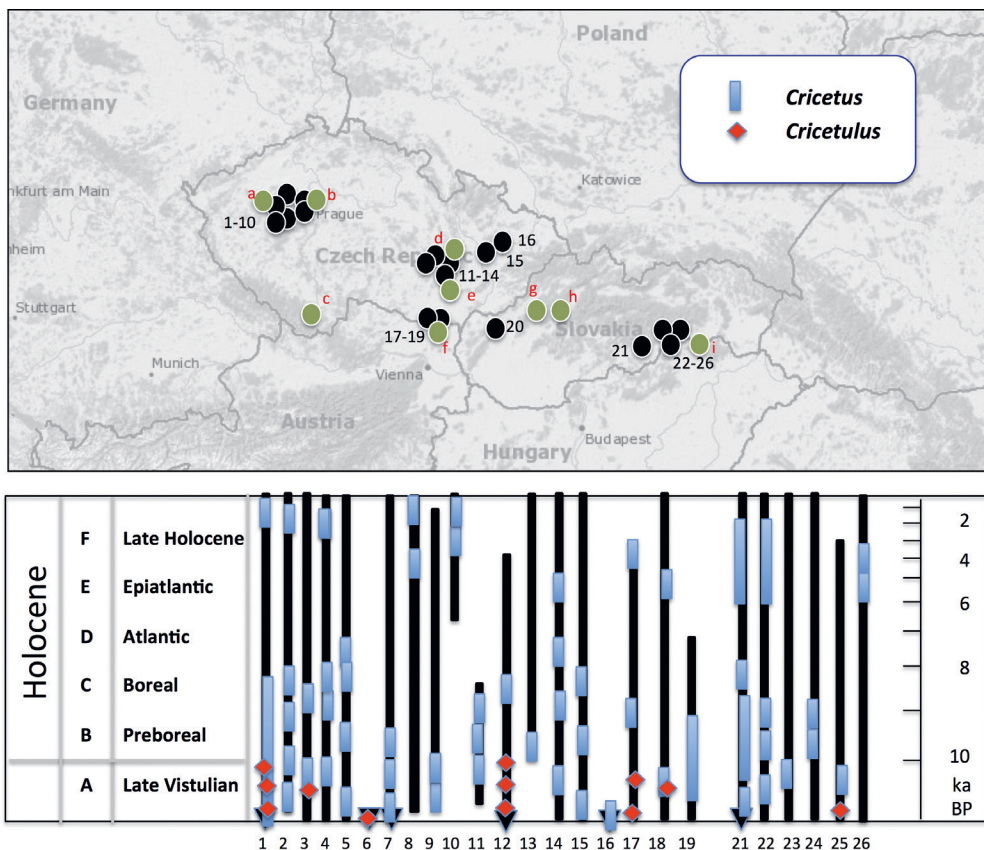


Fig. 1. Overview of the occurrence of hamsters in the Late Vistulian and Holocene sections of the Czech Republic and Slovakia; black marks, red marks – evidence from earlier stages of the Quaternary; blue columns – stratigraphic positions of *Cricetus cricetus* records in individual stratified sequences Q4, red diamonds – *Cricetulus migratorius* records.

Vistulian-Holocene (Q4) sedimentary sequences: 1 – Bišilu (Tetín), 2 – Bacín (Měňany), 3 – Skalice (Měňany), 4 – Skalka nad Čihovou (Karlštejn), 5 – Bašta (Prague), 6 – Chlum 7 (Srbsko), 7 – Vrata, Axamitova brána Cave (Koněprusy), 8 – Kobyła-west, 9 – Železná na Mramoru Cave, 10 – Za hájovou Cave (Koněprusy), 11 – Býčí skála (Adamov), 12 – Holštejnská Cave (Holštejn), 13 – Malý Lesík (Březina), 14 – Srnčí (Ostrov u Macochy), 15 – Velká Kobylanka (Hranice na Moravě), 16 – Tučín, 17 – Martinka rozsedlina (Horní Věstonice), 18 – Soutěška 1, 2 (Horní Věstonice), 19 – Turold N4 (Mikulov), 20 – Dzeravá skála (Malé Karpaty), 21 – Peskö (Bretka), 22 – Maštalná (Brzotín), 23 – Červeného muže Cave (Rožňava), 24 – Červená skála (Silica), 25 – Zbojnicka (Silica), 26 – Hámorská (Plešivec).

Early and Middle Pleistocene (MN17–Q3) sites: a – Q2 Koněprusy C718, b – Q2 Chlum 4, c – Q3, Dobrovkovic 2, d – Q1 and Q3, Mladeč 1 and 2, e – Q3 Turold NE 5 (Mikulov), f – Q2 Červený kopec (Brno), g – Q2 Žirany, h – MN17/Q1 Koliňany, i – Honce (Včeláre), 3, 4, 6, 7, 10, 11, 14.

rative materials are concerned. The non-metric characters proposed by VORONCOV (1982) to distinguish the genus *Phodopus* have not been considered at all.

The Quaternary materials of hamsters available in the Czech Republic and Slovakia present significant contributions to the European fossil record of particular clades (Tables 1 and 2) and in regards to the controversial issues of the topic are undoubtedly worth of reexamination. Some results are reported in the present paper. A special attention was paid to records from the present glacial cycle (Vistulian–Holocene) in order to reconstruct the history of the nowadays population of *Cricetus cricetus* and critically assess the stratigraphic distribution and generic affiliation of particular records of the *Allocricetus-Cricetulus-Phodopus* group.

MATERIAL AND METHODS

Material

The presence of remains of *Cricetus* was confirmed in 89 fossil community samples of 45 sites in the Czech Republic and 41 community samples of 21 sites in Slovakia, representatives of *Allocricetus-Cricetulus* clades were found in 22 community samples in the Czech Republic and 37 samples in Slovakia. Biometrical analyses were undertaken with 465 dental items from 90 samples in the case of *Cricetus* and 330 items from 66 samples in the case of *Allocricetus-Cricetulus*. Besides that we used a comparative material of 20 individuals of extant *C. cricetus* from central Bohemia, 14 *Phodopus sungorus* from a laboratory breed of authors, and a sample of 475 dental items of *Cricetulus migratorius* and *Mesocricetus newtoni* from four Holocene and Late Pleistocene sites in Turkey (Bolu, Mencilar Cave 1, 2) and Bulgaria (Karlukovo 4) collected by the senior author. The material is deposited either in the collection of the Department of Zoology, Faculty of Science, Charles University, or the collection of the Department of Palaeontology, National Museum (Natural History), both in Prague.

The source sites of particular samples are in most instances listed in the tabular checklist of Quaternary sites in the Czech Republic and Slovakia by HORÁČEK & LOŽEK (1988), including references to the primary literature sources reporting them.

Analyses of the structure of the accompanying communities of individual sites are based on the data summarized in the descriptions of individual sites (for glacial sites Q4, e.g. HORÁČEK & SÁNCHEZ-MARCO 1984), for further details concerning Q4 sites see HORÁČEK & LOŽEK (1988) and HORÁČKOVÁ et al. (2015), for Early Pleistocene sites see e.g. FEJFAR & HORÁČEK (1983, 1989).

The geographic setting of individual sites (comp. also Fig. 1) is expressed by their attribution to the following territorial units: (1) Bohemian Karst and Central Bohemia, (2) Southern Bohemia, (3) Northern Bohemia, (4) Western Bohemia, (5) Northern Moravia, (6) Moravian Karst and Brno, (7) Southern Moravia, (8) Western Slovakia, (9) Central Slovakia (including the Tisovec–Muráň Karst), (10) Slovakian Karst, and (11) Northern Slovakia. The stratigraphic setting is summarized in Figs. 1 and 2.

The stratigraphic terms preferably used (biozones MN17, Q1–Q4) follow the concepts by HORÁČEK (1981), HORÁČEK & LOŽEK (1988), and FEJFAR & HEINRICH (1981, 1986), respectively. Within the last glacial cycle (Q4), the individual records are assigned to the following stratigraphic subunits: (w1) Late Eemian – Early Vistulian (MIS5a, b, c – MIS4), (w2) MIS3, (w3) MIS2 (Late Vistulian, LGM), (a) Late Vistulian (after the LGM), (b) Pre-Boreal, (c) Boreal, (d) Atlantic, (e) Epiatlantic and Late Holocene.

The morphological terminology follows the standard usus proposed by SCHAUB (1930), FEJFAR (1970), FAHLBUSCH (1969), and HfR (1995, 1997a, b). The teeth of the mandibular dentition are denoted by lower indices (M_1 – M_3), and the teeth of the maxillary dentition by upper indices (M^1 – M^3).

Biometric analysis

All processed items were photographed at standardized magnification in occlusal view with an Olympus SZX12 stereoscopic microscope in parallel with the calibration scale of the objective micrometer. The

actual measurements were performed using the tpsDig 3.0 software, and the results were simultaneously deposited in an Excel database.

The following variables were measured in accordance with the usual procedures for biometric analysis of the taxa studied (FAHLBUSCH 1969, Hír 1997a, b):

(i) tooth row lengths: M_1-M_3 , M_1-M_2 , M_2-M_3 , M^1-M^3 , M^1-M^2 , M^2-M^3 .

(ii) the length-width dimensions of each tooth (L = length, W = width) in the case of M_1 and M^1 extended by the widths and lengths of anteroconid part of the tooth (La, Wa). A graphical overview of the measured dimensions is given in Fig. 3.

The primary dataset was supplemented with a series of proportional indexes (L/W ratios of particular teeth and corresponding between-teeth L and W ratios) calculated for each item in the Excel. Basic statistics of each subset and between-sample comparisons using standard procedures of univariate, bivariate, and multivariate techniques were computed in Statistica 13. Analyses of the accompanying fauna were processed in an analogous way.

The between-sample comparisons were further supplemented with biometric data from several foreign sites retrieved from respective primary literature sources, including those on the type series *Cricetus cricetus*

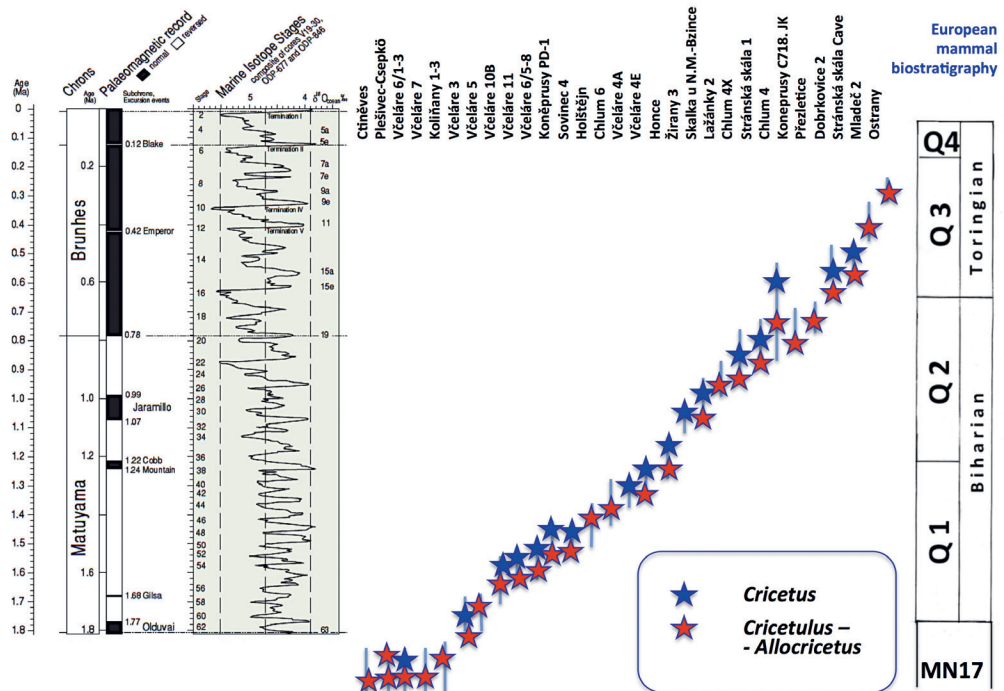


Fig. 2. Overview of Early and Middle Pleistocene sites in the Czech Republic and Slovakia where the occurrence of the hamsters was confirmed: *Cricetus* sp. – blue stars, and *Allocricetus* / *Cricetulus* – red stars. The stratigraphic position of the individual assemblages is indicated, taking into account the biostratigraphic criteria of HORÁČEK & LOŽEK (1988) – see also the diagram of Quaternary biozones on the right and the correlation with climatostratigraphic characteristics, magnetostratigraphy and chronology of the covered period – after HEAD & GIBBARD (2015) (left).

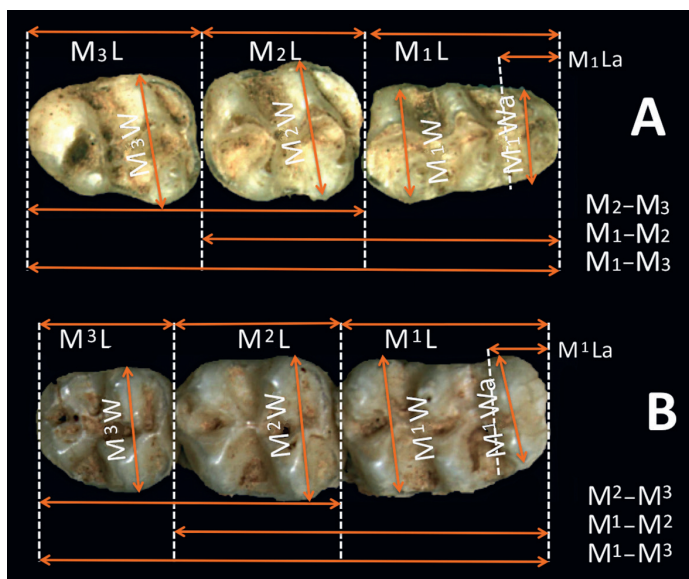


Fig. 3. Dental dimensions measured in this study.

nanus Schaub, 1930 (Q1 Betfia; Hír 1993b) and *C. cricetus praeglacialis* (Q1 Betfia; Hír 1997c). The metric data of the holotype of *Cricetus runtonensis* Newton, 1909 was reconstructed from the illustration of the type specimen in the original paper (NEWTON 1909) reporting M^1-M^3 length = 9.3 mm.

RESULTS

Cricetus cricetus

Occurrence in the current (Q4) cycle

The presence of *Cricetus cricetus*, verified by physical examination of the collection material (usually dental material allowing unambiguous generic identification even in the case of small dental fragments), was confirmed in a total of 110 communities of the Holocene or Vistulian age. The vast majority of the finds come from the context of continuous faunal sequences with reliable stratigraphic delineation covering a period from the late Vistulian to the present, as a rule (Figs. 1, 4). Most of them come from the Bohemian Karst (38 communities, 9 sedimentary sequences), the others are from the Moravian Karst (23 communities, 5 sequences), Northern Moravia (7 communities, 3 localities), Southern Moravia (11 communities, 5 sequences) and the Slovakian Karst (20 communities, 5 sequences). In the vast majority (69 cases), the records come from the layers dated to the transitional section of the latest Vistulian (a: 24) and the early Holocene (Pre-Boreal, b: 18; Boreal, c: 27). Only two records are available from the middle Holocene (Atlantic d), while more records are available from the post-Neolithic period (e: 16 communities in total). The records from deeper stages of the Vistulian are relatively rare (15 in total: 11 from MIS5–MIS3, only 4 from the Late Vistulian LGM supposedly including).

A complementary set of records covers historical findings from classic localities of glacial fauna – Výpustek Cave in the Moravian Karst, Sudslavice near Vimperk, and from the Prague brickyards (Q4wP group: Jinonice, Lysolaje, Košíře, Kotlářka, Svatý Prokop, Meilbek), whose interpretation will be commented in the Discussion.

In the vast majority of cases, the presence of the hamster is documented by fragmentary remains of a single individual (MNI=1:69 communities). More numerous records (MNI>3) are available in only eight communities. In summary, in the spectrum of taxa represented in the

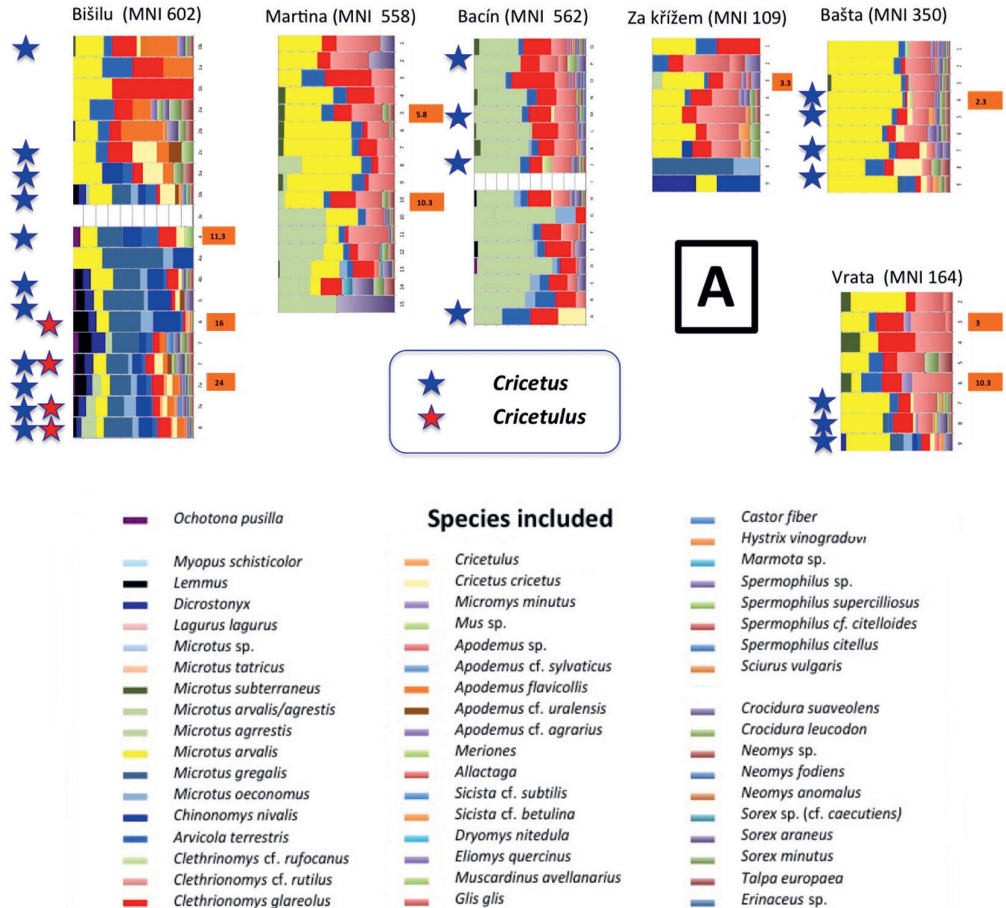


Fig. 4. Occurrence of hamsters (*Cricetus cricetus* – blue asterisks, and *Cricetulus migratorius* – red asterisks) in selected Late Vistulian and Holocene sedimentary sequences. Coloured bars indicate the dominance attribution of particular species of small ground mammals to the communities of particular layers (MNI, %), red boxes – ¹⁴C ka BP; A – selected sites in the Bohemian Karst; B – selected sites in the Moravian Karst; C – selected sites in the Slovakian Karst; D – sites with representation of deeper Vistulian stages.

total Q4 sample (880 communities, MNI=23400), the hamster appears clearly as rather rare sub-recedent element with an overall dominance of a mere 0.55%. In a number of localities (including those with a fairly rich mammalian microfauna – e.g. Dzerava Cave MNI=2013, Šarkanica MNI>3000, Balcarka MNI>800, numerous sections in sandstone areas of northern Bohemia, comp. HORÁČEK & SÁZELOVÁ 2017, etc.) the hamster is invariably absent. On the contrary, in several localities, its presence continuously accompanies a substantial part of the

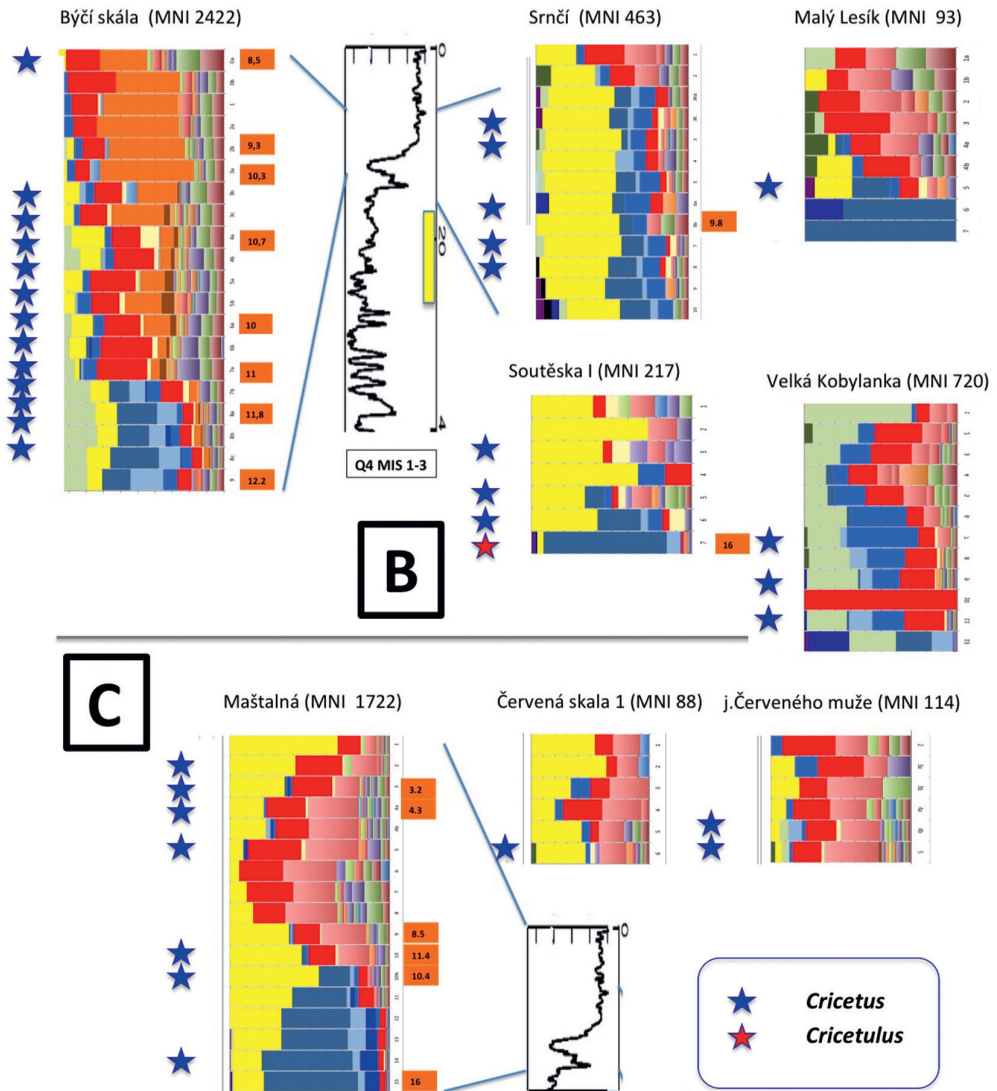


Fig. 4. (continued)

covered sequence (Bišilu, Býčí skála, Bašta, Peskö, Holštejská) – cf. Fig. 4. These facts indicate both a tendency towards islet-like fragmented occurrence and a disposition to continued survival of resident populations in some occurrence islands.

The relative differences in frequency and dominance of accompanying species between communities with hamster present and the respective values in the total assemblage of 880 Q4 communities are graphically surveyed in Fig. 5.

For the communities accompanying the hamster presence this suggests the followings: (i) a relatively high diversity, increased representation of a number of recedent and subrecedent elements characteristic of both glacial and interglacial communities, (ii) a distinctive feature of the dominance structure is a highly increased proportion of demanding open ground elements characterizing the communities of mammoth steppe (*Sicista subtilis* 372%, *Apodemus uralensis* 325%, *Neomys anomalus/milleri* 317%, *Spermophilus* spp. incl. *S. superciliosus* 270%, *Micromys minutus* 241%, *Crociodura leucodon* 233%. *Lemmus lemmus* 182%), (iii) clearly reduced abundance of arboreal and forest interglacial elements (*Sciurus vulgaris*, Gliridae, *Apodemus flavicollis* and *A. sylvaticus*, *Clethrionomys glareolus*, *Microtus subterraneus*, *Sorex* spp.), but also of the leading open ground elements of the LGM communities (*Microtus gregalis*, *Dicrostonyx torquatus*).

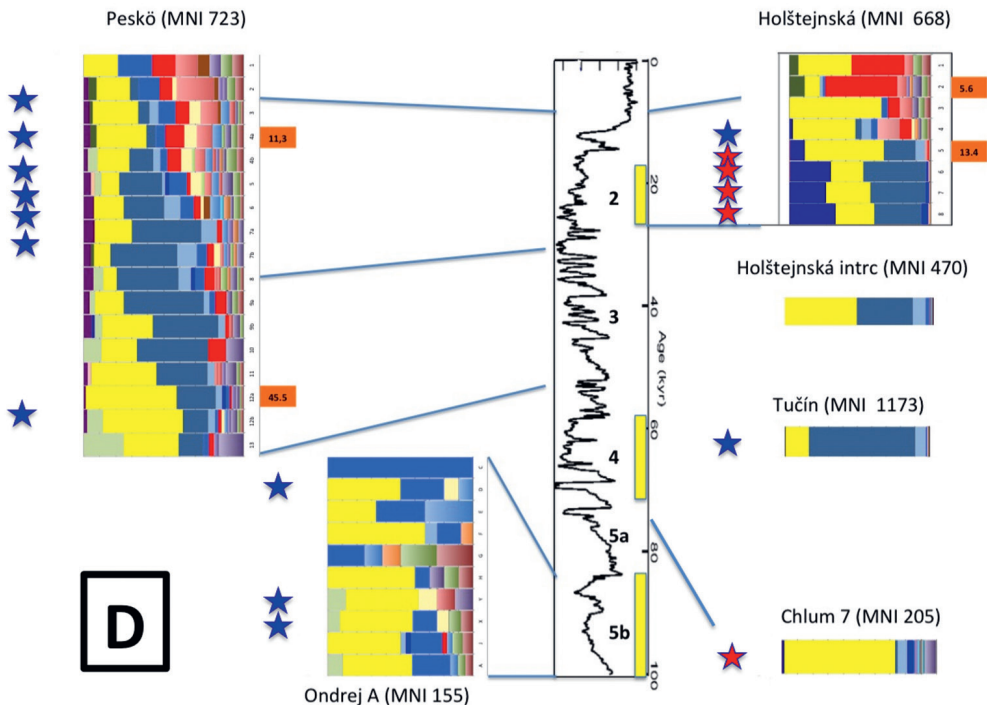


Fig. 4. (continued)

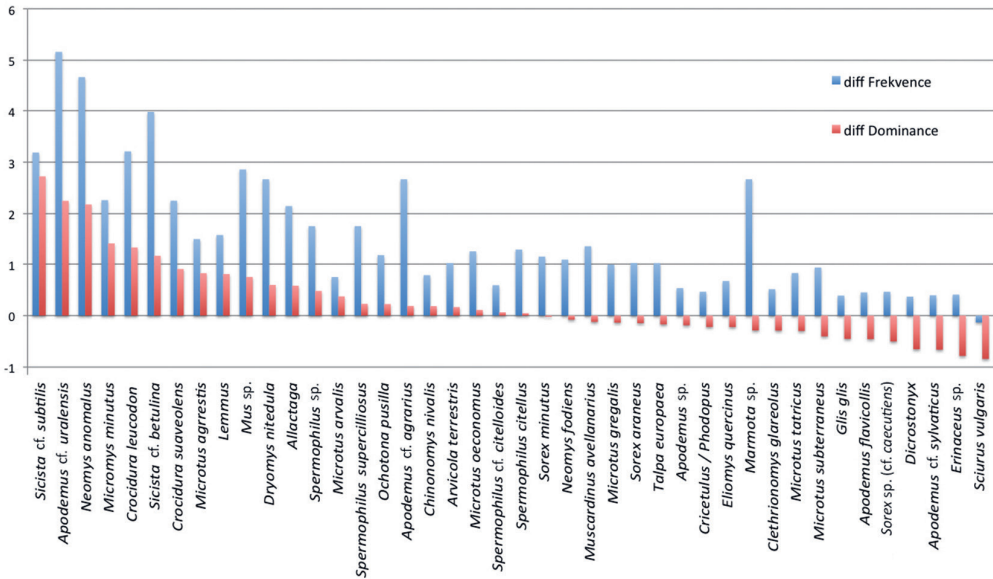


Fig. 5. Small mammal communities accompanying Q4 record of *Cricetus cricetus*: Ratio of frequency (% of sites) and dominance (% abundance – MNI) in communities with hamster (*Cricetus*) presence to respective values in the entire set of Q4 communities (n=880) for the species composing the former set. Arranged by rank of dominance ratio.

Occurrence in the deeper Pleistocene past

The hamster was documented as a recedent or subrecedent element in a total of 31 community samples of the Early Pleistocene sections (3 MN17, 8 Q1, 4 Q2/1–2, 12 Q2/3, 6 Q3). A summary of the occurrence including the stratigraphic position of individual finds is provided in Fig. 2.

Similarly to the Q4 assemblage, in the older sections of the Pleistocene, the presence of the hamster in the respective fossil communities is mostly limited to fragmentary evidence of single individuals, with more numerous assemblages (MNI>5) available only from the localities Honce (Q2/1) and Bzince-Skalka near Nové Město nad Váhom (Q2/2), representative items with complete dentition are also available from the localities Q1 Včeláre 6/8, Q1 Koněprusy PD-1, Q3 Dobrkovice 2, and Tučín.

In a large assemblage of communities from the Early-Middle Pleistocene Transition (EMPT, along the Q2/3 boundary) comprising 88 communities with a total number of individuals MNI=13,264, the hamster is represented by 31 individuals in 14 communities. The average dominance of hamster in the communities in which this species occurs is 16% in this section, which corresponds to the proportions in Q4 communities (12.5%). Thus, it is a relatively rare element also here.

The indexing elements co-occurring with *Cricetus* in the EMPT communities are alongside the euconstat elements of the Q2 section (*Microtus hintoni-gregaloides*, *Sorex runtonensis*, *Talpa minor*, *Mimomys savini*), namely the following taxa (exhibiting higher dominance compared to

Table 1. Basic statistics of dental measurements of *Cricketus* sp. for datasets from individual stratigraphic horizons of Czech and Slovakian record

	$M_1^{-}M_3$	$M_1^{-}M_2$	$M_2^{-}M_3$	M_1W	M_1L	M_1Wa	M_1La	M_2W	M_2L	M_2W	M_2L	M_3W	M_3L	M_3Wa	M_3L	$M_{12}M_{23}$	M_1L/W	M_2L/W	M_3L/W	M_1^1/M_2^1	M_2^1/M_3^1
MNI7	n	0	0	0	1	1	0	2	2	2	2	1	1	1	0	1	1	2	1	0	0
	M	-	-	-	1.530	2.670	1.150	-	1.890	2.265	2.030	2.250	3.250	-	1.745	0.752	1.199	1.444	-	-	-
	min	-	-	-	-	-	-	-	1.680	2.030	-	-	-	-	-	-	1.190	-	-	-	-
	max	-	-	-	-	-	-	2.100	2.500	-	-	-	-	-	-	-	1.208	-	-	-	-
	SD	-	-	-	-	-	-	0.297	0.332	-	-	-	-	-	-	-	0.013	-	-	-	-
Q1	n	0	0	1	6	6	4	2	2	2	2	3	3	6	6	2	2	3	0	0	0
	M	-	-	3.980	1.655	2.728	1.270	0.928	1.645	2.035	1.747	2.393	-	1.658	0.767	1.238	1.367	-	-	-	-
	min	-	-	-	1.450	2.530	1.050	0.770	1.540	1.920	1.540	2.040	-	1.446	0.710	1.229	1.325	-	-	-	-
	max	-	-	-	1.840	2.920	1.550	1.080	1.750	2.150	2.000	2.800	-	1.902	0.856	1.247	1.400	-	-	-	-
	SD	-	-	-	0.151	0.155	0.172	0.128	0.148	0.163	0.234	0.383	-	0.155	0.065	0.013	0.039	-	-	-	-
Q2/1	n	4	5	7	7	7	5	8	8	8	8	7	7	5	8	7	5	8	7	5	4
	M	8.278	5.532	5.330	1.837	3.093	1.280	1.090	2.171	2.626	2.184	2.787	1.044	1.687	0.719	1.210	1.276	0.842	0.887	0.842	0.887
	min	7.770	5.280	4.910	1.720	2.930	1.180	0.960	2.050	2.370	2.030	2.570	0.991	1.576	0.667	1.156	1.195	0.809	0.848	0.809	0.848
	max	8.550	5.760	5.630	1.980	3.220	1.400	1.280	2.300	2.750	2.320	3.070	1.110	1.802	0.814	1.317	1.371	0.879	0.967	0.879	0.967
	SD	0.347	0.234	0.239	0.111	0.088	0.085	0.118	0.089	0.119	0.090	0.177	0.058	0.081	0.056	0.053	0.054	0.032	0.055	0.032	0.055
Q2/2	n	2	3	2	4	5	2	2	3	3	3	3	3	2	4	2	3	3	3	3	2
	M	9.530	5.923	6.260	2.135	3.462	1.620	1.390	2.353	2.810	2.350	2.883	0.990	1.617	0.716	1.194	1.229	0.811	0.812	0.811	0.812
	min	9.300	5.370	6.240	1.940	3.370	1.590	1.300	2.280	2.700	2.300	2.750	0.955	1.543	0.691	1.154	1.122	0.798	0.775	0.798	0.775
	max	9.760	6.440	6.280	2.300	3.550	1.650	1.480	2.440	2.960	2.450	2.950	1.025	1.742	0.740	1.215	1.283	0.834	0.850	0.834	0.850
	SD	0.325	0.536	0.028	0.162	0.085	0.042	0.127	0.081	0.135	0.087	0.115	0.050	0.091	0.034	0.035	0.092	0.020	0.020	0.020	0.053
Q2/3	n	1	1	2	4	3	3	4	4	4	4	3	3	3	3	1	3	4	3	1	1
	M	8.720	5.900	5.510	1.988	3.360	1.533	-	2.268	2.813	2.177	2.873	1.069	1.758	0.802	1.241	1.320	0.848	0.855	0.848	0.855
	min	-	-	-	1.800	3.300	1.500	-	2.240	2.750	2.150	2.800	-	1.657	0.762	1.196	1.302	-	-	-	-
	max	-	-	-	5.520	2.200	3.480	1.600	-	2.300	2.900	2.230	3.000	-	1.833	0.833	1.289	1.345	-	-	-
	SD	-	-	-	0.014	0.193	0.104	0.058	-	0.028	0.063	0.046	0.110	-	0.091	0.037	0.039	0.023	-	-	-
Q3	n	1	1	2	4	4	4	3	5	6	4	4	3	4	4	1	4	5	2	1	1
	M	9.000	6.200	5.435	1.858	3.170	1.525	1.503	2.272	2.367	2.458	2.840	1.235	1.710	0.816	1.107	1.247	0.765	0.870	0.765	0.870
	min	-	-	-	5.020	1.720	3.010	1.350	0.940	1.850	2.000	2.520	-	1.635	0.750	0.706	1.235	-	-	-	-
	max	-	-	-	5.850	2.110	3.450	1.950	2.050	2.640	2.800	3.000	-	1.778	0.924	1.231	1.260	-	-	-	-
	SD	-	-	-	0.587	0.173	0.206	0.287	0.555	0.256	0.375	0.340	0.277	-	0.068	0.076	0.225	0.018	-	-	-

Table 1. (continued)

Q3/3	n	0	0	2	3	3	3	3	1	2	2	2	3	3	0	3	3	2	3	1	1
	M	-	5.455	2.037	3.407	1.640	1.220	2.295	2.820	2.103	2.633	-	1.679	0.803	1.229	1.249	0.801	0.680	-	-	-
	min	-	5.180	1.890	3.300	1.500	1.220	2.250	2.780	1.990	2.360	-	1.577	0.743	1.222	1.156	-	-	-	-	-
	max	-	5.730	2.200	3.470	1.900	1.220	2.340	2.860	2.200	3.090	-	1.825	0.864	1.236	1.405	-	-	-	-	-
	SD	-	0.389	0.156	0.093	0.225	-	0.064	0.057	0.106	0.398	-	0.130	0.061	0.009	0.136	-	-	-	-	-
Q4w	n	4	4	6	10	10	10	6	7	7	10	10	4	10	10	7	10	4	4	4	4
	M	8.713	5.708	5.445	1.873	3.159	1.369	1.067	2.143	2.670	2.027	2.709	1.044	1.690	0.730	1.246	1.335	0.864	0.901	-	-
	min	8.600	5.600	5.000	1.700	3.000	1.140	0.700	2.000	2.500	1.840	2.180	1.000	1.591	0.659	1.209	1.185	0.839	0.806	-	-
	max	8.800	5.800	5.800	2.030	3.360	1.640	1.200	2.250	2.800	2.200	3.000	1.120	1.824	0.862	1.280	1.436	0.875	0.938	-	-
	SD	0.103	0.083	0.281	0.109	0.101	0.171	0.184	0.106	0.118	0.128	0.255	0.053	0.073	0.070	0.021	0.076	0.017	0.063	-	-
Q4wp	n	15	16	18	15	16	15	0	17	18	19	20	15	15	15	17	19	15	15	15	15
	M	7.772	5.194	4.858	1.705	2.892	1.248	-	2.038	2.490	1.977	2.646	1.119	1.707	0.733	1.228	1.342	0.861	0.915	-	-
	min	7.350	4.900	2.300	1.600	2.750	1.150	-	1.850	2.350	1.800	2.400	0.981	1.450	0.675	1.091	1.186	0.800	0.845	-	-
	max	8.230	5.400	5.400	2.000	3.050	1.350	-	2.200	2.620	2.210	2.900	2.283	1.826	0.788	1.316	1.474	0.909	0.964	-	-
	SD	0.261	0.144	0.668	0.107	0.093	0.061	-	0.093	0.080	0.083	0.123	0.324	0.103	0.038	0.065	0.078	0.030	0.041	-	-
Q4A	n	0	2	2	13	11	9	9	12	12	3	3	0	11	9	12	3	1	0	0	0
	M	-	5.165	5.060	1.685	2.900	1.329	0.988	1.976	2.531	1.893	2.537	-	1.627	0.826	1.283	1.339	0.842	-	-	-
	min	-	5.080	4.730	1.240	2.500	0.850	0.730	1.770	2.350	1.820	2.220	-	1.163	0.586	1.114	1.194	-	-	-	-
	max	-	5.250	5.390	2.150	3.150	1.920	1.230	2.160	2.840	2.000	2.800	-	1.855	1.208	1.385	1.423	-	-	-	-
	SD	-	0.120	0.467	0.263	0.180	0.323	0.135	0.118	0.144	0.095	0.294	-	0.227	0.177	0.073	0.126	-	-	-	-
Q4B	n	3	5	4	14	14	14	14	15	16	7	7	3	14	14	15	6	7	4	4	4
	M	7.640	5.176	4.765	1.646	2.929	1.384	1.016	1.979	2.450	1.889	2.407	1.049	1.782	0.833	1.245	1.318	0.872	0.856	-	-
	min	7.310	5.000	4.230	1.490	2.660	1.000	0.830	1.740	1.950	1.470	1.960	1.043	1.613	0.649	1.000	1.165	0.689	0.653	-	-
	max	7.880	5.330	5.110	1.920	3.400	2.170	1.570	2.330	2.660	2.280	2.710	1.057	2.006	1.212	1.420	1.383	0.941	0.956	-	-
	SD	0.295	0.161	0.383	0.137	0.227	0.382	0.190	0.146	0.181	0.245	0.289	0.007	0.103	0.180	0.112	0.079	0.085	0.137	-	-
Q4C	n	3	3	3	11	11	11	11	13	13	8	8	3	11	11	13	8	4	3	3	3
	M	7.573	5.173	4.780	1.833	2.974	1.325	0.957	2.042	2.505	1.953	2.503	1.083	1.629	0.717	1.229	1.283	0.814	0.869	-	-
	min	7.340	5.050	4.610	1.630	2.730	1.070	0.720	1.830	2.270	1.720	2.220	1.058	1.415	0.632	1.141	1.147	0.792	0.833	-	-
	max	7.870	5.300	5.010	2.050	3.220	1.750	1.170	2.230	2.690	2.110	2.880	1.095	1.799	0.866	1.381	1.412	0.832	0.909	-	-
	SD	0.271	0.125	0.207	0.151	0.152	0.266	0.124	0.121	0.134	0.137	0.240	0.022	0.110	0.089	0.076	0.095	0.017	0.039	-	-

Table 1. (continued)

Q4E	n	0	1	4	4	3	4	4	4	5	3	3	0	4	3	3	4	3	1	0	
	M	-	5.690	1.875	3.035	1.420	1.188	2.040	1.188	2.538	1.707	2.513	-	1.618	0.776	1.251	1.478	0.752	-	-	
	min	-	-	1.770	2.880	1.180	1.030	1.930	1.030	2.290	1.500	2.300	-	1.574	0.618	1.187	1.364	-	-	-	
	max	-	-	1.990	3.300	1.540	1.330	2.110	1.330	2.830	1.870	2.690	-	1.658	0.870	1.394	1.537	-	-	-	
	SD	-	-	0.096	0.194	0.208	0.131	0.081	0.131	0.194	0.189	0.198	-	0.038	0.138	0.097	0.099	-	-	-	
		19	19	17	18	17	17	19	19	19	19	19	19	19	17	17	17	19	19	18	18
Recent CR																					
n	19	19	17	18	17	17	19	19	19	19	19	19	19	17	17	17	19	19	19	18	
M	7.595	5.122	4.879	1.636	2.781	1.208	1.211	1.953	2.397	1.921	2.485	1.051	1.704	0.739	1.229	1.293	0.865	0.897	-	-	
min	7.320	4.840	4.390	1.490	2.610	1.050	0.790	1.800	2.250	1.780	2.070	0.984	1.621	0.661	1.135	1.107	0.794	0.699	-	-	
max	7.930	5.400	5.160	1.790	2.960	1.820	2.390	2.070	2.740	2.020	2.680	1.216	1.847	1.152	1.481	1.388	1.004	1.011	-	-	
SD	0.213	0.159	0.224	0.076	0.093	0.188	0.395	0.075	0.117	0.072	0.173	0.054	0.069	0.115	0.077	0.069	0.051	0.072	-	-	
MN17																					
n	0	0	3	3	3	3	0	0	0	0	1	1	0	3	3	3	0	1	0	0	
M	-	-	1.883	2.857	1.517	-	-	-	-	-	1.820	2.410	-	1.520	0.806	-	1.324	-	-	-	
min	-	-	1.850	2.650	1.450	-	-	-	-	-	-	-	-	1.359	0.744	-	-	-	-	-	
max	-	-	1.950	3.050	1.600	-	-	-	-	-	-	-	-	1.649	0.865	-	-	-	-	-	
SD	-	-	0.058	0.200	0.076	-	-	-	-	-	-	-	-	0.147	0.061	-	-	-	-	-	
Q1																					
n	1	1	3	5	4	5	4	3	3	3	2	2	1	5	5	3	2	2	2	1	
M	7.930	5.730	4.390	1.808	2.852	1.564	1.040	1.827	2.143	1.755	2.095	1.189	1.589	0.864	1.181	1.196	0.805	0.719	-	-	
min	-	-	3.810	1.530	2.540	1.270	0.810	1.520	1.860	1.590	1.940	-	1.483	0.830	0.995	1.172	0.791	-	-	-	
max	-	-	4.820	2.110	3.130	1.800	1.290	2.090	2.560	1.920	2.250	-	1.810	0.903	1.322	1.220	0.818	-	-	-	
SD	-	-	0.521	0.263	0.263	0.245	0.196	0.287	0.369	0.233	0.219	-	0.130	0.028	0.168	0.034	0.019	-	-	-	
Q2/1																					
n	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Table 1. (continued)

Q2/2	n	0	1	2	1	1	1	1	1	1	3	3	3	3	0	1	1	1	3	3	1	1	3	3	1	0	
	M	-	6.410	5.295	2.290	3.680	2.000	1.910	2.287	2.853	2.110	2.453	-	1.607	0.873	1.248	1.167	0.802	-	-	-	-	-	-	-	-	-
	min	-	5.230	-	-	-	-	2.220	2.750	2.000	2.200	-	-	-	-	1.239	1.000	-	-	-	-	-	-	-	-	-	
	max	-	5.360	-	-	-	-	2.370	2.950	2.200	2.610	-	-	-	-	1.260	1.275	-	-	-	-	-	-	-	-	-	
	SD	-	0.092	-	-	-	-	0.076	0.100	0.101	0.221	-	-	-	-	0.011	0.147	-	-	-	-	-	-	-	-	-	
Q2/3	n	0	0	0	4	4	1	1	1	1	1	1	1	1	0	4	1	1	1	1	1	1	1	1	0	0	
	M	-	-	-	2.175	3.343	2.060	1.620	2.400	2.550	2.030	2.500	-	1.538	0.858	1.063	1.232	-	-	-	-	-	-	-	-	-	
	min	-	-	-	2.000	3.000	-	-	-	-	-	-	-	1.429	-	-	-	-	-	-	-	-	-	-	-	-	
	max	-	-	-	2.400	3.720	-	-	-	-	-	-	-	1.650	-	-	-	-	-	-	-	-	-	-	-	-	
	SD	-	-	-	0.171	0.295	-	-	-	-	-	-	-	0.091	-	-	-	-	-	-	-	-	-	-	-	-	
Q3	n	2	2	2	3	3	3	3	4	4	3	3	3	2	3	3	3	3	4	3	4	3	2	2	2		
	M	8.735	6.190	5.265	2.233	3.543	1.957	1.273	2.303	2.813	2.177	2.693	1.177	1.595	0.880	1.226	1.235	0.774	0.734	-	-	-	-	-	-		
	min	8.610	6.150	5.090	2.030	3.450	1.830	1.210	2.000	2.660	2.070	2.370	1.131	1.476	0.825	1.157	1.145	0.769	0.687	-	-	-	-	-	-		
	max	8.860	6.230	5.440	2.520	3.720	2.080	1.400	2.650	3.200	2.360	3.010	1.224	1.704	0.912	1.350	1.286	0.780	0.780	-	-	-	-	-	-		
	SD	0.177	0.057	0.247	0.255	0.153	0.125	0.110	0.267	0.259	0.159	0.320	0.066	0.114	0.047	0.085	0.078	0.008	0.066	-	-	-	-	-	-		
Q3/3	n	1	2	1	2	2	2	1	3	3	3	3	3	1	2	2	3	2	3	3	3	3	3	2	1		
	M	8.730	6.185	5.130	2.155	3.565	1.975	1.400	2.373	2.753	2.147	2.447	1.193	1.654	0.917	1.160	1.140	0.756	0.644	-	-	-	-	-	-		
	min	6.120	-	2.100	3.480	1.960	-	2.320	2.640	2.140	2.240	-	1.652	0.887	1.136	1.047	0.753	-	-	-	-	-	-	-	-		
	max	6.250	-	2.210	3.650	1.990	-	2.420	2.870	2.150	2.590	-	1.657	0.948	1.206	1.205	0.759	-	-	-	-	-	-	-	-		
	SD	0.092	-	0.078	0.120	0.021	-	0.050	0.115	0.006	0.183	-	0.004	0.043	0.040	0.083	0.004	-	-	-	-	-	-	-	-		
Q4w	n	2	2	3	3	2	3	2	3	3	3	3	2	2	3	3	3	2	3	3	3	3	2	2			
	M	8.200	5.890	4.907	2.053	3.285	1.687	1.185	2.237	2.587	2.040	2.183	1.188	1.639	0.823	1.157	1.069	0.786	0.661	-	-	-	-	-			
	min	8.000	5.780	4.800	1.910	3.170	1.640	1.140	2.160	2.510	1.920	2.000	1.176	1.619	0.800	1.130	1.042	0.779	0.631	-	-	-	-	-			
	max	8.400	6.000	5.100	2.150	3.400	1.720	1.230	2.300	2.650	2.100	2.350	1.199	1.660	0.859	1.178	1.119	0.792	0.691	-	-	-	-	-	-		
	SD	0.283	0.156	0.168	0.127	0.163	0.042	0.064	0.071	0.071	0.104	0.176	0.016	0.029	0.031	0.024	0.043	0.009	0.043	-	-	-	-	-	-		
Q4wp	n	8	10	7	10	11	9	0	9	10	7	8	7	10	9	9	7	10	8	-	-	-	-	-	-		
	M	7.394	5.280	4.593	1.905	3.038	1.649	-	2.158	2.372	1.969	2.100	1.152	1.611	0.861	1.109	1.075	0.785	0.695	-	-	-	-	-	-		
	min	7.000	5.000	4.000	1.800	2.800	1.500	-	2.000	2.200	1.830	2.000	0.963	1.475	0.741	1.023	1.000	0.734	0.667	-	-	-	-	-	-		
	max	7.700	5.500	5.400	2.050	3.200	1.800	-	2.250	2.600	2.100	2.250	1.250	1.778	0.908	1.198	1.135	0.839	0.726	-	-	-	-	-	-		
	SD	0.231	0.167	0.432	0.093	0.117	0.115	-	0.077	0.134	0.100	0.080	0.092	0.087	0.052	0.053	0.042	0.034	0.021	-	-	-	-	-	-		

Table 1. (continued)

	M ₁ -M ₃	M ₁ -M ₂	M ₂ -M ₃	M ₁ W	M ₁ T ₁	M ₁ W _a	M ₁ T _a	M ₂ W	T ₂	M ₂ W	M ₃ W	T ₃	M ₂ W _a	M ₁ T ₁ W	M ₂ W	M ₃ W	T ₁ W/M ₁ T ₁	M ₃ W	M ₂ W	M ₃ W	T ₁ W/M ₁ T ₁	
Q4A	n	1	2	1	5	5	5	4	4	4	2	2	1	5	5	4	2	2	2	2	2	1
	M	7.780	5.440	4.590	1.990	3.066	1.698	1.220	1.988	2.388	1.805	2.415	1.224	1.542	0.853	1.205	1.338	0.751	0.683	0.751	0.683	1
	min	-	5.260	4.590	1.870	2.940	1.620	1.080	1.870	2.230	1.800	2.180	-	1.463	0.818	1.083	1.211	0.746	-	-	-	2
	max	-	5.620	4.590	2.100	3.190	1.850	1.450	2.080	2.510	1.810	2.650	-	1.611	0.881	1.342	1.464	0.755	-	-	-	2
	SD	-	0.255	-	0.082	0.101	0.094	0.138	0.100	0.116	0.007	0.332	-	0.071	0.024	0.111	0.179	0.007	-	-	-	1
Q4B	n	0	1	0	5	5	5	4	4	4	2	2	0	5	5	4	2	2	1	1	1	0
	M	-	5.440	-	1.932	3.070	1.632	1.212	1.935	2.370	1.885	2.205	-	1.592	0.847	1.226	1.170	0.756	-	-	-	1
	min	-	-	-	1.760	2.920	1.560	1.090	1.870	2.300	1.870	2.180	-	1.532	0.821	1.174	1.166	-	-	-	-	1
	max	-	-	-	2.030	3.190	1.670	1.360	2.070	2.430	1.900	2.230	-	1.744	0.938	1.286	1.174	-	-	-	-	1
	SD	-	-	-	0.112	0.098	0.043	0.114	0.091	0.070	0.021	0.035	-	0.087	0.051	0.048	0.006	-	-	-	-	1
Q4C	n	1	3	2	8	7	6	3	4	4	2	1	1	7	6	3	1	3	1	3	1	1
	M	8.030	5.700	3.425	1.993	3.093	1.537	0.990	2.010	2.498	1.835	2.220	1.239	1.630	0.805	1.237	1.127	0.804	0.671	0.804	0.671	1
	min	-	5.530	2.120	1.530	2.860	1.190	0.760	1.900	2.310	1.700	-	-	1.459	0.717	1.216	-	0.783	-	-	-	1
	max	-	5.860	4.730	2.550	3.310	1.740	1.200	2.150	2.620	1.970	-	-	1.869	0.874	1.278	-	0.838	-	-	-	1
	SD	-	0.165	1.846	0.296	0.148	0.251	0.165	0.128	0.132	0.191	-	-	0.149	0.057	0.035	-	0.029	-	-	-	1
Q4E	n	0	1	1	5	4	4	3	3	3	1	1	0	4	4	3	1	1	0	1	1	0
	M	-	5.370	4.480	1.934	3.278	1.658	1.398	1.820	2.370	1.860	2.020	-	1.706	0.845	1.324	1.086	0.757	-	-	-	1
	min	-	-	-	1.670	3.040	1.440	1.250	1.500	2.300	-	-	-	1.442	0.787	1.156	-	-	-	-	-	1
	max	-	-	-	2.490	3.590	2.230	1.650	2.110	2.440	-	-	-	1.946	0.896	1.533	-	-	-	-	-	1
	SD	-	-	-	0.319	0.229	0.382	0.178	0.306	0.070	-	-	-	0.212	0.049	0.192	-	-	-	-	-	1
Recent CR																						
	n	18	18	19	18	18	18	19	19	19	19	19	18	18	18	19	19	19	18	18	18	18
	M	7.361	5.257	4.484	1.811	2.887	1.485	1.200	2.055	2.353	1.899	2.146	1.173	1.598	0.819	1.147	1.133	0.817	0.748	0.817	0.748	18
	min	6.670	4.660	4.060	1.540	2.530	1.120	0.920	1.780	2.030	1.730	1.960	1.012	1.483	0.655	1.030	0.947	0.741	0.660	0.947	0.741	18
	max	7.900	5.650	5.030	2.030	3.040	1.720	1.630	2.250	2.620	2.170	2.540	1.245	1.738	0.901	1.309	1.415	0.893	0.941	1.415	0.893	18
	SD	0.281	0.241	0.245	0.132	0.148	0.184	0.194	0.119	0.132	0.110	0.184	0.069	0.076	0.071	0.069	0.121	0.043	0.091	0.121	0.043	18

the average values): *Pliomys episcopalis*, *P. coronensis* (=lenki), *Spermophilus* spp., *Lagurus pannonicus*, *Microtus arvalidens*, and in older sections also *Beremendia fissidens*), i.e. elements indicating a warm semi-open landscape with a significant proportion of open habitats.

In summary, the nature of hamster occurrence in the fossil record of the Early Pleistocene sections does not differ much from the Q4 conditions considered above. Its occurrence is rather sporadic, reaching increased abundance in sections with a greater proportion of open landscape indicators. This seems to be the case, especially in the transitional section of Q1 and Q2 biozone and then in the older section of Q3. Although the limited number of localities from deeper sections of the Quaternary past does not allow us to draw more detailed conclusions, it seems that the clearly more frequent occurrence and greater abundance in the Early Pleistocene are linked mainly to localities from the Pannonian area (Slovakian Karst, Lower Považie Basin).

Biometric patterns

A total of 465 fossil items were processed by biometric analysis, comprising a total of 58 maxillary and 31 mandibular tooth rows and 292 teeth (96 M₁, 95 M₂, 75 M₃, 55 M¹, 46 M², 31 M³). A synoptic overview of the biometric characteristics of samples from individual stratigraphic stages is given in Table 1, more detailed comparisons are provided in Figs. 6–8.

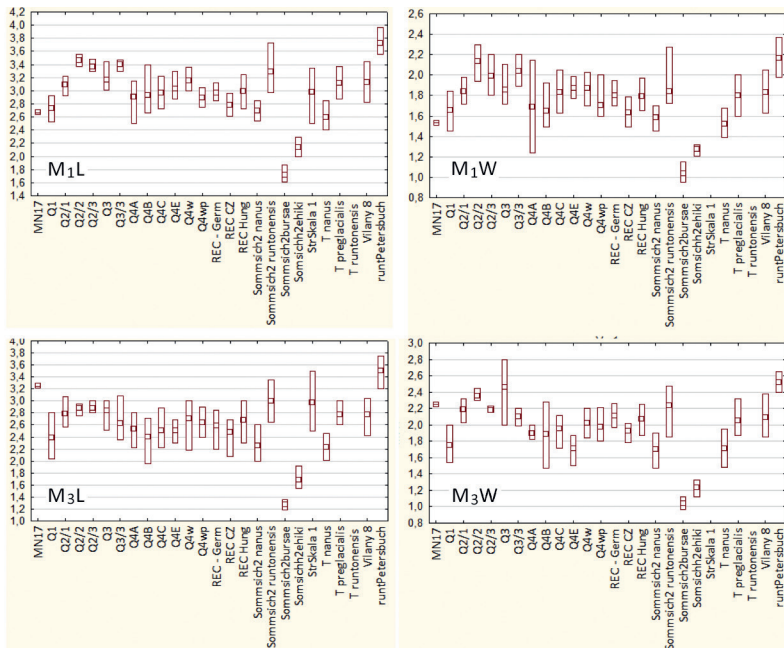


Fig. 6. Mean values and variation ranges of M₁ and M₃ dimensions of *Cricetus* sp. in individual stratigraphic horizons of Czech and Slovakian record supplemented by corresponding literary data (HELLER 1972, FAHLBUSCH 1976, Hír 1993b, 1997c) from selected sites abroad, including type series (T) of *Cricetus nanus* and *C. praeglacialis*.

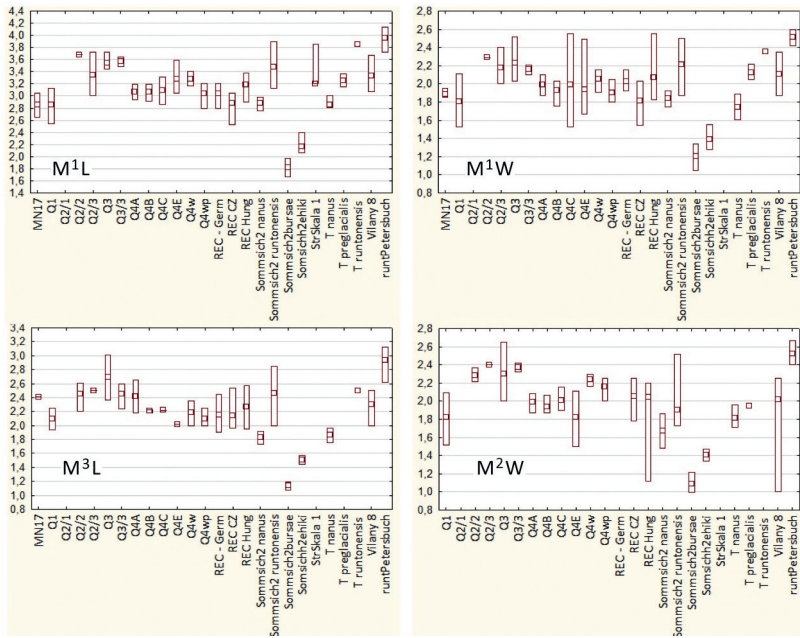


Fig. 7. Mean values and variation ranges of M^1 and M^3 dimensions of *Cricetus* sp. in individual stratigraphic horizons of Czech and Slovakian record supplemented by corresponding literary data (HELLER 1972, FAHLBUSCH 1976, HÍR 1993b, 1997c) from selected sites abroad, including type series (T) of *Cricetus nanus*, *C. runtonensis* and *C. praeglacialis*.

Despite the small number of records in some of these assemblages, limiting detailed analysis, comparisons of these data, as well as analogous comparisons of the variation ratios of individual teeth suggests: (i) the variation ratios in the Late Glacial and earliest Holocene (Q4abc) populations significantly exceed the variation span of the sample of the Recent populations of the Czech Republic, while (ii) in course of the respective period almost all longitudinal dental dimensions exhibit a nearly gradual increase (iii) This trend can also be traced in the samples of the post-Neolithic populations, which, despite some overlap, show somewhat larger dimensions than the Recent populations. (iv) Worth mentioning is that the set of specimens from earlier Vistulian (Q4w: MIS5–MIS2) exceed those of the Holocene populations in mean size and stand above the upper limit of the variation range of the Recent population. (v) The Q2 and Q3 records show the clearest differences in this respect, exceeding all other groups in size. (vi) In contrast, the specimens from the earliest sites covered by our study (MN17–Q1) exhibited the smallest values of the entire material compared. (vii) The specimens from the end of the Q1 biozone (Včeláre 6/8, Včeláre 4A) or from the beginning of the Q2 biozone (Q2/1 Včeláre 4E, Honce) show a transitional state in these respects, roughly corresponding to the size characteristics of the Q4 populations. (viii) Relatively rich material from historical collections from Prague brickworks, accompanying typical forms of the glacial fauna (cf. KAFKA 1893), shows full agreement with the proportions of Recent populations of the Czech Republic.

Comparison with the metric characteristics of the type series of individual Pleistocene taxa (*Cricetus nanus*, *C. praeglacialis*, *C. runtonensis*) and the variation ratios of numerous assemblages from foreign localities (Q3 Petersburg, FAHLBUSCH 1976; Q2 Betfia, Hír 1993b, 1997a, b; Q2/1 Somssich-hegy 2, Hír 1998; Q2/3 Villány 8, Hír 1997c) is in good agreement with the above conclusions (Figs. 6, 7). At the same time, it indicates that in the European fossil record of the hamster, three groups of populations with characteristic stratigraphic distributions corresponding to the nominate taxa *Cricetus nanus* (MN17–Q1), *C. runtonensis* (Q2–Q3) and *C. cricetus* (Q3–Q4) can be quite clearly distinguished – Figs. 9, 10.

Despite the clear metric differences, by the proportions of mandibular and maxillary dentition including individual teeth, the three groups do not show any significant differences.

Genera *Cricetulus*, *Allocricetus* and *Phodopus*

The small hamsters were essentially taken as a single taxonomic operational unit, we omitted the question of taxonomic diversity of the Early Pleistocene records and restricted our study onto the appearance of this group in the present cycle and the generic affiliation of particular records. For that reason, we retrieved a large set of comparative materials illustrating variation in subrecent and/or Holocene populations of *Cricetulus migratorius* and *Mesocricetus newtoni*

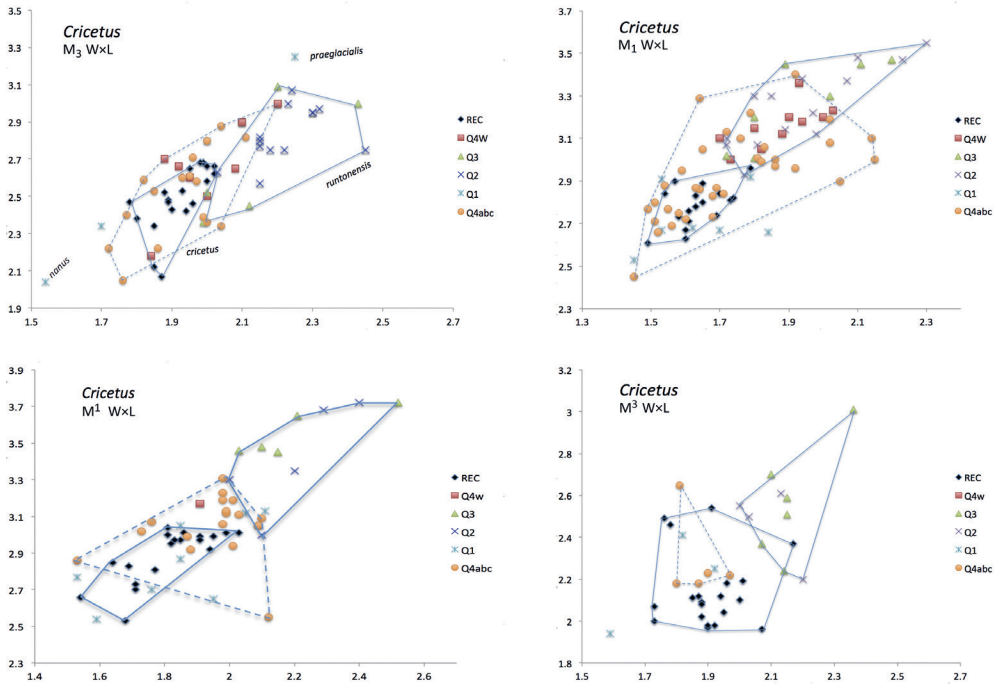


Fig. 8. Scatter plot of length and width dimensions of individual teeth of *Cricetus* sp. from samples of particular stratigraphic horizons of Czech and Slovakian record.

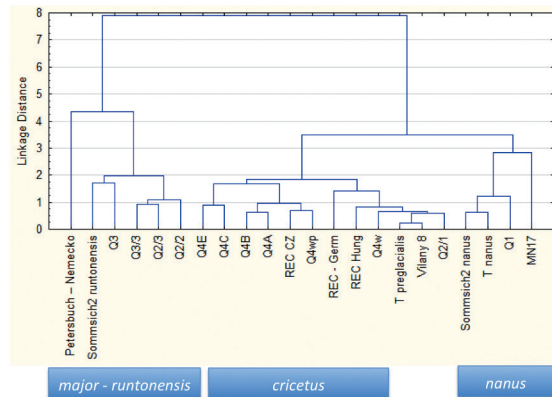


Fig. 9. Ordination of *Cricetus* sp. datasets from individual stratigraphic horizons of Czech and Slovakian record supplemented by corresponding literary data (FAHLBUSCH 1976, Hír 1993b, 1997c) from selected sites abroad, including type series (T) of *Cricetus nanus* and *C. praeglacialis*. Based on set of mandibular teeth dimensions and their proportion indices (UPGMA clustering, Manhattan distance, complete linkage).

in their extant ranges in SE Europa and Asia Minor. In total 312 fossil items and 475 items of comparative material were examined.

Occurrence in the current (Q4) cycle

The presence of small hamsters was confirmed in 21 communities of 15 sedimentary sequences from the Czech Republic and in Dzeravá skala Cave (Malé Karpaty Mts.), Western Slovakia. The absence in other Slovakian localities, especially in the numerous sedimentary sequences of the Slovakian Karst, otherwise rich in diversified micromammal communities, is quite surprising and deserves a special attention. Two records from the Moravian Karst and one from the Bohemian Karst come safely from the subzone Q4a, i.e. the Late Vistulian (after LGM) to the earliest Holocene and can be looked upon as the last appearance datum of *Cricetulus* in our territory. Seven records come from the context of the Late Vistulian communities (w3 = LGM, MIS2), and nine from the earlier Vistulian (w1–w2: MIS3–MIS4). The only records with a more numerous representation of this taxon come from the latter stage (Nad Kačákem, Dzeravá, Bašta Caves), in the others, the record is mostly limited to a single tooth or jaw fragment. In the total set of 880 Q4 communities, it is one of the rarest species, with a frequency of 2.6% and dominance of 0.07% in the total sample. Even in the communities in which it is present, it occurs with an average dominance of only 1.82% (max. 7%). From the analysis of the accompanying communities (Fig. 11) it is evident that the appearance of small hamsters is closely associated with the presence of the taxa otherwise quite rare in Q4 fossil record such as *Marmota* sp., *Allactaga major*, *Lemmus lemmus*, *Chionomys nivalis*, *Lagurus lagurus*, *Hystrix vinogradovi*, *Spermophilus citelloides*, and *S. superciliosus*, i.e., the elements characterizing the more climatically favorable sections of the glacial period with full development of the steppe habitats. The leading elements of the glacial communities *Microtus anglicus* (= *gregalis*), *Dicrostonyx torquatus* or *Microtus arvalis* are also more frequently present than average. At the same time, a relatively wide range of other forms (including insectivores and indicators of

semi-open landscapes) are also present in the individual communities, but their dominance is clearly reduced compared to the average values.

Occurrence in the deeper Pleistocene past

The representation of small hamsters (generally identified as *Allocricetus bursae*) in the older sections of the Pleistocene is significantly more numerous than in the genus *Cricetus*. In the material available from the Czech Republic and Slovakia, they were represented in a total of 43 record units (8 MN17, 8 Q1, 20 Q2, 7 Q3). Moreover, in several localities, there were relatively large groups of multiple individuals (Koněprusy C718, Žirany, Plešivec, Včeláře 6, 4, Turoid NE). As in the fossil record of Q4, it is evident that co-occurrence with representatives of the genus *Cricetus* is the exception rather than the rule (cf. Figs. 5, 11).

Biometric patterns and taxonomic structure of the clade

Table 2 provides a summary of basic statistics for aggregated samples from the individual stratigraphic horizons and comparative material.

A basic comparison of the biometric characteristics, both in terms of mean values and range of variation of individual metric variables, divides the set of populations compared into two groups: (a) a group of small forms of the present cycle (Q4) and (b) a group of populations from the Early and Middle Pleistocene (MN17–Q3), showing distinctly larger dimensions (Figs. 12, 13).

Within group (b), the members of which can be referred to as *Allocricetus bursae* in accordance with general convention, the following facts are noticeable (at least in the case of the mandibular dentition, which is significantly more frequently represented in the fossil record): (i) the mean values of the Q1 and especially MN17 items are clearly higher than those of the Q2 and Q3 age; (ii) all of these samples, however, show a greater range of variation than those of the Q4 biozone and Recent taxa, (iii) this fact can be attributed to the presence of specimens of significantly

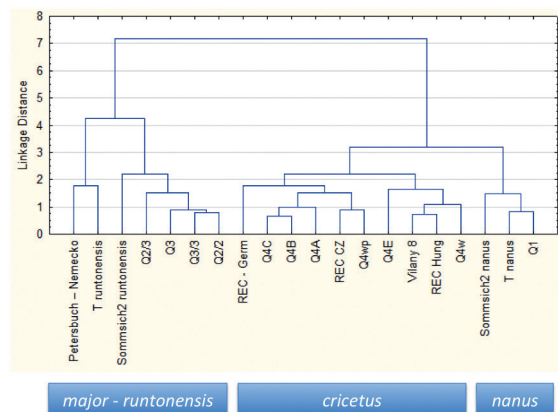


Fig. 10. Ordination of *Cricetus* sp. datasets from individual stratigraphic horizons of Czech and Slovakian record supplemented by corresponding literary data (FAHLBUSCH 1976, HÍR 1993b, 1997c) from selected sites abroad, including type series (T) of *Cricetus nanus*, *C. runtonensis* and *C. praeglacialis*. Based on set of maxillary teeth dimensions and their proportion indices (UPGMA clustering, Manhattan distance, complete linkage).

Table 2. (continued)

Q4w	n	8	9	9	14	14	14	14	14	14	11	11	13	13	6	6	7	7	6
	M	3.854	2.756	2.364	0.978	1.552	0.657	0.621	1.035	1.243	0.944	1.160	1.152	1.585	0.666	1.185	1.244	0.789	0.768
	min	3.730	2.620	2.240	0.890	1.360	0.490	0.360	1.000	1.150	0.860	1.110	1.123	1.360	0.485	1.045	1.088	0.762	0.730
	max	4.000	2.920	2.500	1.120	1.760	0.930	1.090	1.120	1.470	1.050	1.210	1.192	1.725	0.890	1.336	1.326	0.815	0.825
	SD	0.094	0.114	0.075	0.064	0.099	0.129	0.212	0.040	0.101	0.066	0.036	0.025	0.100	0.111	0.090	0.088	0.021	0.033
Recent <i>Photopus</i>																			
n	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14
M	3.646	2.647	2.121	0.921	1.489	0.681	0.586	0.928	1.141	0.853	1.039	1.249	1.619	0.739	1.230	1.220	0.769	0.702	
min	3.480	2.430	2.010	0.840	1.390	0.530	0.430	0.870	1.080	0.790	0.850	1.161	1.469	0.570	1.174	1.063	0.653	0.528	
max	3.870	2.910	2.230	0.990	1.760	0.880	0.840	0.960	1.230	0.910	1.150	1.438	1.869	0.952	1.323	1.322	0.860	0.799	
SD	0.108	0.141	0.075	0.041	0.098	0.107	0.134	0.029	0.040	0.038	0.079	0.084	0.118	0.111	0.043	0.104	0.055	0.084	
Turkey <i>Cricetulus Bolu</i>																			
n	13	26	19	34	35	35	35	32	31	19	19	13	34	34	30	18	25	13	
M	3.878	2.735	2.396	0.969	1.604	0.658	0.502	0.918	1.224	0.884	1.197	1.127	1.668	0.693	1.281	1.320	0.818	0.825	
min	3.700	2.600	2.210	0.780	1.100	0.300	0.350	0.000	1.090	0.400	1.000	1.037	1.458	0.521	1.089	1.020	0.727	0.671	
max	4.220	2.950	2.700	1.200	2.280	0.830	0.730	1.060	1.590	1.000	1.380	1.179	2.092	0.842	1.611	1.610	1.182	1.164	
SD	0.168	0.091	0.126	0.090	0.267	0.096	0.080	0.210	0.096	0.136	0.085	0.036	0.160	0.074	0.140	0.137	0.086	0.115	
Turkey <i>Cricetulus Mencilar</i>																			
n	16	17	16	19	19	19	19	19	19	18	18	16	19	19	19	18	17	16	
M	3.906	2.732	2.425	0.938	1.486	0.659	0.517	0.984	1.227	0.937	1.211	1.122	1.587	0.702	1.251	1.295	0.823	0.814	
min	3.330	2.280	2.030	0.820	1.260	0.560	0.400	0.880	0.980	0.850	1.110	1.036	1.273	0.615	0.980	1.156	0.776	0.763	
max	4.060	2.910	2.520	1.060	1.630	0.990	0.940	1.100	1.290	1.020	1.310	1.165	1.769	1.000	1.455	1.409	0.896	0.911	
SD	0.191	0.151	0.121	0.054	0.088	0.090	0.118	0.048	0.073	0.048	0.054	0.034	0.111	0.081	0.102	0.072	0.038	0.047	
Turkey <i>Mesocricetus Mencilar</i>																			
n	0	1	1	7	7	7	8	8	3	3	0	0	0	7	7	3	0	1	0
M	-	3.980	4.220	1.194	2.100	0.871	0.771	1.337	2.050	-	-	-	-	1.762	0.663	1.539	-	0.942	-
min	-	-	-	1.090	2.050	0.690	0.420	1.180	1.940	-	-	-	-	1.622	0.561	1.406	-	-	-
max	-	-	-	1.270	2.250	1.440	2.010	1.450	2.260	-	-	-	-	1.881	0.723	1.653	-	-	-
SD	-	-	-	0.059	0.068	0.241	0.509	0.140	0.182	-	-	-	-	0.092	0.071	0.125	-	-	-

Table 2. (continued)

Q2	n	5	9	6	21	21	21	12	12	12	6	5	6	21	21	12	5	10	4
	M	4.220	3.293	2.400	1.277	2.040	1.041	0.819	1.204	1.337	1.068	1.174	1.333	1.576	0.821	1.116	1.085	0.714	0.574
	min	4.040	3.000	2.290	1.000	1.660	0.740	0.580	1.050	1.150	0.980	1.020	1.259	1.097	0.673	0.948	0.963	0.641	0.541
	max	4.340	3.610	2.500	2.060	3.260	1.450	1.670	1.540	1.480	1.230	1.640	1.375	1.937	1.171	1.314	1.333	0.843	0.614
	SD	0.137	0.209	0.069	0.246	0.424	0.179	0.257	0.124	0.110	0.087	0.265	0.044	0.160	0.097	0.105	0.150	0.067	0.038
Q3	n	0	0	0	10	10	10	10	1	1	0	0	0	10	10	1	0	1	0
	M	-	-	-	1.207	1.999	1.024	0.731	1.160	1.440	-	-	-	1.662	0.853	1.241	-	0.664	-
	min	-	-	-	1.040	1.880	0.900	0.580	-	-	-	-	-	1.492	0.759	-	-	-	-
	max	-	-	-	1.330	2.170	1.120	0.920	-	-	-	-	-	1.838	1.077	-	-	-	-
	SD	-	-	-	0.086	0.106	0.064	0.123	-	-	-	-	-	0.114	0.088	-	-	-	-
Q4abc	n	0	0	1	2	2	2	2	1	1	0	0	0	1	1	1	0	1	0
	M	-	-	3.200	1.025	1.705	0.915	0.780	1.000	1.340	-	-	-	1.608	0.794	1.176	-	0.971	-
	min	-	-	-	1.020	1.640	0.810	0.710	-	-	-	-	-	-	-	-	-	-	-
	max	-	-	-	1.030	1.770	1.020	0.850	-	-	-	-	-	-	-	-	-	-	-
	SD	-	-	-	0.007	0.092	0.148	0.099	-	-	-	-	-	-	-	-	-	-	-
Q4w	n	4	5	6	12	12	12	9	11	11	6	5	1	11	11	9	2	6	2
	M	3.700	2.968	2.382	1.063	1.717	0.861	0.652	1.020	1.229	1.633	0.938	1.362	1.508	0.779	1.329	0.706	1.228	0.886
	min	3.110	2.800	2.040	0.950	1.620	0.790	0.550	0.910	1.150	0.820	0.900	-	0.451	0.418	1.114	0.343	0.669	0.564
	max	3.990	3.140	2.830	1.180	1.820	0.970	0.760	1.140	1.310	3.110	0.990	-	1.789	0.947	2.508	1.069	3.793	1.207
	SD	0.401	0.141	0.354	0.073	0.059	0.063	0.073	0.059	0.060	1.057	0.041	-	0.366	0.137	0.446	0.514	1.257	0.455
Recent <i>Photopus</i>	n	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
	M	3.632	2.715	2.112	0.976	1.561	0.730	0.615	0.968	1.129	0.826	1.018	1.292	1.611	0.749	1.168	1.232	0.726	0.656
	min	3.350	2.600	1.880	0.810	1.430	0.580	0.500	0.920	1.010	0.740	0.840	1.133	1.333	0.614	1.020	1.105	0.634	0.480
	max	3.820	2.910	2.330	1.110	1.750	0.890	0.710	1.040	1.210	0.880	1.120	1.470	2.012	0.868	1.269	1.329	0.818	0.783
	SD	0.163	0.083	0.151	0.087	0.087	0.106	0.074	0.035	0.052	0.045	0.082	0.106	0.183	0.095	0.069	0.070	0.057	0.078

Table 2. (continued)

	M ₁ -M ₃	M ₂ -M ₃	M ₁ W	M ₁ L	M ₁ Wa	M ₁ La	M ₂ W	M ₂ L	M ₂ W	M ₂ L	M ₃ W	M ₃ L	M ₁₂ W ₃	M ₁ LW	M ₁ WaW	M ₂ LW	M ₃ LW	M ₂ L/M ₁ L	M ₃ L/M ₁ L	M ₂ L/M ₁ L	M ₃ L/M ₁ L
Turkey <i>Cricetulus Bolu</i>																					
n	26	42	42	42	42	42	42	42	42	42	26	26	26	42	42	42	26	42	42	42	26
M	3.838	2.826	2.161	1.036	1.660	0.645	1.024	1.142	0.925	1.051	1.288	1.609	0.867	1.123	1.141	0.689	0.638				
min	3.530	2.420	1.940	0.840	1.430	0.670	0.680	0.660	0.780	0.940	1.095	1.430	0.694	0.750	0.955	0.398	0.571				
max	4.180	3.840	2.490	1.170	1.890	0.960	1.150	1.310	1.100	1.230	1.352	1.929	1.513	1.676	1.295	0.810	0.759				
SD	0.172	0.207	0.107	0.079	0.089	0.161	0.093	0.086	0.110	0.068	0.058	0.057	0.120	0.119	0.145	0.082	0.067	0.040			
Turkey <i>Cricetulus Mencilar</i>																					
n	19	29	22	36	36	35	34	34	34	22	22	22	19	36	35	34	22	29	29	19	19
M	3.802	2.830	2.153	1.060	1.708	0.652	1.050	1.229	0.866	1.014	1.304	1.737	0.922	1.172	1.179	0.703	0.602				
min	3.270	2.410	1.940	0.910	1.480	0.630	0.460	0.710	1.040	0.680	0.850	1.242	1.432	0.589	0.982	0.972	0.629	0.553			
max	4.130	3.070	2.390	1.350	2.300	1.130	0.820	2.160	2.790	1.060	1.140	1.359	6.061	3.394	1.465	1.417	0.815	0.671			
SD	0.201	0.145	0.105	0.096	0.175	0.088	0.076	0.219	0.300	0.084	0.070	0.035	0.746	0.434	0.106	0.120	0.040	0.033			
Turkey <i>Mesocricetus Mencilar</i>																					
n	2	8	3	14	14	14	9	9	9	4	4	4	2	14	14	9	4	8	8	2	2
M	5.635	4.389	3.327	1.412	2.488	1.284	0.848	1.518	1.900	1.378	1.755	1.214	1.774	0.945	1.269	1.281	0.826	0.712			
min	5.590	3.980	3.310	1.020	1.800	0.940	0.690	1.280	1.640	1.300	1.580	1.211	1.547	0.648	1.037	1.088	0.704	0.690			
max	5.680	5.430	3.340	1.890	3.180	2.500	1.250	2.190	2.270	1.480	2.120	1.216	2.056	2.451	1.432	1.582	1.211	0.734			
SD	0.064	0.502	0.015	0.248	0.369	0.408	0.155	0.275	0.215	0.078	0.250	0.003	0.154	0.445	0.157	0.224	0.165	0.031			
Turkey <i>Mesocricetus Bolu</i>																					
n	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bulgaria <i>Cricetulus Karlukovo</i>																					
n	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
M	5.645	4.095	3.365	1.335	2.295	1.055	0.865	1.565	1.900	1.385	3.610	1.217	1.720	0.791	1.220	2.560	0.828	1.575			
min	5.580	4.040	3.280	1.310	2.290	1.050	0.710	1.450	1.880	1.340	1.510	1.203	1.684	0.772	1.143	1.127	0.817	0.657			
max	5.710	4.150	3.450	1.360	2.300	1.060	1.020	1.680	1.920	1.430	5.710	1.232	1.756	0.809	1.297	3.993	0.838	2.493			
SD	0.092	0.078	0.120	0.035	0.007	0.007	0.219	0.163	0.028	0.064	2.970	0.020	0.051	0.026	0.109	2.027	0.015	1.299			

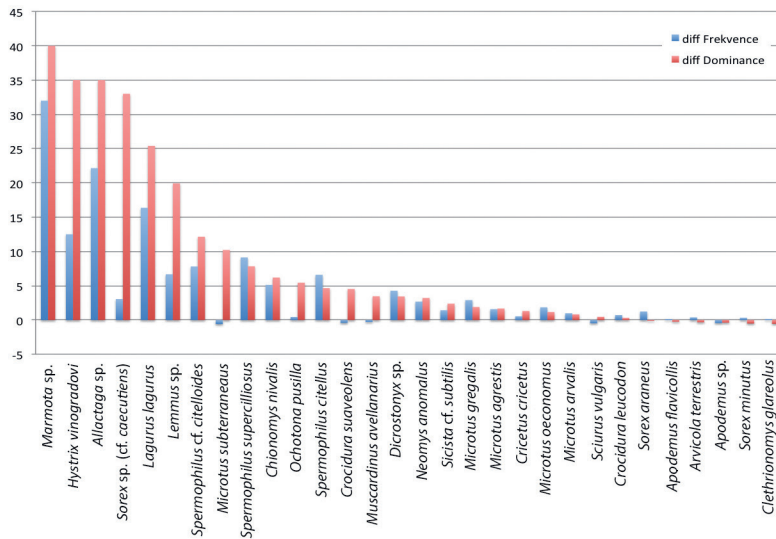
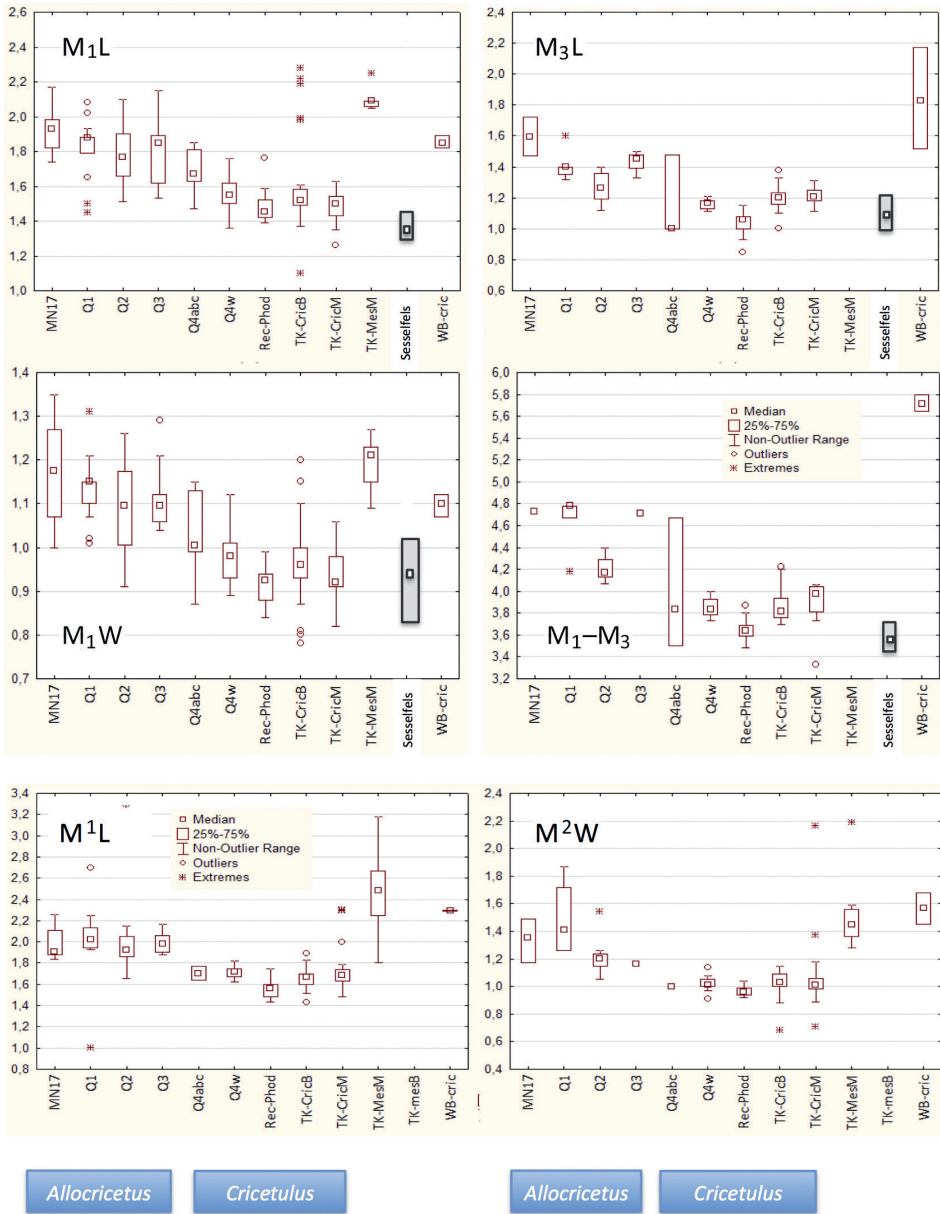


Fig. 11. Small mammal communities accompanying Q4 record of *Cricetulus migratorius*: Ratio of frequency (% of sites) and dominance (% abundance – MNI) in communities with *Cricetulus* presence to respective values in the entire set of Q4 communities (n=880) for the species composing the former set. Arranged by rank of dominance ratio.

larger than average size – at least some of them fall within the variation span of the largest form of the group – *Allocricetus ehiki* – clearly the case in the MN17 Plešivec, Q1 Včeláre 4, Q2 Chlum 4 samples. Unfortunately, the limited scope of our material does not allow us to test the hypothesis of a discrete position of this form, but the fact that the statistical distribution of dimensions in MN17 and Q1 samples does not meet the normality criterion (cf. results of the Shapiro-Wilks test in Fig. 14) seems to support it. (iv) Bivariate comparisons (Fig. 13) suggest a rather continuous distribution within a very wide range of variation, exceeding the range of variation of the Q4 populations (including comparative sets of Recent species). (v) However, the outliers appear to be confined to populations of a few localities (cf. maximum values for Turol NE7 for Q3, Plešivec for MN17, Chlum 4 for Q2, minimum values for Q2 Koněprusy C718, JK). Unfortunately, however, our material is clearly insufficient for quantitative testing of the locality effect. (vi) Although the largest individuals from these sites encroach on the edge of the variation range of the Recent *Mesocricetus newtoni*, the overall shape of the variation field of the Early and Middle Pleistocene specimens clearly corresponds to the pattern of variation of the Q4 populations and the comparative samples of *Cricetulus migratorius*, respectively (Figs. 12, 13). (vii) The Q2 and Q3 sets of items show a high probability of normal distribution that does not suggest the presence of multiple taxa (cf. Fig. 14).

In the case of group (a) – small hamsters of biozone Q4 – the following can be stated: (i) a very compact group is the set of items of the Vistulian age (Q4w = MIS5b–MIS2). Here, the values of the individual variables fall within a relatively narrow range with perfectly normal distributions with mean values corresponding to the sets of the compared Recent samples; (ii)



Allocricetus

Cricetulus

Allocricetus

Cricetulus

Fig. 12. Mean values and ranges of variation of selected dimensions of mandibular and maxillary dentition of small hamsters in sets of individual stratigraphic horizons from the Czech Republic and Slovakia (MN17–Q4) and sets of Holocene records of *Cricetulus migratorius* and *Mesocricetus newtoni* from Turkey (TK), a sample of Recent *Phodopus sungorus*, a Q4w population from the Sesselfelsgrötte (VAN KOLFSCHOTEN 2014) and a Q4W2 sample from the Bulgarian site Karlukovo 4 (BW).

the sparse late glacial and earliest Holocene specimens show, in contrast, clearly higher mean values and a wider range with the presence of items exceeding the upper margin of the variability of the glacial specimens and the Recent forms compared, (iii) At the same time, items from the lower limits of the variation range (Bišilu 6) are encountered here, corresponding to some items of the glacial communities of supposedly the MIS3 age (Balcarcka, Bašta 9, Dzeravá 5,

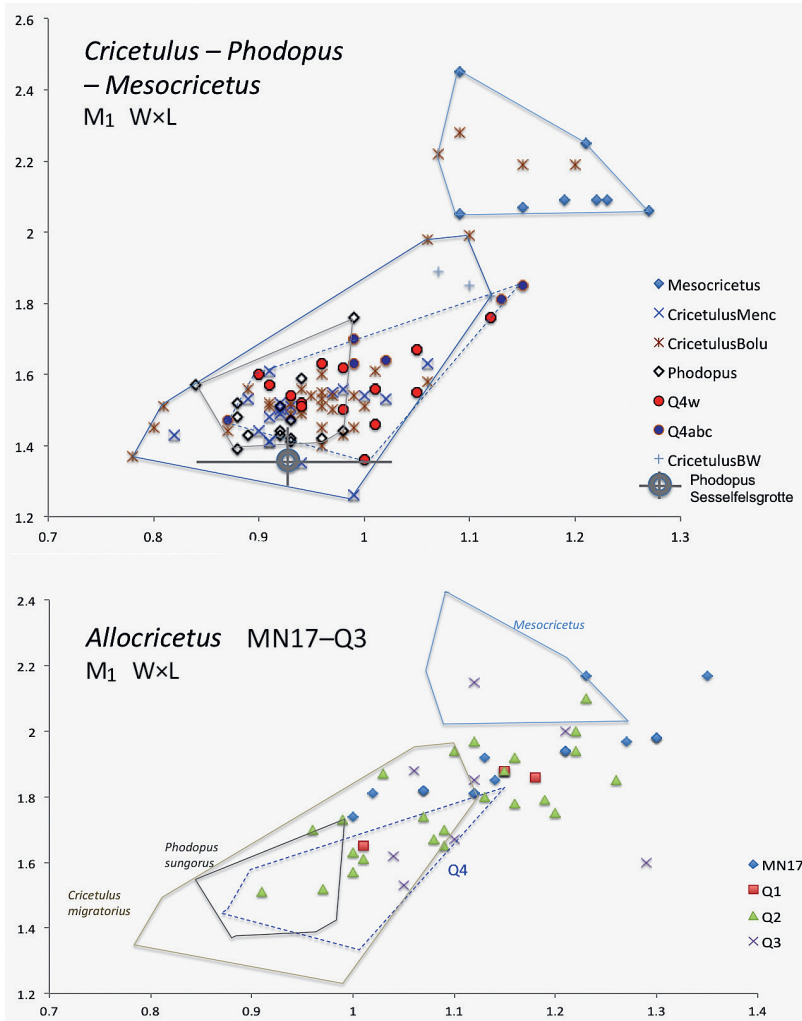


Fig. 13. Scatter plots of M_1 width to length in small hamsters from Czech and Slovakian localities of different stratigraphic sections, in the Holocene assemblages of *Cricetulus migratorius* and *Mesocricetus newtoni* from Turkey (TK), a sample of Recent *Phodopus sungorus*, a Q4w population from the Sesselfelsgrotte (VAN KOLFSCHOTEN 2014) and a Q4W2 sample from the Bulgarian site Karlukovo 4 (BW).

Martinka 10). In these cases, it is, therefore, appropriate to consider an alternative determination option – referring them, in analogy with the proposal of VAN KOLFSCHOTEN (2014), to *Phodopus sungorus*.

In this context, it should be recalled that the main argument for the above determination is the extremely small size of the single teeth outside the variation range of most fossil populations and Recent populations of *Cricetulus migratorius* (cf. VAN KOLFSCHOTEN 2014). However, the relatively large comparative assemblage of *Cricetulus migratorius* from two late Holocene localities in the current distribution area (Pontic region of Turkey) shows a much wider range

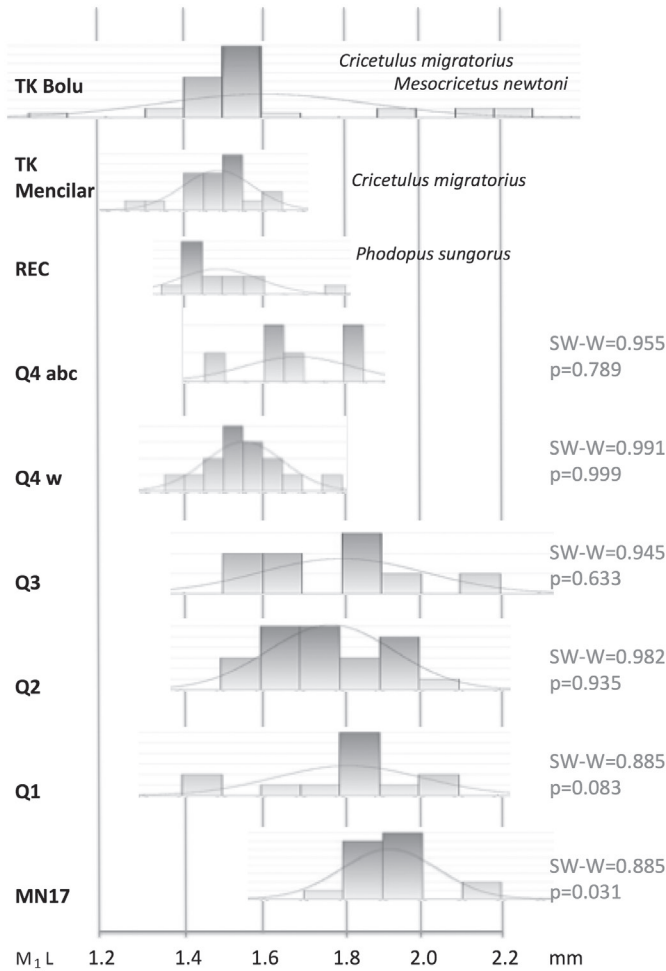


Fig. 14. Frequency diagrams of the M_1 length (M_1L) in small hamsters from Czech and Slovakian localities of different stratigraphic horizons, in the Holocene assemblages of *Cricetulus migratorius* and *Mesocricetus newtoni* from Turkey (TK), in and values of the Shapiro-Wilks test for normality of distribution (right).

of variation than that indicated by most literature sources, especially regarding the presence of extremely small individuals (Figs. 12–14). With this in mind, our analysis shows that the size variation range of *Phodopus sungorus* falls entirely within the range of variation of the compared population of *Cricetulus migratorius* (Figs. 12, 14). In other words, size characteristics alone are not, at least in the case of individual specimens, a sufficient guarantee of a reliable determination. For this reason, we have extended the comparisons to take into account the state of the non-metric characters distinguishing the genus *Phodopus* proposed by VORONCOV (1982). Namely, (i) the absence of the para- and metafossets of the maxillary molars which present in most specimens of *Cricetulus* (central enamel islands – clearly visible, e.g., in Plate 5/2d), this condition being related to (ii) the generally very shallow median groove separating the lingual and labial cusps of the teeth. As a consequence, already at a relatively low degree of abrasion (iii) adjacent tubercles merge into broad lophs reminiscent of the situation in the genus *Meriones*, less clearly this tendency is also evident on the mandibular molars. (iv) The cingulum posterior on the maxillary molars is only indistinct, (v) the cingulum anterior on M² runs out lingually into a distinct process. In our set of Recent *Phodopus sungorus*, we confirmed the above characters to varying degrees, although not in all specimens (cf. e.g. the presence of fossets on Plate 5/1a). Analogously, however, especially in the case of characters (i), (iv), and (v), we found the same condition in some specimens of *Cricetulus migratorius* from the Turkish series. Thus, also in this case, the discriminating capacity of these characters seems to refer rather to mean states in larger population samples than to categorical differences between each item of the respective genera. Within the Q4 record, one specimen from the Nad Kačákem Cave (Plate 4/5a) and another from Bišilu 6 (Plate 4/4), might indicate a possible correspondence with the above dental characters of the genus *Phodopus*. In all cases, however, these are mandibular dentitions, maxillary elements where the respective discrimination characters should be properly developed are absent in our collection.

Leaving aside the above controversial items, it can be concluded that, given the wide range of variability of the compared Recent taxon, the vast majority of our Q4 fossil evidence can be co-identified with the Recent species *Cricetulus migratorius*. This conclusion is supported also by the results of the factor analysis (PCA) of the entire set of mandibular variables (including the proportional indices) which shows nearly identical slope of the regression line of the factor variables F1 and F2 in the *Cricetulus migratorius*, Q1, Q2, and Q4w, distinctly different from that for the Recent *Phodopus sungorus* samples.

DISCUSSION

The revision of Quaternary hamster records in the Czech Republic and Slovakia, the results of which are summarized in this paper, is undoubtedly not complete. The material from the Moravian Museum collection and possible other sources have not been physically revised and biometrically assessed. However, published records from these collections are included in the survey which covers with a very high probability a substantial part of the material available from the territories of these countries. Our results are thus believed to provide a reliable platform for further analyses. Discussing them we will address just a few elementary questions: (i) what the Quaternary record from the Czech Republic and Slovakia says about the range history of particular hamster clades?, (ii) what trends in phenotype dynamics do they show?, (iii) how to evaluate alternative concepts on the species composition of this group in their light?, and (iv) what can be said about the past of the extant forms?.

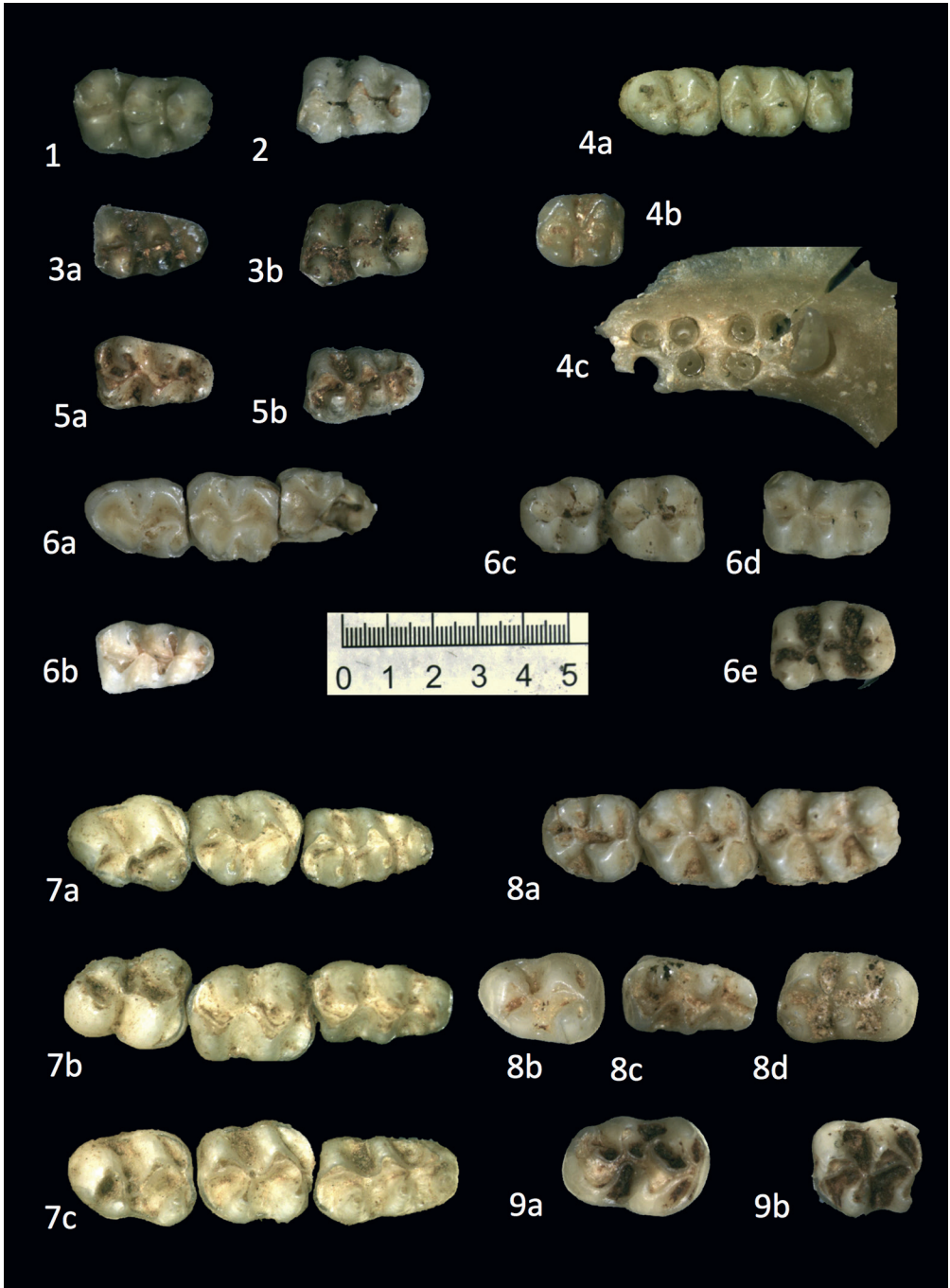
History of *Cricetus cricetus*

The origin of the genus *Cricetus* has traditionally been assigned to records of large forms of hamsters from a number of localities of the Late Miocene and Early Pliocene of the Mediterranean region (MEIN & FREUDENTHAL 1971, FREUDENTHAL et al. 1998, KALIN 1999). The expansion of that group behind the limits of the Mediterranean in that time was obviously related to aridization associated with the Messinian Salinity Crisis (ca. 5.3 Ma). Most of the records of that age were identified as *Cricetus kormosi* Schaub, 1930, a species described from the Hungarian Late Miocene (MN13) site Polgárdi 2, similar to a larger form described later from another profile of that site, *Cricetus polgardiensis* Freudenthal et Kordos, 1989. Several other species of the genus *Cricetus* have been described from Mediterranean localities of the earliest Pliocene (MN14, MN15): *C. angustidens* Déperet, 1891 (MN15 Betterie du Serrat), *C. barrieri* Mein et Michaux, 1970 (MN14 Barrieri), *C. lophidens* de Bruijn, Dawson et Mein, 1970 (MN14 Maritsa), including derived genera isolated on western Mediterranean islands (AGUSTÍ et al. 2012). Isolated records from this section are also available from Central Europe (Podlesice, FAHLBUSCH 1972; Ivanovce, FEJFAR 1970). However, a detailed revision of all these forms (FREUDENTHAL et al. 1998) has shown that, especially in the arrangement of the maxillary molars, they differ significantly from the patterns characterizing the Recent genus and must be classified in a distinct genera *Pseudocricetus* Topachevski et Skorik, 1992 and *Apocricetus* Freudenthal, Mein et Suárez, 1998.

The oldest records of the genus *Cricetus* s.str. thus appear only during the MN17 biozone, in parallel with the development of xerothermic open ground formations preceding the expansion of the genus *Microtus* (cf. our sites Včeláre 6, 7, Koliňany 3; FEJFAR & HORÁČEK 1983). This view is in good agreement with the results of molecular phylogenetic reconstructions (NEUMANN et al. 2006), which place the origin of the genus in the Late Pliocene. As our results show, the hamsters of this section, as in the succeeding Q1 biozone, are characterized by a gracile dentition and overall smaller size falling at the lower limits of the variation range of the Recent species. It is a rare element represented only by single individuals in most localities. The situation clearly changes from the beginning of the Q2 biozone. Especially in the older section characterized by the increased representation of warm open landscape elements, we encounter communities in which the hamster acts as a distinct subdominant element (in our material Honce, Skalka u Nové Mesta nad Váhom – Bzince, in Hungary, especially in Somssich-hégy 2; Hír 1998). Compared to the small hamsters of the earliest Pleistocene, the form from the beginning of the Q2 biozone is clearly distinguished by a larger size around the upper limit of the variation range of Recent populations. An even more pronounced size shift is then evident at the end of the Q2 biozone and in Middle Pleistocene (Q3) populations. Although the hamster is documented from a relatively large number of communities in these sections, it is represented usually only with a very small number of individuals (cf. e.g. SABOL & ZERVASNOVÁ 2014). Morphometric characters of hamsters from different localities of these sections often show quite considerable differences. This corresponds to the large range of cutoff values for individual dimensions in the overall set of these horizons. Certain differences in morphometric variation between a few sites where the hamster is represented by a larger number of individuals (Somssich-hegy 2, Villány 8, Solymár, Petersbuch) may give the impression of distinct separate taxa which can further be combined by

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Plate 1. Dental specimens of *Cricetus* from selected MN17, Q1 and Q2/1 sites: 1 – MN17 Včeláre 6/1, 2 – Včeláre 6/3, 3 – MN17 Včeláre 7, 4 – Q1 Koněprusy PD-1, 5 – Q1 Včeláre 6/7, 6 – Q1 Včeláre 4E, 7 – Q1 Honce, 8 – Q1 Včeláre 6/8, 9 – Q1 Včeláre 11.

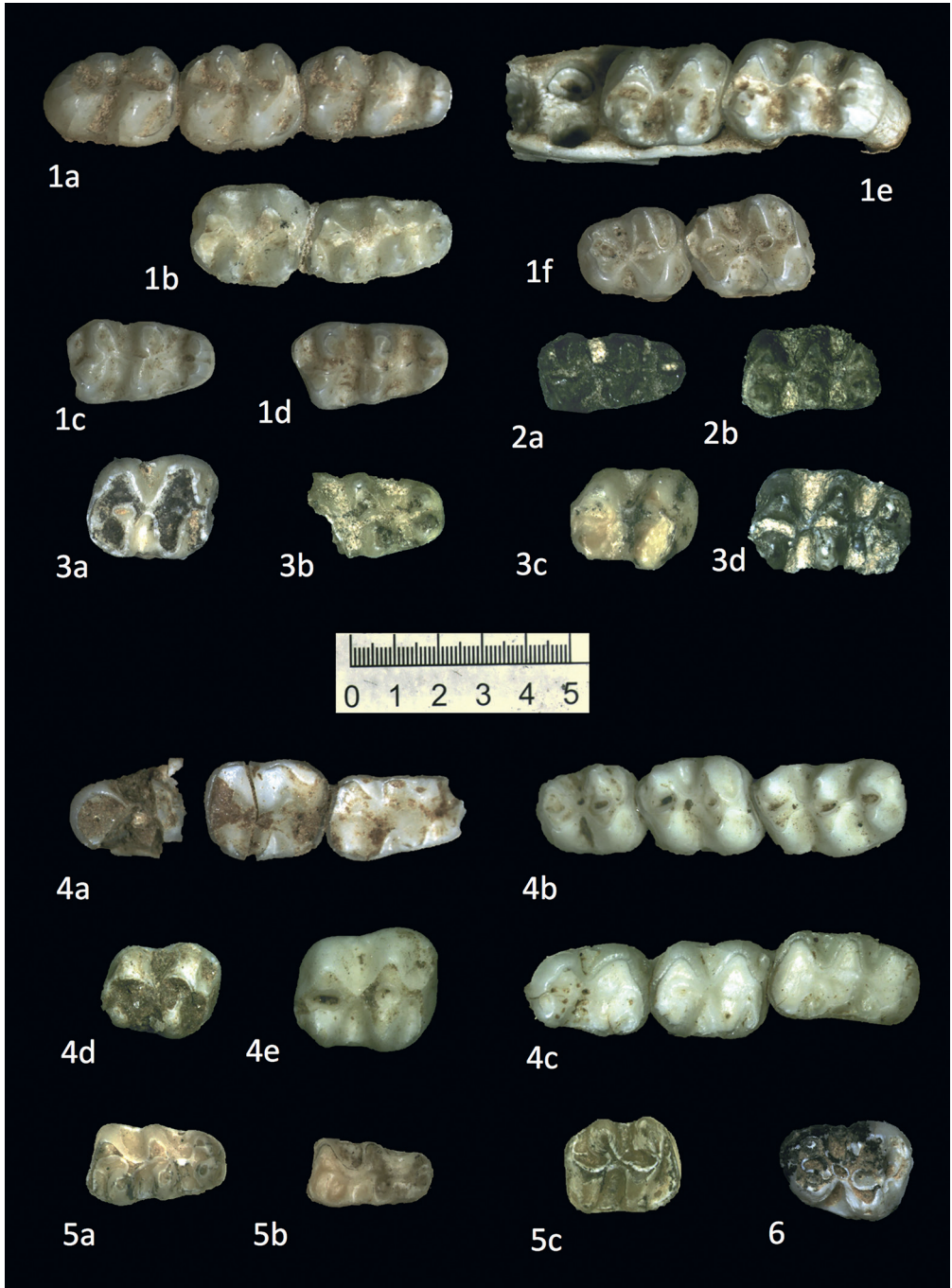


presumptive ad hoc criteria into disparate evolutionary lineages. A result of similar procedures is the concept summarized by HÍR (1997a, b, c, 1998) according to which the Quaternary fossil record consists of four independent evolutionary units, classified at the level of separate species: (i) MN17–Q1 *Cricetus nanus*, extinct at the end of Q1, (ii) Q2–Q3 *C. runtonensis*, characterized by a gradual increase in size, (iii) lineage *C. preaglacialis* – *C. cricetus* represented by smaller specimens appearing sporadically in the Q2, Q3 biozone communities indicating a gradual increase in size, and (iv) a group of Q3 and Q4 glacial giant hamsters documented at Peterbuch sites (FAHLBUSCH 1969) and described as *C. major* from Výpustek Cave (WOLDŘICH 1880). In this context, it should be noted that FAHLBUSCH (1969), considering the stratigraphic position of the examined population from Q3 of the Peterbuch locality standing between the stratigraphic position of the type localities Q2 *C. runtonensis* (UFB West Runton) and Q4w *C. major* (Výpustek), proposes their co-identification under the priority name *C. major*, and, due to the lack of metric overlap with the Recent population, a separate species status for this taxon, distinct from the Recent *C. cricetus*. Coidentification of both the taxa was criticized by PRADEL (1985) while MAUL (1999) and MAUL & PARFITT (2010), based on a comparison of type specimens of *C. runtonensis* and *C. major*, emphasize the distinctiveness of these forms and propose their separate species status. Another topic for discussion in these contexts might be the question of the real stratigraphic position of the type material of *C. major* – for it is by no means granted that it comes from the same context as the collections of typical glacial macrofauna from this locality (LIEBE 1879). The infillings of quite diverse age appear in Výpustek Cave (pers. obs.) and whether all items collected during exploring of the cave in the 19th century came indeed from a single site is not clear.

At this point, however, we will confine ourselves to summarizing the overall picture provided by the fossil record evaluated in this paper to assess the Quaternary history of hamsters. It suggests a more or less continuous increase in size in the sequence MN17-Q1-Q2/1-Q2/2-Q2/3 (cf. Fig. 6), which does not provide much support for the considerations of radical speciation and extinction events at the Q1/Q2 boundary. The increased frequency of the hamster in Q2 biozone communities suggests the possibility of a continuous occurrence and pan-European distribution in that stage, possibly with short-term temporal fluctuations and temporal fixation of local phenotypic specificities within the wide variation range of the large-size form characteristic of the Q2–Q3 period. At least in some phases of this period, short-term abundance cycles (characteristic of the extant species), which greatly amplify the potential for temporal microevolutionary dynamics are likely to occur (as indicated by the numerous occurrences in some localities – see above). In the mid-Pleistocene (Q3), the cyclical appearance of large-scale extinctions in interglacial stages with continuous woodland cover in Central Europe are likely to add to this. Moreover, the extent and spatial dislocation of refugial areas of interglacial occurrence in the more arid southern regions of Central Europe may have varied considerably between particular glacial cycles. Under these circumstances, the phylogenetic history and range dynamics of the species under study might take the form of a coarse mosaic of diverse microevolutionary events, of which the very limited fossil record that is actually available shows only tiny fragments. Attempts to assemble the fragments of this mosaic into separate species or species lineages, delimited mostly by rather faint diagnostic criteria operating often by mean

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Plate 2. Dental specimens of *Cricetus* from selected Q2 and Q3 sites: 1 – Q2/2 Skalka u Nového Mesta nad Váhom – Bzince, 2 – Q2 Chlum 4X, 3 – Q2 Stránská skála 1/6, 4 – Q3 Dobrkovice 2, 5 – Q3 Stránská skála Cave, 6 – Q3 Mladeč 7/20.



size differences only, are to be considered quite premature. In this respect, our conclusions fully support KOWALSKI's (2001) proposal to consider the entire group of Quaternary records of the genus *Cricetus* as a monotypic clade, with distinguishing phenotypically distinct chronological forms as temporally or regionally defined subspecies (i.e., *Cricetus cricetus nanus*, *C. c. runtonensis*, *C. c. major*).

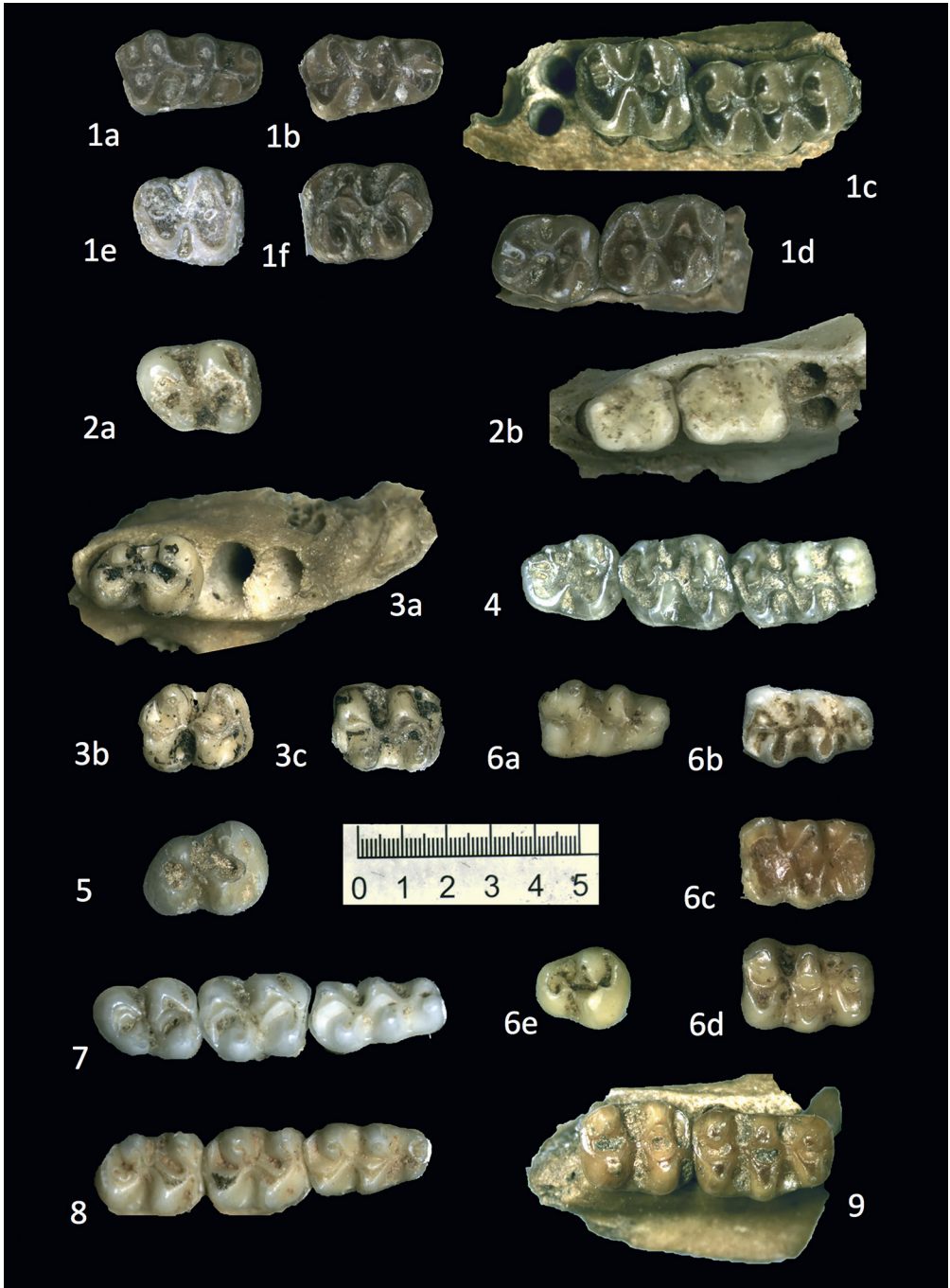
The form of the present glacial cycle Q4, *C. cricetus cricetus*, is very strongly defined in this respect. The Eemian interglacial, with a very rapid onset of the forest phase and a long-term continuous forestation of the whole Central European area, very probably led to the almost complete regional extinction of the studied species. With the gradual disintegration of the woodland cover at the end of the interglacial (MIS5a–5d) and especially in the warmer parts of the older glacial period (MIS3), the populations probably spread gradually from refugial islands in the Pannonian area and from the eastern European steppe zone. In the LGM (MIS2) communities, the hamster is absent with a few exceptions, but local survival in scattered microrefugia must be taken into account, as its presence and the significant onset of distribution can be detected immediately with the warming of the Late Glacial (subzone Q4a). It is then almost continuously recorded in all sites of the planar and colline regions also in the Early Holocene – Pre-Boreal (Q4b) and Boreal (Q4c). With the extensive spread of the forest in the late Boreal and Atlantic (Q4d), local extinctions in most of the area are to be expected. In the Pannonian region (incl. Slovakian Karst) it reappears almost simultaneously with the onset of Neolithic deforestation, while in the Czech Republic its re-expansion, following the post-Neolithic development of the cultural steppe, seems to be somewhat delayed. Comparison of the biometric characteristics of the Q4 populations then provides the following picture: (i) the specimens from the glacial section (Q4w – with the most evidence for earlier glacial phases), show invariably larger sizes than those of the late glacial and Holocene age, (ii) the smallest average sizes within the Q4 fossil record appeared in the populations from the end of the glacial period, a gradual increase in size is evident during the Holocene, and (iii) in general, the largest size is exhibited by the populations of the post-Neolithic age, which in this respect is very clearly distinct from the sample of Recent populations with the smallest size in the entire Q4 material. (iv) A large sample of historical collections from Prague brickyards, supplementing the collections of typical glacial macrofauna (KAFFKA 1893), shows identical metric characteristics of the Recent population. This fact suggests that these are very likely the remains of Recent individuals that died in their burrows in loess substrate, not evidence of the abundant presence of the hamster during the LGM as recalled in the secondary literature.

Cricetulus, *Allocricetus*, and *Phodopus* in Central Europe

In contrast to the genus *Cricetus*, records of small hamsters are a regular component of most Central European communities of the Early and Middle Pleistocene, although even here they appear as a rather recedent element, the more numerous assemblages with subdominant representation of this taxon are limited to a few localities. The above-mentioned records are generally assigned to the species *Allocricetus bursae* Schaub, 1930 described from MN15 site Csárnota 2 (KRETZOI 1956).

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Plate 3. Dental specimens of *Cricetus* from selected Q4 communities: 1 – Tučín, 2 – Zkamenělý zámek – jeskyně, 3 – Srbsko, Cave in Bříč, 4 – Rokytnice, cave, 5 – Srnčí 5, 6 – Peskö 4, 7 – Býčí skála, 8 – Červeného muže 4, 9 – Koněprusy, Za hájovnou Cave.

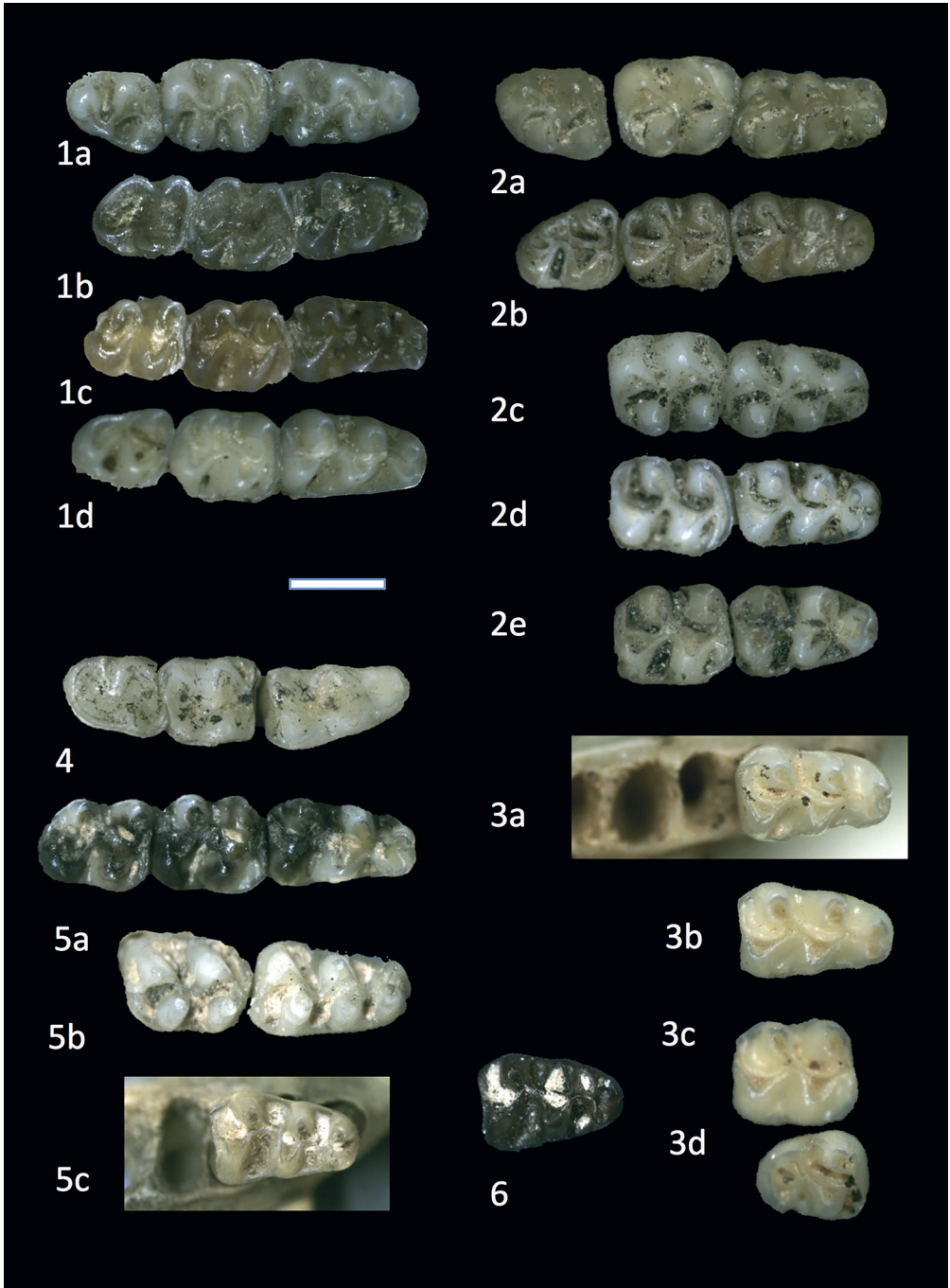


As confirmed by the results of our investigation, in terms of phenotypic characteristics, small hamster specimens from MN17–Q3 biozones represent a fairly uniform group with more or less identical variation characteristics, including mean values of individual biometric variables. This conclusion does not concern the specimens with significantly larger dimensions corresponding to the diagnostic characteristics of the form *Allocricetus ehiki* Schaub, 1930. According to Hír (1997c), this species was restricted to the earliest Pleistocene (MN17–Q1: Villány 3, Osztramos 3), but in our material individuals with similar characteristics also stand out in communities of the late Q2 section (Chlum 4X = MIS22). With these exceptions, the small hamsters included in *Allocricetus bursae* represent a broadly uniform eufrequent component of European Early and Middle Pleistocene communities with overlapping distributions into Eastern Europe and the Near East, from where several forms formally distinguished at the subspecies or species level have been described within this group. However, their immediate relationships to *A. bursae* are quite unambiguous (CUENCA BESCOS 2003) and validity is often considered questionable (KOWALSKI 2001, VAN DEN HOEK OESTENDE et al. 2015). Even the oldest records of this taxon from MN14 of the Iğdeli locality (ALPASLAN et al. 2010) show perfect agreement with Pleistocene forms as well as with Holocene Turkish samples of *Cricetulus migratorius*. This fact alone leads to deep doubts about whether the separation of Pliocene, Early and Middle Pleistocene populations into a separate genus *Allocricetus* is sufficiently justified. Also, Hír (1993a, 1995) shows that the two taxa – *Allocricetus bursae* and *Cricetulus migratorius* – exhibit extensive overlap in metric and non-metric characters, and that the size characteristics by which they differ reveal only on larger assemblages allowing the application of quantitative statistical comparisons. For these reasons, VAN DEN HOEK OESTENDE et al. (2015) propose to abolish the generic status of *Allocricetus* and to include all forms of this fossil genus in the genus *Cricetulus*. KOWALSKI (2001) then considers directly also the species *Allocricetus bursae* as a synonym of the Recent *Cricetulus migratorius*. The results of our investigations show identical features of variation dynamics in all fossil populations, including subrecent material of the extant species from Turkey, and a noticeable tendency towards a decrease in mean size throughout the MN17 to Q4 section (Figs. 12–14). In short, they suggest that the whole that group represents just a single evolutionary unit, the prior name for which is *Cricetulus* Milne-Edwards, 1867.

The Recent *Cricetulus migratorius* is one of the most widespread species of the western Palaearctic: its range extends from central Mongolia and Baluchistan to central Russia and Ukraine, Transcaucasia, Iran, and Turkey, extending westwards into eastern Bulgaria and Romania (KRYŠTUFEK & VOHRALÍK 2009). In this area, it inhabits a very wide range of open and semi-open habitats from the coastal plains to the subnivean zone of the highlands. The extraordinary ecological plasticity is matched by quite pronounced phenotypic variability (LEBEDEV 2000, LEBEDEV et al. 2018b). Molecular phylogenetic analyses show that it is the most derived clade of the entire genus with sister relationships to *Allocricetulus eversmanni*. The phylogenetic analyses further demonstrated that the genus *Cricetulus* in the traditional concept represents a polyphyletic group, and regarding a distant position of *C. migratorius* it is necessary to separate this species into a separate genus, for which LEBEDEV et al. (2018a) propose the name *Nothocricetulus*. Molecular phylogeographic analysis of its genetic varia-

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Plate 4. Mandibulary dentition of *Phodopus* and *Cricetulus*: 1 – *Phodopus sungorus*, Recent, 2 – *Cricetulus migratorius*, Holocene Turkey: a, b – Safranbolu, Mencilar Cave, c–e Bolu travertin, 3 – *Cricetulus migratorius* Q4W Karlukovo 4 (Bulgaria), 4 – *Cricetulus migratorius* Q4 Tetín, Bišilu, 5 – *Cricetulus migratorius* Q4W2 Srbsko, Nad Kačákem Cave, 6 – *Cricetulus migratorius* Q4W2 Dzeravá Cave 9.



bility shows a basal divergence of the Tian Shan population and a clear divergence of populations from the eastern part of the range (Iran-Uzbekistan-Kazakhstan-Mongolia subspecies *C. m. migratorius*) and a group of populations from the western part of the range (*C. m. phaeus*) with haplotypes WI (Southern Volga, Central Russia), WII (Caucasus region), WIII (Turkey), and WIV (Armenia). A surprising finding is that the western and eastern groups are separated by a fairly recent divergence following a stretch of a drastic reduction in genetic diversity. The molecular dating of that divergence is 130–160 ka. The common presence of both western and eastern haplotypes in the western regions of Central Asia (Kazakhstan) identifies this region as the center of divergence and the source region of subsequent range expansion (LEBEDEV et al. 2018b). A palaeobiogeographic scenario with which these findings might be consistent must thus assume, however, a large-scale extinction of ancestral populations over the vast majority of the original range of *Cricetulus bursae*. The conditions of the Eemian interglacial, the onset of which was characterized by extreme oceanization and climatic humidity, with a very rapid onset of closed forest formations, and its persistence throughout the MIS5e section (130–110 ka; WOILLARD 1978, ZAGWIJN 1996, BREWER et al. 2008), provides fairly robust support to the above scenario. In these contexts, two points should be highlighted that our results make very clear: (i) the presence of hamsters is already documented in the early phases of the Vistulian glaciation (MIS5a–5c, ?MIS4) and especially in the climatically optimal section of the glacial (MIS3); (ii) the morphometric characteristics of these populations, however, clearly differ from the quite homogeneous group of Early and Middle Pleistocene populations of *C. bursae*. This fact gives the impression that this is an evolutionary unit of a different origin than the earlier resident European populations of *C. bursae*. Such a possibility seems to be in very good agreement with the above-mentioned assumption of expansion from the Central Asian refugium at the end of the Eemian Interglacial or the older phases of the Vistulian. In this respect, then, it is appropriate to consider, against the proposal of KOWALSKI (2001), the possibility of more narrowly defining *C. migratorius* as a set of populations shaped by the range dynamics of the present glacial cycle from a common ancestor in the refugial population surviving the Eemian Interglacial in Central Asia. The evolutionary characterization of this Recent species presented by LEBEDEV et al. (2018b) is consistent with this: it is a highly diversified complex of closely related populations with multiple speciation tendencies in statu nascendi.

With regard to the topic of our work, it should be summarized that in Central Europe, such a defined form of *C. migratorius* occurs at least discontinuously probably during most of the Vistulian glaciation, especially in the phases of relative warming with the development of a diversified mosaic of open or semi-open steppe habitats (MIS3, late glacial Q4a). Contrary to expectations, however, *C. migratorius* is invariantly absent in communities of relatively dry preboreal (Q4b) and boreal sections (Q4c), where other forms of warmer open landscapes become more widespread. Thus, an explanation by other biotic factors should be taken in account – e.g. competitive exclusion with mice of the genus *Apodemus*, which are absent in glacial communities (even in most of the current range of *Cricetulus migratorius*) and become the dominant component of Central European communities during early Holocene.

A question to which our investigation has not provided a clear answer remains the presence of the genus *Phodopus* in the European fossil record. Despite the few specimens in our assemblage, which metrical characteristics might suggest such a determination, we cannot unequivocally prove their affiliation to the taxon. Conversely, an assessment of the variability of a relatively large assemblage of Holocene specimens from the recent range of *C. migratorius* in Turkey has shown a range of variation exceeding that of the *Phodopus sungorus* comparative material,

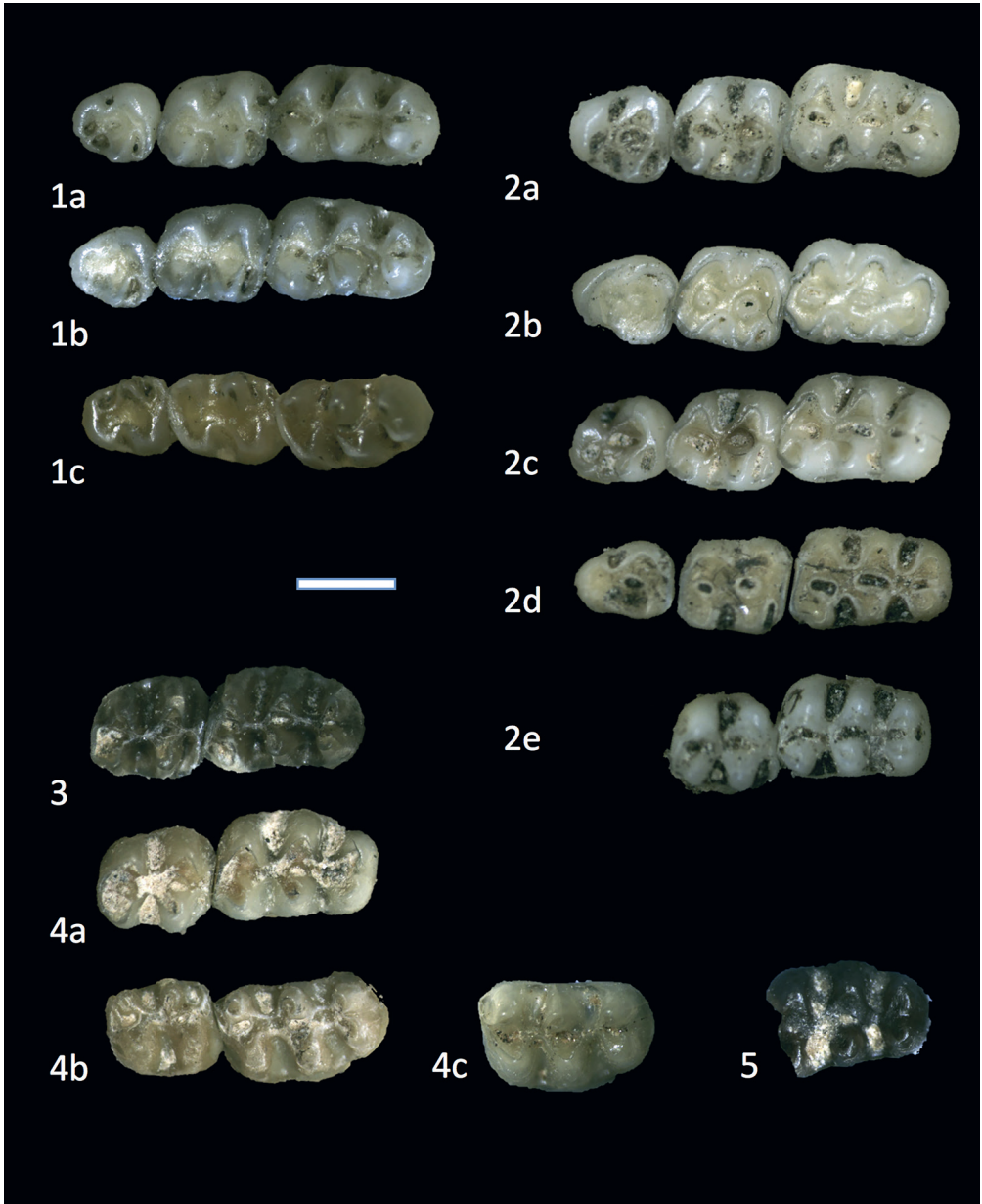


Plate 5. Maxillary dentition of *Phodopus* and *Cricetulus*: 1 – *Phodopus sungorus*, Recent, 2 – *Cricetulus migratorius*, Holocene Turkey: a, b – Safranbolu, Mencilar Cave, c – e – Bolu travertin, 3 – *Cricetulus migratorius* Q4W2 Tetin, Bišilu, 4 – *Cricetulus migratorius* Q4W2 Srbsko, Nad Kačákem Cave, 5 – *Cricetulus migratorius* Q4W2 Dzeravá Cave 9.

which calls the applicability of metric characteristics as an unambiguous identification criterion rather robustly into question. With this in mind, we thus identify all our Q4 small hamster material as *C. migratorius*, leaving the question of the presence of the genus *Phodopus* in Europe as an open topic for further analysis.

CONCLUSIONS

In response to the questions posed in the introduction of this paper, the following can be stated:

(i) Although the genus *Cricetus* appeared throughout the entire Quaternary period (i.e. MN17–Recent), the number of records, especially in the deeper horizons of the Pleistocene, is surprisingly low; with the exception of a few sites from the Q2 biozone, *Cricetus* is clearly a rare element whose occurrence was very patchy in both temporal and spatial terms.

(ii) In the case of small hamsters (traditionally referred to as *Allocricetus bursae* in older sections) the situation is somewhat different. Particularly in the Early Pleistocene (MN17–Q2) it is a regular element of most communities, in some cases acting as a subdominant element.

(iii) Both for *Cricetus* and *Cricetulus*, the key break in range history appeared with the Eemian interglacial stage, obviously due to the distinctly oceanic climate and large-scale spread of forest formations. For the clades under study, this was very probably the stage of almost complete extinction over most of central Europe.

(iv) Subsequent range expansions at the beginning of the Vistulian Glaciation then give way to a broad expansion with a peak of distribution during the glacial optimum of MIS3. The situation in the LGM (MIS 2) is unclear, the absence of hamsters in most records from this stage suggests a significant pattern of range regression.

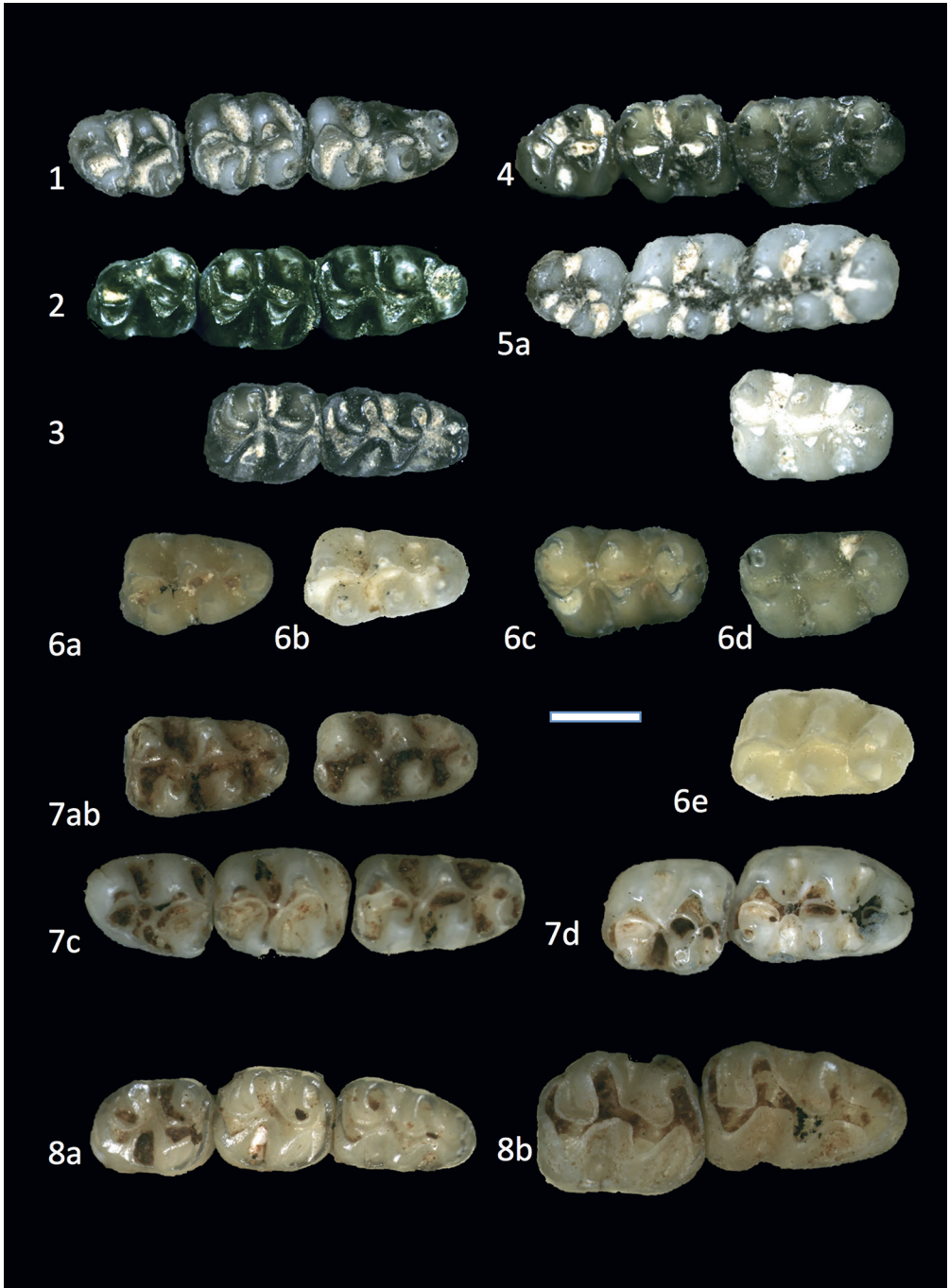
(v) With warming and the development of variegated open habitats at the end of the glacial period, a renewed range expansion appeared both in *Cricetus cricetus* and *Cricetulus migratorius*. While the latter species is no longer documented in the following sections of the early Holocene, the hamster undergoes a well-marked Early Holocene range expansion in the Central European area.

(vi) In contrast to the abundant record from the Pre-Boreal and Boreal in most lowland and upland areas, the hamster is absent from the Late Boreal and Atlantic communities, except in southern Slovakia. Considering the mosaic nature of the natural conditions of Central Europe, it can be assumed that the range regression in that time may not have been, despite the development of closed forest formations, associated with complete extinction in that region. Especially in the southern areas, further hamster occurrence is documented already in the early phases of Neolithic deforestation, and on a wider scale with the post-Neolithic expansion of the cultural steppe. The population from this section shows metric features related to those of the Boreal populations but is distinctly different from the Recent populations.

(vii) The presence of the genus *Phodopus* in the Central European fossil record could not be clearly confirmed by the material available from the Czech Republic and Slovakia.

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Plate 6. Dentition of small hamsters (*Allocricetus*) in selected Q1–Q2 sites: 1 – M_{1-3} Q2 Koněprusy C718/H, 2 – M_{1-3} Q2 Koněprusy C718/f5, 3 – M_{1-2} Q2 Koněprusy C718/H7, 4 – M_{1-3} Q2 Koněprusy C718/H5, 5 – Q2 Koněprusy C718/H (a – M_{1-3} , b – M^1), 6 – Q2 Koněprusy Med1/23 (a, b – M_1 , c, d, e – M^1), 7 – Q1 Včeláre 5 (a, b – M_1 , c – M_{1-3} , d – M^{1-2}), 8 – Q1 Včeláre 10B (a – *A. bursae* M_{1-3} , b – *A. ehiki* M_{1-2}).



Comparisons of phenotype patterns and size trends based on multiple samples from different stratigraphic horizons provided relatively robust support for a simplified view of the taxonomic composition of the groups.

(*) Within the genus *Cricetus*, first appearing during the MN17 biozone, a clear tendency towards an increase in body size can be noted during the Early and Middle Pleistocene, culminating at the end of the Q2 biozone and in some Middle Pleistocene (Q3) populations by the presence of extremely large forms clearly exceeding the variation range of Recent populations, to which the other evidence of the present glacial cycle (Q4) is quite clearly associated despite changes in mean values. Although the extreme forms of the individual stratigraphic sections show considerable mutual differences, for which they use to be classified as distinct species in the mainstream literature (MN17–Q1 *C. nanus*, Q2–Q3 *C. runtonensis-major*, Q4 *C. cricetus*), the full range of evidence suggests a rather different picture: a mosaic of temporal and local variations that do not fit the idea of sharply distinct chronotaxa. The conclusion of these comparisons, then, is to support the view that the European fossil record of the genus *Cricetus*, despite numerous local and temporal phenotypic variations, represents a single biological species whose temporal phenotypic variants can be distinguished at the subspecies level (Fig. 15).

(**) Analogous conclusions are reached in the case of the second group. For this group, it is clear that the set of hamster specimens from the communities of the present glacial cycle (Q4) falls quite clearly within the range of variation of the Recent species *Cricetulus migratorius*. The group of specimens from the Early Pleistocene sections (MN17–Q3), traditionally separated into a separate fossil genus *Allocricetus*, differs from the Q4 specimens in general by a larger size but shows a clear correspondence in all dental characters as well as an identical pattern of

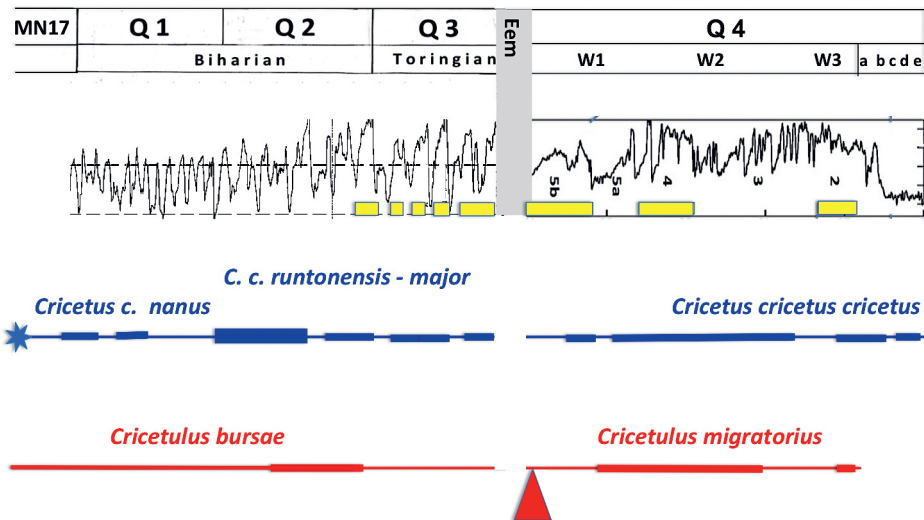


Fig. 15. A graphical summary: A simplified draft of the Quaternary range dynamics of hamsters in Central Europe. Note assumed range regressions in the Middle and Late Pleistocene interglacials, particularly the Eemian. See text for details.

variation dynamics. Thus, our findings support the view that this is a single genus within which it is appropriate to distinguish a relatively homogeneous group of Early and Middle Pleistocene populations with distinct differences from the Q4 form, at the species level, as the separate taxon *Cricetulus bursae* (Schaub, 1930).

(***) Finally, it should be noted that the above interpretations are in very good agreement not only with the alternative views of some paleontologists (e.g. KOWALSKI 2001) but also with the current output of molecular phylogenetics.

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APPENDIX

List of biometrically analyzed fossil dental items – no. of region, name of site / layer (M₁-M₂-M₃-M¹-M²-M³)

Cricetus cricetus

- MN17**: 10 Včeláre 7 (1-0-0-0-0-0); 10 Včeláre 6/1 (0-0-0-1-0-0); 10 Včeláre 6/3 (0-0-0-1-0-0); 10 Včeláre 10B (0-1-0-1-0-1); 10 Včeláre 11 (0-1-1-0-0-0);
- Q1**: 10 Včeláre 6/5–6/8 (4-1-1-3-1-1); 5 Mladeč 1/3 (0-0-0-0-0-1); 10 Včeláre 4E (1-0-0-1-0-0); 10 Včeláre 4A (1-0-0-1-1-1); 1 Koněprusy PD-1 (0-1-1-1-2-1);
- Q2**: 10 Honce 1-střed (7-8-7-0-0-0); 8 Skalka u Nového Mesta / Bzince (7-4-5-2-3-3); 6 Červený kopec PKX (2-3-2-0-0-0); 6 Stránská skála 1 (0-1-0-1-0-0); 1 Koněprusy C718 (1-1-1-2-1-2);
- Q3**: 5 Mladeč 2 (0-1-1-0-0-0); 2 Dobrkovice 2 (3-2-3-2-4-2); 6 Stránská skála Cave (1-2-0-1-0-0); 5 Tučín (3-2-3-2-3-3);
- Q4W**: 11 Gánovce/EF (1-0-0-0-0-0); 11 Ondrej (1-0-0-0-0-0); 1 Bišilu 8 (1-1-1-0-0-0); 1 Bišilu 7 (1-0-1-0-0-0); 9 Pěšků 12b (0-0-1-0-0-0); 1 Bišilu 6 (0-0-1-0-0-0); 6 Srnčí 7b (1-0-0-1-0-0); 2 Sudslavice NM (3-4-3-1-2-2); 1 Turské Maštale NM (0-1-1-0-0-0); 1 Praha-brickyards NM (16-19-20-9-10-8);
- Q4a**: 1 Bišilu 5 (0-1-0-0-0-0); 1 Skalka nad Čihovou 7 (0-1-0-0-0-0); 1 Srbsko – SSj (0-0-0-0-2-1); 3 Rokytnice (1-0-0-1-1-1); 6 Býčí 7bc (1-0-0-0-0-0); 6 Býčí 8c (0-2-2-1-1-0); 6 Srnčí 8 (0-1-0-0-0-0); 6 Býčí 8a (1-0-0-0-0-0); 7 Soutěska II/6 (1-0-0-1-0-0); 7 Turold N4 (5-2-2-2-1-1); 9 Pěšků 7b (0-3-0-0-0-0); 10 Maštálná 14 (1-0-0-0-0-0); 10 Maštálná 9 (1-0-0-0-0-0); 10 Maštálná 10 (1-2-0-0-0-0); 10 Červená Skála (1-1-0-0-0-0);
- Q4b**: 1 Bišilu 3b (3-4-1-0-0-0); 1 Bišilu 3a (0-1-0-0-0-0); 1 Bašta 5 (0-1-0-0-0-0); 6 Býčí 4a (0-1-0-0-0-1); 6 Býčí 4b (3-3-3-0-0-0); 6 Býčí 3c (1-1-1-1-1-0); 6 Býčí 6bc (1-1-1-0-0-0); 6 Býčí 6a (1-1-1-1-1-0); 6 Býčí 5b (0-0-0-1-0-0); 6 Býčí 3b (1-1-0-0-1-1); 6 Býčí 5a (0-0-0-1-0-0); 6 Býčí 3a (1-0-0-0-0-0); 6 Býčí 1 (1-0-0-0-0-0); 6 Zazděná 7 (1-1-1-1-1-0); 7 Martinka-rozsedlina 5 (0-1-0-0-0-0); 9 Pěšků 6 (1-0-0-0-0-0);
- Q4c**: 1 Bacín F (0-1-0-0-0-0); 1 Bacín H (0-1-0-0-0-0); 1 Bacín J (0-0-1-0-0-0); 1 Bacín M (0-1-0-0-0-0); 1 Skalka nad Čihovou 5 (0-1-0-0-0-0); 1 Skalka nad Čihovou 4 (0-0-0-1-1-0); 6 Srnčí 5 (0-0-1-0-0-0); 6 Srnčí 3 (0-0-1-0-0-0); 6 Holštejská 4 (0-0-1-0-0-0); 7 Martinka I/4 (0-1-0-1-1-0); 9 Pěšků 4 (1-1-0-3-1-1); 9 Pěšků 4a (1-1-0-1-1-1); 9 Pěšků 4b (1-1-0-1-1-1); 10 Červeného muže 4b (1-1-1-0-0-0); 10 Červeného muže 5 (1-1-1-0-0-0); 10 Hámorská 4 (0-0-0-0-0-0); 10 Červeného muže (0-0-0-1-0-0); 10 Zbojnická 5 (1-1-0-0-0-0);
- Q4e**: 1 Bišilu 2c (0-1-0-0-0-0); 1 Bacín A (1-1-0-1-0-0); 7 Martinka-rozsedlina 1 (1-1-0-0-0-0); 9 Pěšků 2 (0-1-1-0-1-0); 9 Pěšků 3 (1-1-2-0-1-1); 10 Hámorská 3 (0-0-0-1-0-0); 10 Hámorská 2 (0-0-0-1-1-0); 10 Maštálná 3 (0-0-0-1-0-0); 10 Maštálná 4 (1-0-0-0-0-0); 10 Maštálná 5 (0-0-0-1-0-0).

Cricetulus / Allocricetulus bursae

MN17: 3 Ctiněves (1-0-1-0-0-0); 10 Plešivec Csöpké (3-3-0-2-1-2); 10 Včeláre 3a (1-0-0-0-0-0); 10 Včeláre 3 (2-1-0-0-0-0); 10 Včeláre 5 (2-2-2-3-2-0); 10 Včeláre 6a (0-2-0-5-0-0); 10 Včeláre 10B (2-3-1-2-2-1); 10 Včeláre 11 (2-3-1-1-0-2); 10 Včeláre 14 (2-2-0-1-1-0);

Q1: 10 Včeláre 3B (1-0-0-1-0-0); 10 Včeláre 6/5 (1-1-0-0-0-0); 5 Sovinec 4 (1-1-0-0-0-0); 10 Včeláre 4E (0-0-0-1-0-0); 10 Včeláre 4A (0-0-0-0-1-1);

Q2: 10 Honce 1 (1-2-1-1-1-2); 8 Žirany 3 (6-2-1-6-1-0); 8 Skalka u Nového Mesta-Bzince (2-1-0-0-0-0); 1 Koněprusy 15-31 (1-0-0-2-0-0); 1 Chlum 4 X/1 (1-0-0-2-0-0); 1 Chlum 4 X/2 (1-0-0-0-1-0); 1 Koněprusy JK (2-2-1-1-1-0); 1 Koněprusy C718/D (1-1-1-0-0-0); 1 Koněprusy C718/E (1-1-1-0-0-0); 1 Koněprusy C718/f (1-1-1-0-0-0); 1 Koněprusy C718/f5 (5-5-5-0-0-0); 1 Koněprusy C718/H2 (2-2-2-3-3-3); 1 Koněprusy C718/H3 (1-1-1-0-0-0); 1 Koněprusy C718/H5 (0-0-0-1-1-1); 1 Koněprusy C718/H4 (0-0-0-5-4-1); 1 Koněprusy C718/H6 (1-1-1-0-0-0); 1 Koněprusy C718/H7 (1-1-1-0-0-0); 1 Chlum 4C/5 (1-1-0-0-0-0);

Q3: 2 Dobrkovice 2 (3-2-2-0-0-0); 6 Stránská skála Cave (2-0-0-3-0-0); 7 Turoid NE 7 (4-2-0-4-0-0); 7 Turoid NE 1-2-8 (2-1-1-3-0-0); 11 Pažica-Rozsedlina (1-0-0-0-0-0).

Cricetulus migratorius

Q4W: 1 Chlum 7 (0-1-0-0-0-0); 8 Dzeravá 9 (0-1-0-1-0-0); 1 Nad Kačákem (7-5-5-6-5-2); 8 Dzeravá 5 (1-0-0-0-0-0); 5 Balcarka (2-1-1-2-2-2); 6 Holštejnská 7 (1-0-0-0-0-0); 6 Pekárna 6 (1-0-0-0-0-0); 7 Martinka-rozsedlina 10 (0-0-0-1-0-0); 8 Dzeravá 3 (0-0-0-1-0-0); 1 Bišilu 6 (2-2-1-0-0-0); 6 Holštejnská 6 (1-0-0-0-0-0); 7 Martinka-rozsedlina 7 (0-0-0-1-0-0-);

Q4a: 1 Skalice I/7 (1-1-1-0-0-0); 7 Soutěska 9 (1-0-0-0-0-0); 7 Soutěska II/5 (0-0-0-1-1-0); 9 Pěšků 5 (1-1-1-0-0-0); 1 Bašta 9 (1-1-1-0-0-0).

Comparative samples Q4

Turkey: Bolu – Travertin II (36-33-19-41-41-25); Mencilar Cave (14-13-13-45-33-23);

Bulgaria: Karlukovo Cave 4 (3-3-3-2-2-2);

Phodopus sungorus: Recent (14-14-14-11-11-11).