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GENUS *APODEMUS* IN THE PLEISTOCENE OF CENTRAL EUROPE: WHEN DID THE EXTANT TAXA APPEAR?

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Abstract: The extant species of the genus *Apodemus* represent the most common small mammals of Central Europe. Unfortunately, their phylogenetic past is only poorly known. With the aid of detailed biometric analyses we tried to identify the first appearance of the phenotypic patterns characterizing the extant populations. We examined dental material of *Apodemus* from 53 community samples from the territory of the Czech Republic and Slovakia dated from the early Villanyian (MN 16/17) to the late Middle Pleistocene (Q 3) with particular respect to their correspondence with the morphometric characteristics of the extant species. While the Toringian (Q 3) interglacial samples invariably include forms identical with the extant taxa *A. flavicollis*, *A. sylvaticus* and supposedly *A. uralensis* (including the items corresponding to *A. maastrichtiensis*), the samples of Early Pleistocene age (MN 17 – Q 2) exhibited clear differences in the variation pattern which results in questioning the possibility of their co-identification with the respective extant species. In most instances they varied within the limits in resembling *A. sylvaticus* but exceeded its variation ranges in some non-metric characters. Regarding serious doubts on real taxonomic status of other named fossil species we propose to denote these Plio-Pleistocene *sylvaticus*-like phenotypes provisionally with the prior name *A. atavus* Heller, 1936.

Key words: *Apodemus*, Pleistocene, Pliocene, Central Europe, dental phenotype

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Introduction

The wood mice of the genus *Apodemus* are the most common murid rodents throughout the Palaearctic region (Niethammer 1978, Musser et al. 1996). The genus, phenotypically established within the early radiation of murid rodents during the Vallesian (Martín-Suárez and Mein 1998, Freudenthal and Martín-Suárez 1999) is characterized by rapid adaptive radiations (Serizawa et al. 2000, Suzuki et al. 2003, 2008). Initial divergence most likely started somewhere in Eastern or Central Asia, and resulted in diversification into two or three Asian clades – *Apodemus*, *Argenteus*, *Gurkha* group (*A. gurkha*) and a single European clade – *Sylvaemus* (Serizawa et al. 2000, Suzuki et al. 2003, 2008, Liu et al. 2004).

Currently, more than 20 species are recognized (Musser et al. 1996, Musser and Carleton 2005) and subdivided into 3–4 of the above mentioned subgenera (Serizawa et al. 2000, Suzuki et al. 2003, 2008, Liu et al. 2004). All the West Palaeartic representatives except for *A. agrarius* (subgenus *Apodemus*) belong to the subgenus *Sylvaemus*, the clade regularly represented in the European fossil record since the Turolian. Presumably, it was already established there in the Late Miocene (MN 13; van Daam 1997, Martín-Suárez and Mein 1998, Horáček et al. 2013), shortly after the westward expansion of the murids in MN 10. In contrast, all extant species of the subgenus *Sylvaemus* (including the European representatives, *A. alpicola*, *A. flavicollis*, *A. mystacinus*, *A. epimelas*, *A. sylvaticus* and *A. uralensis*) are, according to molecular data (Bellinvia et al. 1999, Serizawa et al. 2000, Filippucci et al. 2002, Michaux et al. 2002, Bellinvia 2004, Suzuki et al. 2008), mutually closely related and separated by only shallow divergences (less than 10% in mtDNA), which suggests their radiation from a common ancestor during the Pliocene and Early Pleistocene age, supposedly due to the effects of the climatic changes at that time (Zachos et al. 2001).

The fossil record of the genus in Europe is almost continuous since the Late Miocene, the taxon appears in the vast majority of the Pliocene and Pleistocene assemblages

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throughout the whole of Europe. Kowalski (2001) listed it in 460 Late Pliocene and Pleistocene assemblages from 24 countries. In most instances the Quaternary fossil records are co-identified with extant European species, particularly the medium-sized species *A. sylvaticus.* Kowalski (2001) reported 227 records of *A. sylvaticus* dated from the late Villanyian (Villány 3, Schernfeld, Mas Rembault 2, Tegelen, Betfia 13, Akulaevo) and Early Biharian (32 sites) to Middle and Late Pleistocene. The other extant species are reported relatively exceptionally in the fossil record (Kowalski 2001): 31 *A. flavicollis* (except for one Villanyian and three Biharian records – Trassanel, Voigtstedt, Atapuerca, Karaj Dubina, all of them Middle and Late Pleistocene age), 7 *A. agrarius*, no record of *A. uralensis* and *A. alpicola*. In addition at least 65 records mostly of the Villanyian and Early Biharian age were reported under the names denoting nominal fossil species *A. alsomyoides* Schaub, 1938 (MN 17, Villány 3, Hungary), *A. argyropuloi* Topačevskij, 1973 (Q 1, Tarchankut, Ukraine), *A. atavus* Heller, 1936 (MN 15, Gundersheim, Germany), *A betfiensis* Terzea, 1995 (MN 17, Betfia 13, Romania), *A. dominans* Kretzoi, 1959 (MN 15, Csarnóta 2, Hungary), *A. occitanus* Pasquier, 1974 (MN 16, Arondelli, Italy), *A. jeanteti* Michaux, 1967 (MN 17, Seynes, France), *A. maastrichtiensis* van Kolfschoten, 1985 (Q 3, Maastricht-Belvedere 2, the Netherlands), *A. maximus* Thaler, 1972 (Q 1, Monte Pellegrino, Italy), *A. leptodus* Kretzoi, 1956 (Q 1, Villány 5, Hungary), some of them partly referred to the extinct genus *Parapodemus* Schaub, 1930.

The European fossil species of the genus *Apodemus* can be subdivided into two phenotypic groups often considered to represent separate clades which co-occurred from the Late Miocene and Pliocene: (i) large-sized forms with large broad molars, resembling the extant *A. mystacinus* and *A. epimelas*, represented by the species *A. barbarae*, *A. schaubi*, *A. gudrunae*, *A. gorafensis*, *A. jeanteti*; possibly related to the extant clade *A. mystacinus-epimelas* and/or the fossil genus *Rhagapodemus* Kretzoi, 1959 (*frequens* Kretzoi, 1956, *primaevius* Hugueney et Mein, 1964, *hautimagnesis* Mein et Michaux, 1970, *athensis* Bruijn et Meulen, 1975); and (ii) forms with smaller molars and M1 with almond-shaped outline , resembling the recent species *A. sylvaticus* and *A. flavicollis*, represented by the remaining named species e.g. *A. atavus*, *A. dominans* etc. (Martín-Suárez and Mein 1998, Storch 2004, Nesin and Storch 2004). In addition to the fossil taxa, *A. sylvaticus* and *A. flavicollis* have been reported in numerous European localities since the Early Pleistocene (Pasquier 1974, Michaux and Pasquier 1974, Storch 1974, Popov 1994, Argenti and Kotsakis 1999, Maul and Parfitt 2010, Minwer-Barakat et al. 2011, Marcolini et al. 2013).

However, the actual status and relationships between particular species within these groups are often considered doubtful and biased due to poor comprehension of the taxonomical relevance of formal diagnostic characters and patterns of phenotype variation. Among others this also concerns the two taxa to which most of the Pliocene records are ascribed, i.e. *atavus* and *dominans*, considered either quite distinct lineages (Martín-Suárez and Mein 1998) or, more recently, extreme phenotypes of a single species (Fejfar and Storch 1990, Martín-Suárez and Mein 2004, Minwer-Barakat et al. 2005, García-Alix et al. 2008, Colombero et al. 2014).

It should be stressed that identification at species level traditionally presents a serious problem, even in the case of extant species for which a far more complete record is available. Though individual extant species differ in mean body size, each of them shows a broad range of within-species variation and extensive between-species overlaps in the states of any morphometric traits (comp. e.g. Filippucci et al. 1996, Reutter et al. 1999, Frynta and Mikulová 2001, Spitzenberger 2001, Barčiová and Macholán 2009, Jojić et al. 2012). Just recently, with regard to the discriminatory bias of morphometric characters, differences in the distress call were proposed as the most reliable criterion for species identification (Ancillotto et al. 2016). Obviously, species identification is even more complicated in the case of fragmentary fossil material, which is often restricted to isolated molar teeth (Heinrich and Maul 1983a, b). It is no wonder that the species identification of fossil *Apodemus* was frequently regarded as provisional (cf.) and/or not provided at all (e.g. 119 out of 460 records in Kowalski 2001). In any case, species identification within the genus *Apodemus* is generally a very difficult task and in the case of a fragmentary fossil record this problem seems to be even more pertinent. Both fossil and recent species show a considerable variability in size and morphology over time (Pasquier 1974, Freudenthal and Martín-Suárez 1990), the fossil forms are often not properly diagnosed, their actual status and relationships to extant taxa, and consequently the history of extant species should be considered as rather unclear.

The recently proposed alternative approach to species identification (for more details see Knitlová and Horáček 2017) enabled retrieval of reliable information on the history of extant species from the mid-European Late Pleistocene and Holocene fossil record of the genus *Apodemus* which suggested that: (i) the genus is invariably absent in MIS 3 – MIS 2 assemblages but regularly appears during the Late Vistulian; (ii) all the Late Vistulian remains of the genus belong to *A. flavicollis*, the species clearly predominating in the fossil record until the Late Holocene; (iii) *A. uralensis* accompanied it in all the studied area (the Czech Republic and Slovakia) until the late Boreal when it disappeared from the fossil record (except for Pannonia); (iv) contra to expectation, *A. sylvaticus* appeared later in the Early Holocene, first in the western part of the region and, until Atlantic, was relatively rare (the regular appearance of the species is mostly in the post-Neolithic period); (v) *A. agrarius* appeared sparsely from the Boreal with maximum frequency during the post-Neolithic period. Worth mentioning is that contrary to former interpretations, the picture resulting from the novel analyses of the fossil record conformed precisely to the picture proposed by molecular phylogeography (Libois et al. 2001, Michaux et al. 2003, 2004, 2005).

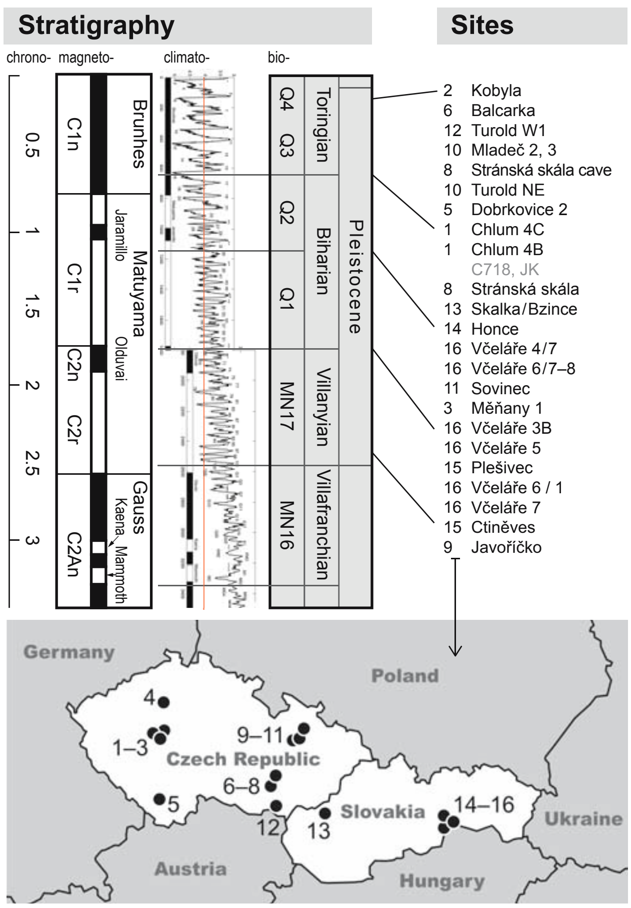
Here, we applied the same approach with material of the genus *Apodemus* from the Late Pliocene to Middle Pleistocene assemblages from the Czech Republic and Slovakia to reveal (i) the degree of phenotype correspondence between the extant forms and samples from different stratigraphic horizons, (ii) the differences in variation pattern in different stratigraphic horizons, and (iii) the period from which the phenotypic setting of extant species was established.

Instead of attempts to establish a definite identification of Plio/Pleistocene forms and discussion on the taxonomic status of fossil species, we propose a provisional solution with respect to the complicated nature of the task and inherent bias.

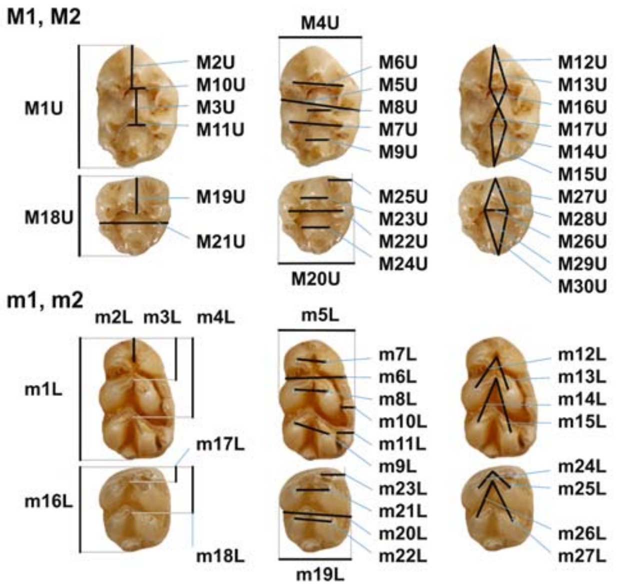
Material and methods

The study is essentially based on material of the genus *Apodemus* from the faunal assemblages of the Late Pliocene and Pleistocene age deposited in the collection of the Department of Zoology, Charles University, Prague. The material was collected during last 50 years, mostly by the senior author. The study covers dental and cranial remains of *Apodemus* spp. in 53 community samples from 16 sites in the Czech Republic (CZ) and Slovakia (SK). Geographical position and the stratigraphical context of individual localities is shown in Text-fig. 1. A list of the respective sites is in Table 1. The statigraphical position of particular samples is expressed in terms of the standard European biostratigraphic scale (Fejfar and Heinrich 1983, Bernor et al. 1996) and alternatively in terms of the Neogene (MN) or Quaternary (Q 1–4) mammalian biozones (Mein 1976, 1989, Horáček and Ložek 1988, Agustí et al. 2001).

The Plio-Pleistocene material under study comprised 361 remains identified as *Apodemus* spp. (mostly isolated teeth and jaw fragments). All items were photographed with the aid of an Olympus SZX12 stereomicroscope, and further



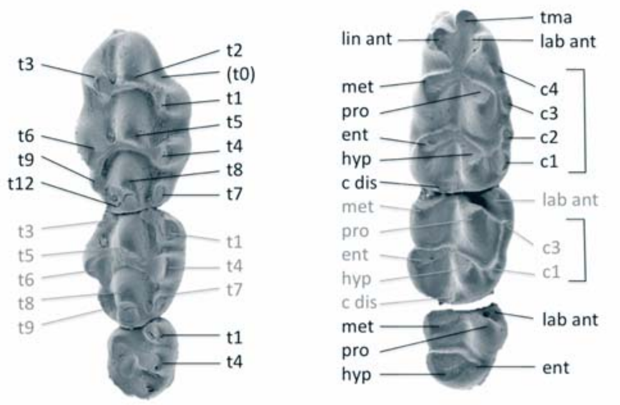
Text-fig. 1. Geographical position and stratigraphic context of the Pleistocene sites from the Czech Republic and Slovakia containing *Apodemus* material analyzed in this paper.



Text-fig. 2. Definition of the metric characters applied in this study, for non-metric characters see Appendix 1.

measured using tpsDig image analysis software (by F. J. Rohlf) with an accuracy of 0.01 mm.

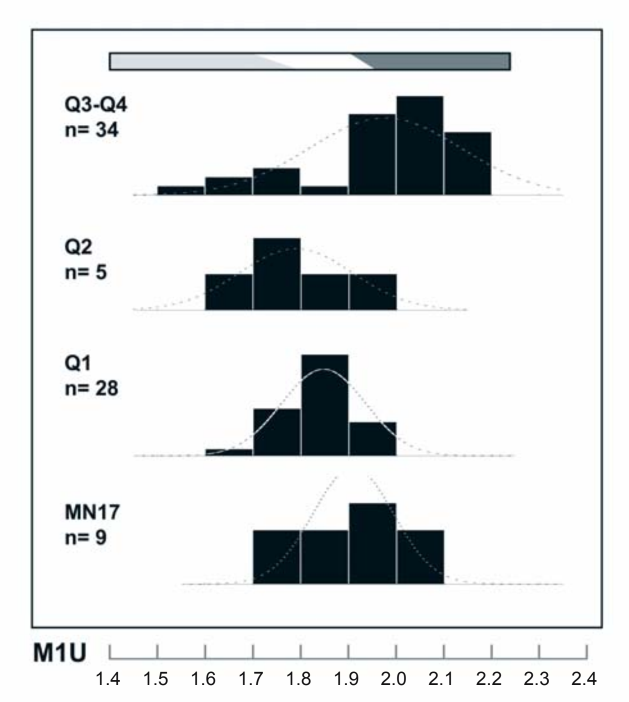
In total, 57 dental dimensions were measured (see Text-fig. 2), supplemented with 4 proportional ratios (M2U/M1U, M14U/M15U, m3L/m1L, m6L/m5/L) and 25 non-metric variables (including the degree of tooth abrasion, see App. 1). The supplementary variables expressing the size of molar surfaces (SURM1, SURM2, SURm1, SURm2) were computed by multiplying molar length by molar width. The degree of tooth wear and the states of 24 non-metrical characters were scored using predefined scales (0–9) subdividing the span of the observed variation (see App. 1 for details). Further, the number of roots on M1–2 or the number of alveoli for M1–2 in the maxillary fragments were determined. All measurements were taken by the same author (M.K.). Cusp nomenclature follows Horáček et al. (2013), see Text-fig. 3. Maxillary molars are marked in upper case (M1 – M3) and mandibular molars in lower case (m1 – m3).



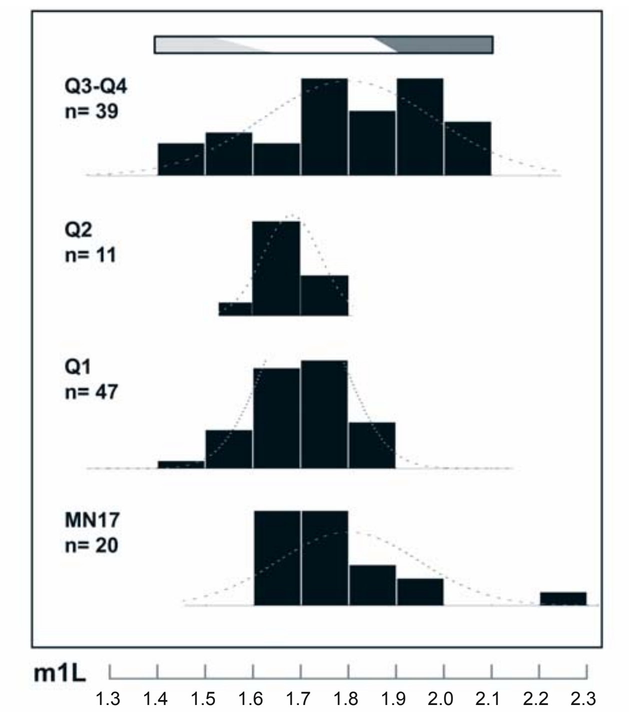
Text-fig. 3. Cusp nomenclature of murid molars as applied in this paper (after Horáček et al. 2013).

Table 1. List of the Czech and Slovak Pleistocene localities containing *Apodemus* remains which were examined in this study.

No	Locality abbr.	Name (administrative localisation, region)	*Apodemus* spp.				Detailed primary data
			M1	M2	m1	m2	
		THE CZECH REPUBLIC – BOHEMIA					
1	CHL4B	Chlum 4C (Srbsko, Bohemian Karst)	1	5	15	4	Horáček (1979), Horáček (1982), Horáček and Ložek (1988)
	CHL4C	Chlum 4B (Srbsko, Bohemian Karst)	3	1	1	4	
	CHL7	Chlum 7 (Srbsko, Bohemian Karst)	1	0	0	0	Horáček and Sánchez-Marco (1984)
2	KOBY	Kobyla-Chlupáčova sluj (Koněprusy, Bohemian Karst)	1	2	3	3	Horáček and Ložek (1988)
3	MENA	Měňany 2 (Měňany, Bohemian Karst)	1	0	1	0	
4	CTIN	Ctiněves (Ctiněves, Litoměřice distr.)	3	0	1	1	Horáček and Ložek (1988)
5	DOB2	Dobrkovice 2 (Kájov-Dobrkovice, Český Krumlov distr.)	1	0	0	0	Fejfar (1965)
		THE CZECH REPUBLIC – MORAVIA					
6	BALC	Balcarka (Ostrov u Macochy, Moravian Karts)	3	0	1	0	Horáček and Ložek (1988)
7	STRS	Stránská skála (Brno, Moravian Karts)	0	1	0	4	Ložek (1964), Musil et al. (1995)
8	STRC	Stránská skála cave (Brno, Moravian Karst)	0	0	0	1	Kučera et al. (2009)
9	JAVO	Javoříčko (Luká, Olomouc distr.)	0	1	5	4	Horáček and Ložek (1988)
10	MLAD	Mladeč 2, 3 (Mladeč, Olomouc distr.)	27	12	21	17	Horáček and Ložek (1984, 1988)
		Mladeč 1 (Mladeč, Olomouc distr.)	0	1	1	0	Horáček and Ložek (1984, 1988)
11	SOVI	Sovinec (Jiříkov-Sovinec, Bruntál distr.)	1	2	0	1	Horáček and Ložek (1988)
12	TUW1	Turold W1 (Mikulov, Břeclav distr.)	0	1	0	0	Horáček (1983), Horáček and Ložek (1983)
	TUNE	Turold NE (Mikulov, Břeclav distr.)	1	0	1	0	Horáček (1983), Horáček and Ložek (1983)
		SLOVAKIA					
13	BZIN	Skalka u N. M. n. V. (= Bzince) (Bzince, Topoľčany distr.)	2	1	2	1	Ložek and Horáček (1984)
14	HONC	Honce (Honce, Slovak Karst)	1	2	0	1	Horáček and Ložek (1987)
15	PLES	Plešivec (Plešivec, Slovak Karst)	3	4	11	2	Ložek and Horáček (1988)
16	VCEL	Včeláre 4/7 (Dvorníky-Včeláre, Slovak Karst)	1	1	15	4	Horáček (1985)
	VC6/7-8	Včeláre 6/7-8 (Dvorníky-Včeláre, Slovak Karst)	15	8	24	15	Horáček (1985)
	VC3B	Včeláre 3B (Dvorníky-Včeláre, Slovak Karst)	6	3	5	0	Horáček (1980, 1985)
	VC5	Včeláre 5 (Dvorníky-Včeláre, Slovak Karst)	3	4	7	3	Horáček (1985)
	VC6/1	Včeláre 6/1 (Dvorníky-Včeláre, Slovak Karst)	5	3	6	4	Fejfar and Horáček (1983), Horáček (1985)
	VC7	Včeláre 7 (Dvorníky-Včeláre, Slovak Karst)	1	0	0	0	Horáček (1985)
	TOTAL		**80**	**52**	**120**	**69**	



Text-fig. 4. Frequency diagram of metric variation (M1 length = M1U) in samples of *Apodemus* spp. representing particular Pleistocene biozones (MN 17 – Q 3), compared to variation span in the Recent samples of *A. uralensis*, *A. sylvaticus* and *A. flavicollis* (a heading strip).



Text-fig. 5. Frequency diagram of metric variation (m1 lenght = m1L) in samples of *Apodemus* spp. representing particular Pleistocene biozones (MN 17 – Q 3), compared to variation span in the Recent samples of *A. uralensis*, *A. sylvaticus* and *A. flavicollis* (a heading strip).

The procedure of phenotype categorization based on variation of extant species was applied: individuals falling in zones of overlap and those exhibiting the character states restricted to particular extant species were treated as different parataxa (for more detailed information see Knitlová and Horáček 2017). Diagnostic criteria for the respective parataxa were established based on morphometric characteristics: (i) length of molars (M1U, M18U, m1L, m16L) and (ii) surface area of molars (SURM1, SURM2, SURm1, SURm2) (see tab. 2 in Knitlová and Horáček 2017). All examined molars were categorized into parataxa 1–5 (1 – *A. uralensis*, 2 – *A. uralensis*/*A. sylvaticus*, 3 – *A. sylvaticus*, 4 – *A. sylvaticus*/*A. flavicollis*, 5 – *A. flavicollis*) based on the above mentioned morphometric criteria. For each item, three different determination techniques were used independently: SPA – preliminary identification "by eye" based on overall phenotype appearance; SPB – categorization based on molar length variables and SPC – categorization based on area variables.

The set of morphometric data was further analysed with the aid of a multivariation approach. A standard PCA of fossil samples and a series of discrimination functions were computed using different sets of metric and non-metric variables, with the samples of extant species as the primary source of discrimination factors. The biometric data for extant samples (n = 225) were retrieved from a previous study (Knitlová and Horáček 2017) as well as the default discrimination functions based on metric variables (applied in Text-fig. 6). Corresponding comparisons, based on a most robustly discriminating set of both metric and non-metric m1 and M1 variables respectively, are presented in Text-figs 7 and 8. Regarding the numerical scoring of the non-metric variables utilise in this study, for the purpose of multivariate comparisons their states were treated as metrical characters.

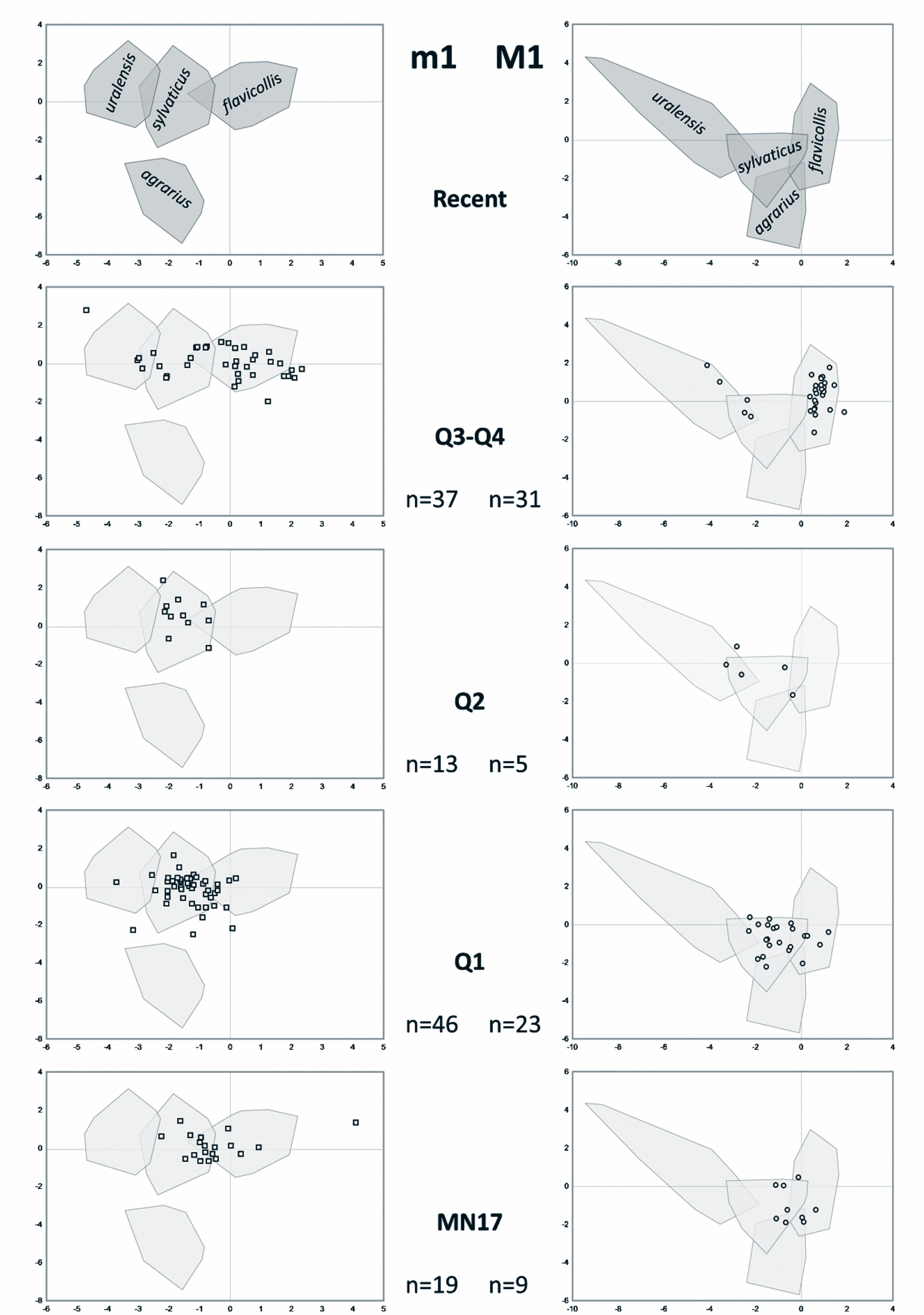
For each individual of the Recent and fossil samples, an average difference from the mean values for extant species (*A. uralensis*, *sylvaticus*, *flavicollis*) was computed separately for metric and non-metric characters. For metric characters the difference was expressed as a ratio of individual and mean state, for the non-metric as an absolute value of the respective numerical difference. The variation pattern was expressed in the form of plot of metric to non-metric values (Text-fig. 9).

Statistical analyses were performed in Microsoft Excel and Statistica Software 13.

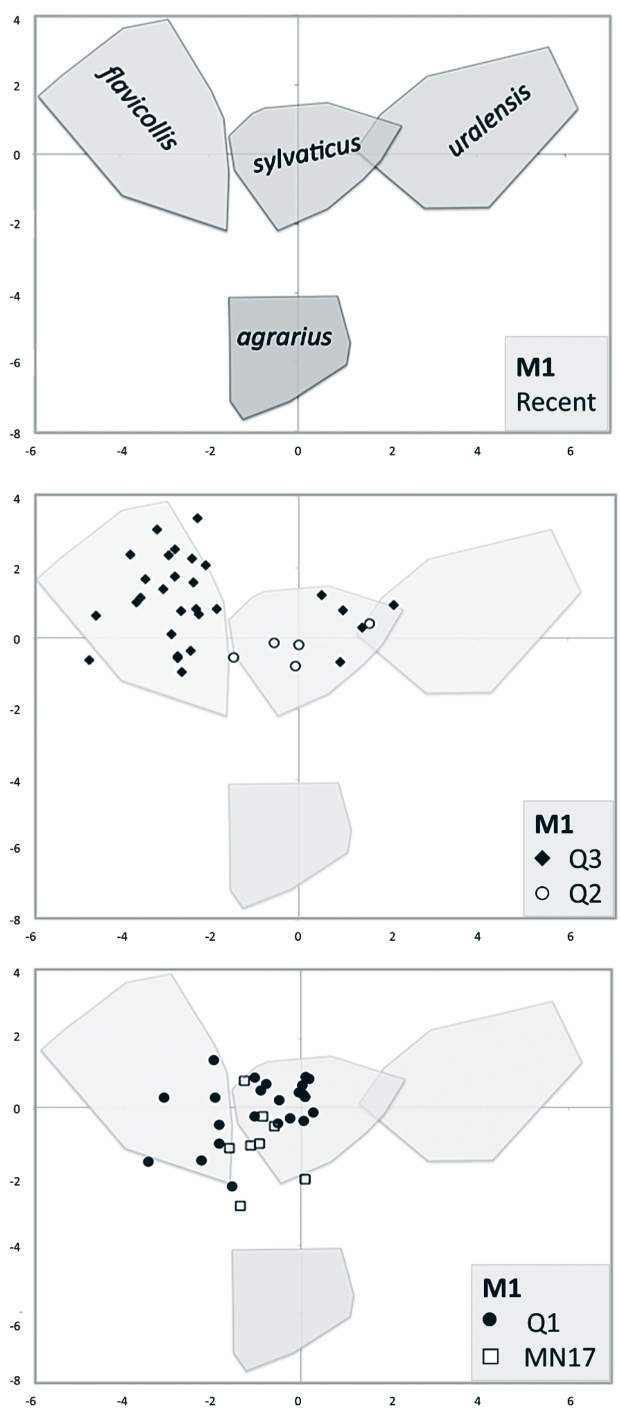
Results

Out of 321 molars (80 M1, 52 M2, 120 m1, 69 m2) studied, 12 teeth were not categorized into any parataxa and excluded from most of morphometric analyses due to damage or a high degree of tooth wear. One tooth (m1 from Včeláre 7) was not classified into any parataxa due to significantly exceeding the upper limit of the variability of the Recent population of the largest Central European species (*A. flavicollis*, m1L = 2.05 mm). This specimen was identified as the genus *Rhagapodemus* (m1L = 2.29 mm) (see App. 2).

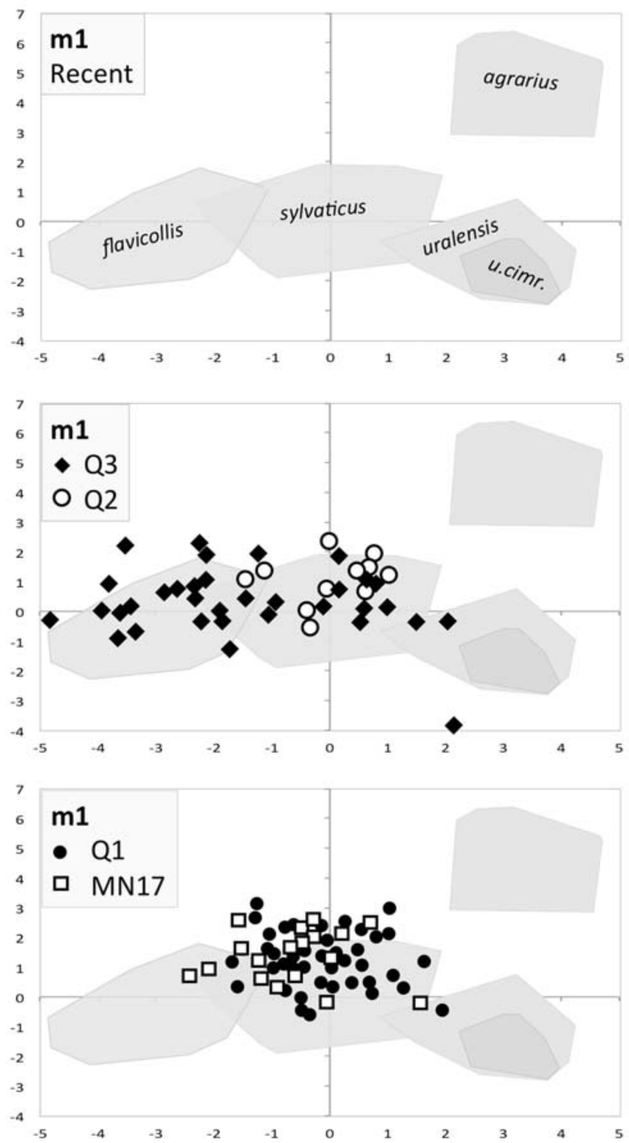
No item exhibited the characteristics of *A. agrarius*. This also concerns the M2 from Mokrá 1 with indistinct t3



Text-fig. 6. Plot of discriminant scores (R1/R2) of individual m1 and M1 teeth of *Apodemus* spp. from particular Pleistocene biozones superimposed onto a plot of variation ranges for the respective variables for the Recent *Apodemus* sample (based on the discrimination analysis of metric variables of M1 and m1).



Text-fig. 7. Plot of discriminant scores (R1/R2) of individual M1 of *Apodemus* spp. from particular Pleistocene biozones superimposed onto a plot of variation ranges for the respective variables for the Recent *Apodemus* sample (based on the discrimination analysis of total set of characters, both metric and non-metric).



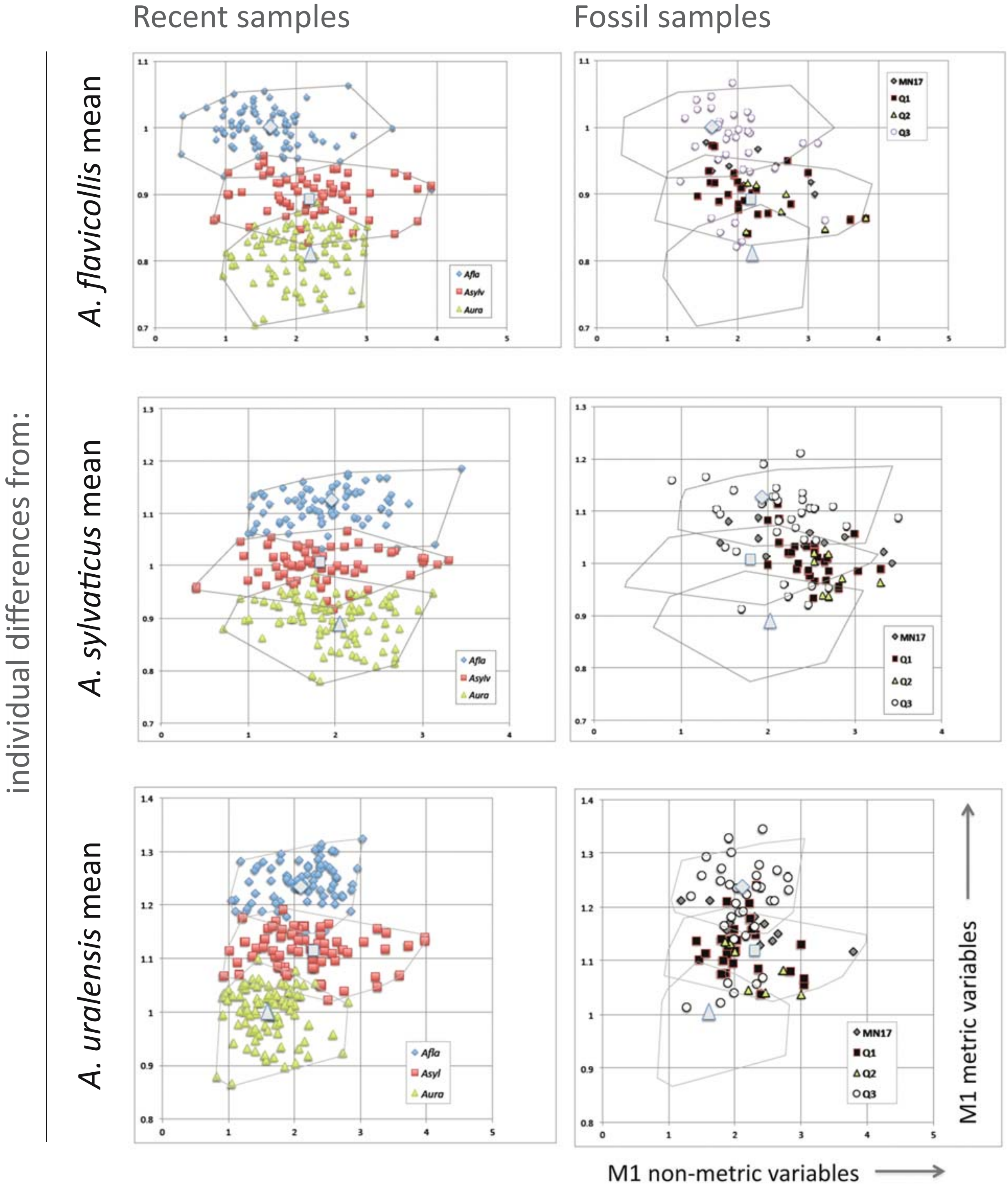
Text-fig. 8. Plot of discriminant scores (R1/R2) of individual m1 of *Apodemus* spp. from particular Pleistocene biozones superimposed onto a plot of variation ranges for the respective variables for the Recent *Apodemus* sample (standardized discrimination scores based on nine most significant variables).

for which it was formerly identified as "*A*. cf. *agrarius*" by Horáček (1984).

Phenotype categories (parataxa)

Data on size variation in specific stratigraphic horizons are presented in Text-figs 4 and 5. A clear difference can be seen between the Middle Pleistocene (Q 3) and earlier horizons (MN 17 – Q 2). While in the former more recent horizons, the *Apodemus* sample exhibits a bi- or trimodal distribution with peaks corresponding to extant species *A. uralensis*, *sylvaticus* and *flavicollis* (the most common species), similar to the Late Pleistocene-Holocene pattern, in the latter it show a unimodal distribution centered on the variation range exhibited by extant *A. sylvaticus*. In short, the vast majority of the Villanyian and Biharian items fall within the variation range of recent populations of *A. sylvaticus*, but most of them differ from extant species due to the well-developed t12 in M1 – M2 (comp. App. 3).

The identification of individual items in terms of arbitrary phenotype categories (parataxa), established based on variation within extant species, revealed the same picture. All parataxa (1–5) were represented in the Pleistocene material examined. On the basis of morphometric criteria



Text-fig. 9. Mean individual differences in non-metric and metric variables of M1 from respective mean values of extant *A. flavicollis*, *A. sylvaticus* and *A. uralensis* in the Recent samples (left) and fossils of particular Pleistocene biozones (right), superimposed to variation ranges and centroids of the former ones.

(SPB, SPC), most of the fossil record was assigned to parataxon 2 (38 molars), parataxon 3 (91 molars), parataxon 4 (74 molars) and parataxon 5 (93 molars), while the other parataxon, 1, was clearly less abundant – 12 molars (see also the results of the frequency analysis of M1U values in Text-fig. 4 and m1L values in Text-fig. 5).

A detailed survey of the determination results for particular community samples is in Appendix 2. In terms of individual parataxa it can be summarized as follows:

Parataxon 1 – *A. uralensis* s. str.: 12 molars (5 M1, 4 m1, 3 m2) from 6 community samples (Q 1: Mladeč 1B; Q 2: Chlum 4, 4C/4=Y; Q 3: Mladeč 2, 2 4m, 2 7/20)

Parataxon 2 – *A. uralensis*/*A. sylvaticus*: 38 molars (9 M1, 2 M2, 18 m1, 9 m2) from 18 community samples (MN 17: Javoříčko III; Q 1: Včeláre 4E, 5B, 5 base 90, 4/7, 6/3, 6/7, 6/8; Q 1/Q 2: Mladeč 3 7/10; Q 2: Chlum 4, 4C/4=Y, 4C/6, 4C/6/7; Stránská skála 1/6; Q 3: Mladeč 2, 2 1m, 2 vrch; Turold NE 8/1+2 base)

Parataxon 3 – *A. sylvaticus* s.str.: 91 molars (22 M1, 9 M2, 47 m1, 13 m2) from 27 community samples (MN 17: Ctiněves 25; Javoříčko IV; Plešivec E, 6556; Včeláre 6/1c, 6/1, 3, 7; Q 1: Měňany 2; Sovinec 4; Včeláre 3B/1, 4E, 5B, 5 base 90, 4/7, 6/3, 6/7, 6/8; Q 1/Q 2: Honce; Q 2: Bzince; Chlum 4C/4=Y, 4C/6/7; C "x"; Stránská skála 1/6; Q 3: Mladeč 2, 2 1m; Turold NE 8/1+2 base)

Parataxon 4 – *A. sylvaticus*/*A. flavicollis*: 74 molars (13 M1, 22 M2, 17 m1, 22 m2) from 33 community samples (MN 17: Chlum 7; Ctiněves 23, 25; Javoříčko III, IV; Plešivec E; Včeláre 6/1c, 6/1, 3; Q 1: Mladeč 1; Sovinec 4, 4 (353); Včeláre 3B/1, 4E, 5B, 5 base 90, 4/7, 6/3, 6/7, 6/8; Q 1/Q 2: Honce; Q 2: Bzince A; Chlum 4/C3, 4C/4=Y, 4-3~6, 4B/10b, 4K/3B; Stránská skála 7; Q 3: Dobrkovice II; Mladeč 2, 2 4m, 2 7/20; Q 4: Kobyla 6)

Parataxon 5 – *A. flavicollis*: 93 molars (27 M1, 15 M2, 31 m1, 20 m2) from 18 community samples (MN 17: Javoříčko III; Plešivec A4, E; Včeláre 6/1, 3; Q 1: Včeláre 3B/1, 4E, 5B, 4/7, 6/3, 6/8; Q 2: Chlum 4; Stránská skála cave; Q 3: Mladeč 2 4m; Turold W1; Q 4: Balcarka; Kobyla 6, 9)

Number of roots

In the total of 80 M1 examined, 12 of them are three-rooted, 45 four-rooted, 14 M1 are in maxillary fragments and in 14 M1 the roots are not preserved. The representation of three-rooted and four-rooted M1 in individual community samples is listed below: three-rooted M1 – 12 molars in 8 community samples (MN 17: Chlum 7; Plešivec E; Q 1: Včeláre 3B/1, 5B, 6/8; Q 2: Chlum 4C/4=Y; Q 3: Mladeč 2; Turold NE8/1+2 base); 4-rooted M1 – 45 molars in 17 community samples (MN 17: Ctiněves 23, 25; Plešivec 6556; Včeláre 6/1c; Q 1: Měňany 2; Včeláre 3B/1, 5B, 6/3, 6/7; Q 1/Q 2: Honce; Q 2: Bzince; Q 3: Dobrkovice; Madeč 2; 2 4 m, 2 vrch; Q 4: Balcarka; Kobyla 9).

In the total of 52 M2 studied, only one M2 had 3 roots (Q 1: Včeláre 6/8), 27 M2 are four-rooted, 13 M2 are in maxillary fragments and in 11 M2 the roots are not preserved.

In the total of 28 fragments of upper jaw examined, 8 of them have 3 alveoli for M1 (MN 17: Včeláre 6/1; Q 1: Mladeč 1; Sovinec 4 (353); Včeláre 6/7, 6/8); 18 have 4 alveoli for M1 (Q 1: Včeláre 5B, 5 base 90, 6/7, 6/8; Q 2: Bzince B; Chlum 4C/6; Q4: Kobyla 9), in 2 fragments alveoli are not preserved (Q 2: Bzince B; Chlum 4B/10b). None of studied maxillary fragments had 3 alveoli for M2 (11 maxillary fragments had 4 alveoli for M2, the remaining alveoli are not preserved). We found no clear relationship between the number of roots and categories of the phenotypic classification (parataxa). At the same time, both the presumptive plesiomorphic condition (3 roots) and derived condition (4 roots) appeared in all stratigraphic horizons at roughly the same frequencies, no clear trend could be identified.

Multivariate comparisons

All discriminant analyses exhibiting for a given set of characters (m1, M1, etc.) the best discrimination capacity, revealed roughly the same picture (comp. Text-figs 6, 7 and 8). The Q 3 samples are clearly split into clusters corresponding to extant species with that of *A. flavicollis* as the most frequent. Only a few items fall beyond the limits of the variation ranges of extant samples. The Q 2 material exhibited the least variation, clearly corresponding to the variation range of *A. sylvaticus*. In contrast, Q 1 and MN 17 samples showed relatively broad variation centred within the variation span of *A. sylvaticus* but exceeding it both up to the marginal areas of *A. flavicollis* and *uralensis* clusters and beyond the variation ranges of extant species. The centroids of Q 1 and particularly MN 17 samples are shifted relatively far from the centroid of extant *A. sylvaticus*, being close to the overlap zone of *sylvaticus*/*flavicollis* clusters.

Quantitative pattern of phenotype variation

A comparison of extant and fossil forms with respect to individual differences from mean states of metric and nonmetric variables in three extant species (Text-fig. 9) revealed a picture which clearly supports the above mentioned patterns. There is a perfect correspondence in population variation pattern between Q 3 samples and extant populations but clear differences between MN 17 and Q 2 samples. Regarding the relationship to *A. uralensis* and *A. flavicollis*, it appears that almost all items of MN 17 to Q 2 age fall in the clusters of *A. sylvaticus*. Nevertheless, regarding the relationship to the mean of *A. sylvaticus*, they show considerable difference from the cluster characterizing the variation pattern of extant *A. sylvaticus* (including the centroid position) particularly in the value of non-metric characters.

Discussion

The classification of fossil species of the genus *Apodemus* is exclusively based on odontological characters. Martín-Suárez and Mein (1998) list for most of them a default generic state and orientation of their phylogenetic morphoclines: (i) a stephanodont pattern of M1, M2 forming a nearly continuous crest connecting cusps t4-5-9-8, with gradual inflation of t8 and appearance of t7 at its labial base; (ii) the cusps t6 and t9 grow closely connected; (iii) cusp t12 is large in the fossil forms, in the majority of more recent forms it tends to be reduced (supposedly due to the increase in volume of t8); (iv) M1 with t1 in an anterior position and three or four roots; (v) M2 without t1bis; (vi) typically, no longitudinal connections between cusps of lower molars while the cusp pairs tend to form chevrons; (vii) a distinct tma cusp on m1, as a rule.

All the items included in our study corresponded well to these diagnostic features. Both in metric and non-metric characters the Pleistocene samples covered almost the whole variation range of the Recent and Holocene populations of extant mid-European species, *uralensis*, *sylvaticus* and *flavicollis*, including extensive zones of between-species overlap (comp. Knitlová and Horáček 2017). Application of diverse techniques quantifying the degree of correspondence between the extant and Pleistocene samples of course revealed considerable differences. While the samples of Middle Pleistocene age (Q 3) corresponded quite perfectly to extant phenotype diversity of the genus in the pattern of variation span, position of centroids, quantitative patterns of within-species variation (both in metric and non-metric characters) and even frequency of individual species (with dominating *A. flavicollis*), the samples from all stages of the Early Pleistocene (MN 17 – Q 2) show in all these respects clear differences from the Recent forms.

In this respect, our results robustly support the conclusion by Pasquier (1974) that based on phenotypic traits *A. sylvaticus* and *A. flavicollis* appeared initially as two separate species at the beginning of the Middle Pleistocene. The shift in the phenotype pattern at the Q 2/Q 3 boundary, at which point the phenotypes characterizing the extant species were being established, is synchronous with analogical rearrangements in other clades (*Sorex runtonensis- S. araneus*, *Mimomys savini-Arvicola*, *Microtus gregaloides-M.gregalis* etc. – comp. e.g. Horáček and Ložek 1988). This could have been driven by dramatic climatic and environmental changes originated at the Early-Middle Pleistocene transition (Head and Gibbard 2005).

The Early Pleistocene record of the genus is dominated with a form corresponding in overall size to extant *A. sylvaticus* but at the same time showing significant differences from the extant species. However, what is the actual taxonomic relevance of these differences and, correspondingly, relevance of the differences between the samples from particular Early Pleistocene localities (clearly pronounced in MN 17 and older samples) cannot be answered with any certainty at the moment. Whether more species were part of the group, and which would reflect actual taxonomic diversity of the genus in Europe during the course of the Late Cenozoic past, the status of particular nominate fossil species and their relationship to extant taxa, remains with the present state of knowledge unknown. Answering these questions is confounded by multiple factors – from the fragmentarity of the fossil record (a lack of abundant population samples) to poor comprehension of some aspects of character variation and their phylogenetic significance. Many times it has been stressed that species identification of the Pliocene *Apodemus* is particularly difficult, because – notwithstanding the broad variation – some of the characters discriminating them are mostly symplesiomorphies, e.g. a three-rooted M1 and M2, a relatively well developed t12 in the M1 and M2 and the presence of the cingular cuspid c1 in the m1 and m2 (Martín-Suárez and Mein 1998, 2004, Minwer-Barakat et al. 2005, García-Alix et al. 2009, Hordijk and de Bruin 2009). In addition, in the Early Pleistocene forms, the situation is almost the same (Marchetti et al. 2000).

Considering the *sylvaticus*-like Early Pleistocene form, comprising the major bulk of the samples surveyed, two names are available and frequently used (comp. Kowalski 2001): *A. atavus* Heller, 1936 and *A. dominans* Kretzoi, 1959. Under these names, a medium-sized species is reported from many localities in Europe since the latest Miocene up to the Early Pleistocene (Rietschel and Storch 1974, Fejfar and Storch 1990, Bolliger et al. 1993, Martín-Suárez and Mein 1998, 2004, Marchetti et al. 2000, Minwer-Barakat et al. 2005, García-Alix et al. 2009, Hordijk and de Bruin 2009, Colombero et al. 2014). Nevertheless, the distinction between *A. atavus* and *A. dominans*, based on morphology, is often regarded as highly problematic (Popov 2004, Hordijk and de Bruijn 2009, Vasileiadou et al. 2012).

The diagnosis of *A. atavus* Heller, 1936 (type locality Gundersheim, MN 16) is based on the following characters (Heller 1936): always well-developed t7 and t12, t3 with short posteriorly directed spur, separated t4 and t7 until a fairly advanced stage of wear and three roots on the slender M1 and an always well-developed tma, the spur of the protoconid/metaconid chevron connected to the lingual cusp of the anteroconid complex and a variable number of labial accessory cuspulids on the m1, large posterior heel of m2 that usually protrudes over the outline. Rietschel and Storch (1974) gave as diagnostic criterion of *A. atavus* that the c1 of m2 is large. Yet, in larger samples that character appears to be highly variable: some specimens have a well-developed c1, and in other cases it is much reduced (Minwer-Barakat et al. 2005). In the collection from the type locality, Gundersheim, no m2 are available. The majority of the small Pliocene *Apodemus* with individualized t7 are attributed to *A. atavus* (Heller 1936, Rietschel and Storch 1974, Maul 1990, Bollinger et al. 1993, Mörs et al. 1998, van Kolfschoten et al. 1998, Marchetti et al. 2000).

Diverse opinions were proposed concerning the phylogenetic relationships of *A. atavus*. (i) *A. atavus* does not show an ancestor-descendant relationship with any western European Miocene taxon, it may be an Asian immigrant (Martín-Suárez and Mein 1998). The geographic distribution of *A. atavus* extends throughout the Palaearctic region (Cai and Qui 1993, Martín-Suárez and Mein 1998), chronologically from the latest Miocene to the Early Pleistocene (Minwer-Barakat et al. 2005). It is a species with relatively conservative morphology, with few differences between the oldest and the youngest populations (Minwer-Barakat et al. 2005). (ii) *A. atavus* should be considered as a direct ancestor of the extant species *A. sylvaticus* (Rietschel and Storch 1974, Fejfar and Storch 1990, Martín-Suárez and Mein 1998). This relationship may be corroborated by some remains of *A. atavus* from Willerhausen (Rietschel and Storch 1974), where the exceptional preservation of bones and soft tissues allowed the authors to note that the habitus and size of the two species are similar and that *A. atavus* differs solely in a few characters such as the shorter ulna and femur and the more prominent t12 in M1 and M2. (iii) According to Martín-Suárez and Mein (1998), *A. atavus* could be a common ancestor of *A. sylvaticus* and *A. flavicollis* in the Early Pleistocene of Europe. (iv) Most of the Early Pleistocene European samples of *Apodemus* can be considered as *A. atavus*, finally including the Late Biharian populations as proposed by Marchetti et al. (2000) who reported the largest population sample (more than 500 remains) from the site Monte La Mesa, Italy.

A. dominans Kretzoi, 1959 (type locality Csarnóta 2, MN 15b) was reported in Europe since the latest Miocene to the Pleistocene. According to Martín-Suárez and Mein (1998), *A. dominans* represented a very conservative lineage leading from the Late Miocene to the Pleistocene. According to Rietschel and Storch (1974) and Pasquier (1974), *A. dominans* could be an ancestor of *A. flavicollis*. Fejfar and Storch (1990) suggested that putative distinctive characters of *A. dominans* including the presence of a prominent t12 on M1, M2, three radiculated upper molars, and the presence of rearward facing c1 on m1 and m2 should be regarded as symplesiomorphies of the genus. The size differences between *A. dominans* from the type locality of Csarnóta 2 (van de Weerd 1976) and *A. atavus* from Gundersheim 4

(Fejfar and Storch 1990), supposedly close to its type site, are very slight. However, some authors (Storch and Dahlmann 1995, Mörs et al. 1998, Popov 2004, Hordijk and de Bruijn 2009, Vasileiadou et al. 2012) assigned per analogia to common occurrence of extant *sylvaticus* and *flavicollis* some specimens to *A. dominans* and *A.* cf. *dominans* as a separate species because of their slightly larger mean values with respect to those of *A. atavus* from Gundersheim 4. However, Fejfar and Storch (1990) argued that the minute size differences between the two forms does not provide a reliable criteria to support their independent status and consider *Apodemus dominans* to be a junior synonymum of *Apodemus atavus* (including *A. occitanus* synonymized with *dominans* already by de Bruijn and van der Meulen 1975), the view later also accepted by Martín-Suárez and Mein (2004), Minwer-Barakat et al. (2005), García-Alix et al. (2008), and Colombero et al. (2014).

Our results revealing the differences in variation pattern, particularly in non-metric characters, between the extant *sylvaticus* and the Early Pleistocene medium-sized form suggest that the extant and fossil form present distinct entities, a fact worth being emphasized by denoting the latter as a separate taxon. With regard to the above discussed taxonomic conclusions we propose as a provisional solution (until a detailed comparison is made of Pliocene and Early Pleistocene populations) to denote all the medium-sized *sylvaticus*-like forms from the mid-European Early Pleistocene with the prior name *A. atavus* Heller, 1936.

The other question to be discussed concerns the rare small-sized items which partly fall in the range of extant *A. uralensis* (comp. parataxon 1), appearing mostly in the early Middle Pleistocene assemblages. The fossil taxon which come here in account is *A. maastrichtiensis* van Kolfschoten, 1985 (type locality Maastricht-Belvedere, Middle Pleistocene, with further records from Q 3 sites Fransche Kamp, Wageningen, Miesenheim). Its diagnosis is as follows (van Kolfschoten 1985): the M1 with 3–4 roots (mostly 3) and t9 which is smaller than t6 and a narrow, elongated t7. The t3 of the M2 is incipient or absent, t7 and t9 are small. The slopes of the m1 and m2 cusps are more or less vertical and the angle formed by the chevrons is obtuse. The tma of m1 is isolated in most of the specimens. The m2 antero-labial cusp is small. *A. maastrichtiensis* differs from all other *Apodemus* species in the extreme steepness of the cusp slopes in its lower molars. From *A. uralensis* it differs in the size of the t3 of M2 which is more strongly developed in *A. uralensis*. Only a small number of specimens of *A. uralensis* (2 out of 114) show a reduction in t3 (Steiner in Niethammer 1978). The t9 of M1 and M2 of *A. uralensis* are also larger than those of *A. maastrichtiensis*. In addition several specimens from our Q 2 and Q 3 sites (Mladeč 3, Chlum 4) and also the teeth from MN 17 sites (Ctiněves, Javoříčko III) clearly show a closer correspondence to *A. maastrichtiensis* in its diagnostic characters than to *uralensis*. What is actual significance of these relationships and what was the Pleistocene history of the small-sized *Apodemus* remains an important task for further study.

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References

Agustí, J., Cabrera, L., Garces, M., Krijgsman, W., Oms, O. et al. (2001): A calibrated mammal scale for the Neogene of Western Europe: State of the art. – Earth-Science Reviews, 52: 247–260. https://doi.org/10.1016/S0012-8252(00)00025-8

Ancillotto, L., Mori, E., Sozio, G., Solano, E., Bertolino, S., Russo, D. (2017): A novel approach to field identification of cryptic *Apodemus* wood mice: calls differ more than morphology. – Mammal Review, 47: 6–10. https://doi.org/10.1111/mam.12076

Argenti, P., Kotsakis, T. (1999): Fossil *Apodemus* (Rodentia: Muridae) in Italy: the biochronological meaning. – In: Proceedings of the 2nd FIST Congress. Geoitalia, 1: 59–61.

Barčiová, L., Macholán, M. (2009): Morphometric key for the discrimination of two wood mice species, *Apodemus sylvaticus* and *A. flavicollis*. – Acta Zoologica Academiae Scientiarum Hungaricae, 55: 31–38.

Bellinvia, E. (2004): A phylogenetic study of the genus *Apodemus* by sequencing the mitochondrial DNA control region. – Journal of Zoological Systematics and Evolutionary Research, 42: 1–9. https://doi.org/10.1111/j.1439-0469.2004.00270.x

Bellinvia, E., Munclinger, P., Flegr, J. (1999): Application of the RAPD technique for a study of the phylogenetic relationships among eight species of the genus *Apodemus*. – Folia Zoologica, 48: 241–248.

Bernor, R. L., Fahlbusch, V., Andrews, P., de Bruijn, H., Fortelius, M. et al. (1996): The evolution of western Eurasian Neogene mammal faunas: A chronologic, systematic, biogeographic and paleoenvironmental synthesis. – In: Bernor, R. L., Fahlbusch, V., Mittmann, H. W., (eds), The evolution of western Eurasian Neogene mammal faunas. Columbia University Press, New York, pp. 449–471.

Bollinger, T., Engesser, B.,Weidmann, M. (1993): Première découverte de mammifères pliocènes dans le Jura Neuchâtelois. – Eclogae Geologicae Helvetiae, 86: 1031–1068.

Cai, B., Qiu, Z. (1993): Murid rodents from the Late Pliocene of Yangquan and Yuxian, Hebei. – Vertebrata PalAsiatica, 31: 267–293.

Colombero, S., Pavia, G., Carnevale, G. (2014): Messinian rodents from Moncucco Torinese, NW Italy: palaeobiodiversity and biochronology. – Geodiversitas, 36: 421–475. https://doi.org/10.5252/g2014n3a4 de Bruijn, H., van der Meulen, A. J. (1975): The early Pleistocene rodents from Tourkobounia-1 (Athens, Greece). – Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, B, 78: 314–338.

Fejfar, O. (1965): Die unter-mittelpleistozäne Mikromammalien-Funa aus Dobrkovice, Südböhmen. – Berichte der Geologische Gesellschaft DDR, 10: 57–65.

Fejfar, O., Heinrich, W.-D. (1983): Arvicoliden-Sukzession und Biostratigraphie des Oberpliozäns und Quartärs in Europa. – Schriftenreihe für Geologische Wissenschaften, 19/20: 61–109.

Fejfar, O., Horáček, I. (1983): Zur Entwicklung der Kleinsäugerfaunen im Villányium und Alt-Biharium auf dem Gebiet der ČSSR. – Schriftenreihe der geologischen Wissenschaften, Berlin, 19-20: 111–208.

Fejfar, O., Storch, G. (1990): Eine pliozäne (ober-ruscinische) Kleinsäugerfauna aus Gundersheim, Rheinhessen. 1. Nagetiere: Mammalia, Rodentia. – Senckenbergiana lethaea, 71: 139–184.

Filippucci, M. G., Macholán, M., Michaux, J. R. (2002): Genetic variation and evolution in the genus *Apodemus* (Muridae: Rodentia). – Biological Journal of the Linnean Society, 75: 395–419.
https://doi.org/10.1111/j.1095-8312.2002.tb02080.x

Filippucci, M. G., Storch, G., Macholán, M. (1996): Taxonomy of the genus *Sylvaemus* in western Anatolia: morphological and electrophoretic evidence (Mammalia: Rodentia: Muridae). – Senckenbergiana Biologica, 75: 1–14.

Freudenthal, M., Martín-Suárez, E. (1990): Size variation in samples of fossil and recent murid teeth. – Scripta Geologica, 93: 1–34.

Freudenthal, N., Martín-Suárez, E. (1999): The Miocene land mammals of Europe. – Geobios, 38: 401–409.

Frynta, D., Mikulová, P. (2001): Discriminant analysis of morphometric characters in four species of *Apodemus* (Muridae: Rodentia) from Eastern Turkey and Iran. – Israel Journal of Zoology, 47: 243–258.
https://doi.org/10.1560/UN22-P31P-PHKD-8D6X

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M. (2008): Muridae (Rodentia, Mammalia) from the Mio-Pliocene boundary in the Granada Basin (southern Spain). Biostratigraphic and phylogenetic implications. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 248: 183–215.
https://doi.org/10.1127/0077-7749/2008/0248-0183

Head, M. J., Gibbard, P. L. (2005): Early–Middle Pleistocene transitions: an overview and recommendation for the defining boundary. – In: Head, M. J., Gibbard, P. L. (eds), Early–Middle Pleistocene transitions: the land–ocean evidence. Special Publication, Geological Society of London, 247: 1–18.
https://doi.org/10.1144/GSL.SP.2005.247.01.01

Heinrich, W.-D., Maul, L. (1983a): Skelettreste von Nagetieren (Rodentia, Mammalia) aus dem fossilen Tierbautensystem von Piesede bei Malchin. Teil 1. Taxonomische und biometriche Kennzeichung des Fundgutes. – Wissenschaftliche Zeitschrift der Humboldt Universität zu Berlin, Mathematisch-naturwissenschaftliche Reihe, 32: 729–743.

Heinrich, W.-D., Maul, L. (1983b): Skelettreste von Nagetieren (Rodentia, Mammalia) aus dem fossilen Tierbautensystem von Piesede bei Malchin. Teil 2. Paläoökologische und faunengeschichtliche Auswertung des Fundgutes. – Wissenschaftliche Zeitschrift der Humboldt Universität zu Berlin, Mathematisch-naturwissenschaftliche Reihe, 32: 745-752.

Heller, F. (1936): Eine oberpliozäne Wirbeltierfauna aus Rheinhessen. – Neues Jahrbuch für Mineralogie, Geologie und Palaöntologie, Abteilung B, 76: 99–160.

Horáček, I. (1979): Výplně 4. sluje na Chlumu u Srbska a jejich význam pro kvartérní stratigrafii [The 4th Cave in Chlum near Srbsko and its significance for Quaternary stratigraphy]. – Český kras, 4: 19–34. (in Czech with English summary)

Horáček, I. (1980): Včeláre 3 – nová staropleistocenní lokalita Slovenského krasu [Včeláre 3 – a new Early Pleistocene site in the Slovak karst]. – Slovenský kras, 18: 183–192. (in Czech with English summary)

Horáček, I. (1982): Výzkum fosilních obratlovců v CHKO Český kras [Reaseach on fossil vertebrates in the Bohemian karst]. – Památky a příroda, 1982(2): 106–111. (in Czech)

Horáček, I. (1983): Pokryvné uloženiny a fosilní výplně [Subsurface deposits]. – In: Bosák, P. (ed.), Krasové jevy vrchu Turold u Mikulova [Karst phenomena of Turold Hill near Mikulov]. Studie ČSAV, 5/84: 105 pp. (in Czech with English summary)

Horáček, I. (1984): Mokrá 1 – nová lokalita staropleistocenní fauny v Moravském krasu [Mokrá 1 – new locality with Early Pleistocene fauna in Moravian karst]. – Československý kras, 34: 55–60. (in Czech with English summary)

Horáček, I. (1985): Survey of the fossil vertebrate localities Včeláre 1-7. – Časopis pro mineralogii a geologii, 30: 353–366.

Horáček, I., Knitlová, M., Wagner, J., Kordos, L., Nadachowski, A. (2013): Late Cenozoic history of the genus *Micromys* (Mammalia, Rodentia) in Central Europe. – PLoS ONE, 8: e62498 (19 pp.).
https://doi.org/10.1371/journal.pone.0062498

Horáček, I., Ložek, V. (1983): Paleontologické doklady a jejich stratigrafické zhodnocení. [Paleontological records and their stratigraphical meaning]. – In: Bosák, P. (ed.), Krasové jevy vrchu Turold u Mikulova [Karst phenomena of Turold Hill near Mikulov]. – Studie ČSAV, 5/84: 105 pp. (in Czech with English summary)

Horáček, I., Ložek, V. (1984): Z výzkumu výplní Mladečských jeskyní u Litovle [Fossil deposits of Mladečské Cave near Litovel]. – Československý kras, 35: 98–100. (in Czech with English summary)

Horáček, I., Ložek, V. (1987): Staropleistocenní fauna z Honců ve Slovenském krasu [Early Pleistocene fauna from Honce, Slovak karst]. – Československý kras, 38: 133–134. (in Czech with English summary)

Horáček, I., Ložek, V. (1988): Palaeozoology and the Mid-European Quaternary past: scope of the approach and selected results. – Rozpravy ČSAV, řada MPV, 98: 1–102.

Horáček, I., Sánchez-Marco, A. (1984): Comments on the Weichselian small mammal assemblages in Czechoslovakia and their stratigraphical interpretation. – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 1984(9): 560–576.

Hordijk, K., de Bruijn, H. (2009): The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). – Hellenic Journal of Geosciences, 44: 21–103.

Jojić, V., Blagojević, J., Vujošević, M. (2012): Two-module organization of the mandible in the yellow-necked mouse: a comparison between two different morphometric approaches. – Journal of Evolutionary Biology, 25: 2489–2500. https://doi.org/10.1111/j.1420-9101.2012.02612.x

Knitlová, M., Horáček, I. (2017): Late Pleistocene-Holocene paleobiogeography of the genus *Apodemus* in Central Europe. – PLoS ONE, 12 (3): e0173668 (23 pp.). https://doi.org/10.1371/journal.pone.0173668

Kowalski, K. (2001): Pleistocene rodents of Europe. – Folia Quarternaria, 72: 1–389.

Kučera, J., Sůvová, Z., Horáček, I. (2009): Stránská skála jeskyně: glacialní společenstvo hlodavců (Rodentia) ze staršího středního pleistocenu [Early Middle Pleistocene glacial communitity of rodents (Rodentia): Stránská skála Cave (Czech Republic)]. – Lynx, n. s., 40: 43–69. (in Czech with English summary)

Libois, R., Michaux, J. R., Ramalhinho, M. G., Maurois, C., Sara, M. (2001): On the origin and systematics of the northern African wood mouse (*Apodemus sylvaticus*) populations: a comparative study of mtDNA restriction patterns. – Canadian Journal of Zoology, 79: 1503–1511. https://doi.org/10.1139/z01-106

Liu, X., Wei, F., Li, M., Jiang, X., Feng, Z., Hu, J. (2004): Molecular phylogeny and taxonomy of wood mice (genus *Apodemus* Kaup, 1829) based on complete mt DNA cytochrome b sequences, with emphasis on Chinese species. – Molecular Phylogenetics and Evolution, 33: 1–15. https://doi.org/10.1016/j.ympev.2004.05.011

Ložek, V. (1964): Quartärmollusken der Tschechoslowakei. – Rozpravy ÚÚG, 31: 1–374.

Ložek, V., Horáček, I. (1984): Staropleistocenní fauna z jeskyně Na Skalce u Nového Mesta nad Váhom [Early Pleistocene fauna from Na Skalce Cave near Nové Mesto nad Váhom]. – Československý kras, 35: 65–75. (in Czech with English summary)

Ložek, V., Horáček, I. (1988): Vývoj prírody Plešivecké planiny v poledové dobe [Postglacial history of Plešivecká plainina, Slovak Karst]. – Ochrana prírody, Bratislava, 6A: 151–175. (in Slovak with English summary)

Marchetti, M., Parolin, K., Sala, B. (2000): The Biharian fauna from Monte La Mesa (Verona, northeastern Italy). – Acta Zoologica Cracoviensia, 43(1): 79–105.

Marcolini, F., Masini, F., Petronio, C. (2013): The rodents of the Pirro Nord fauna (Foggia, Southern Italy). – Palaeontographica, Abteilung A: Palaozoologie-Stratigraphie, 298(1-6): 73–85. https://doi.org/10.1127/pala/298/2013/73

Martín-Suárez, E., Mein, P. (1998): Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys* and *Rhagapodemus* (Rodentia, Mammalia). – Geobios, 31: 87–97. https://doi.org/10.1016/S0016-6995(98)80099-5

Martín-Suárez, E., Mein, P. (2004): The Late Pliocene locality of Saint-Vallier (Drôme, France). 11. Micromammals. – Geobios, 37(Supplement 1): S115–S125. https://doi.org/10.1016/S0016-6995(04)80011-1

Maul, L. (1990): Überblick über die unterpleistozänen Kleinsäugerfaunen Europas. – Quartärpaläontologie, 8: 153–191.

Maul, L. C., Parfitt, S. A. (2010): Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK: morphometric data, biostratigraphy and taxonomic reappraisal. – In: Stuart, A. J., Lister, A. M. (eds), The West Runton Elephant and its Cromerian Environment. Quaternary International, 228: 91–115. https://doi.org/10.1016/j.quaint.2009.01.005

Mein, P. (1976): Biozonation du Neogene Mediterranean a partir des Mammiferes. – In: Seneš, J. (ed.), Proceedings of the VIth Congress R.C.M.N.S., vol. 2. IGCP, Bratislava, pp. 78–81.

Mein, P. (1989): Updating of MN zones. – In: Lindsay, E. H., Fahlbusch, V., Mein, P., (eds), European Neogene mammal chronology. Plenum Press, New York, pp. 73–90.

Michaux, J. R., Chevret, P., Filippucci, M. G., Macholán, M. (2002): Phylogeny of the genus *Apodemus* with a special emphasis on the subgenus *Sylvaemus* using the nuclear IRBP gene and two mitochondrial markers: cytochrome b and 12S rRNA. – Molecular Phylogenetics and Evolution, 23: 123–136. https://doi.org/10.1016/S1055-7903(02)00007-6

Michaux, J. R., Libois, R., Filippucci, M. G. (2005): So close and so different: comparative phylogeography of two small mammal species, the yellow-necked fieldmouse (*Apodemus flavicollis*) and the woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. – Heredity, 94: 52–63. https://doi.org/10.1038/sj.hdy.6800561

Michaux, J. R., Libois, R., Paradis, E., Filippucci, M. G. (2004): Phylogeographic history of the yellow-necked fieldmouse (*Apodemus flavicollis*) in Europe and in the Near and Middle East. – Molecular Phylogenetics and Evolution, 32: 788–789. https://doi.org/10.1016/j.ympev.2004.02.018

Michaux, J. R., Magnanou, E., Paradis, E., Nieberding, C., Libois, R. (2003): Mitochondrial phylogeography of the woodmouse (*Apodemus sylvaticus*) in the Western Palearctic region. – Molecular Ecology, 12: 685–697. https://doi.org/10.1046/j.1365-294X.2003.01752.x

Michaux, J., Pasquier, L. (1974): Dynamique des populations de mulots (Rodentia, *Apodemus*) en Europe durant le Quaternaire. Premières données. – Bulletin de la Société géologique de France, 7: 431–439. https://doi.org/10.2113/gssgfbull.S7-XVI.4.431

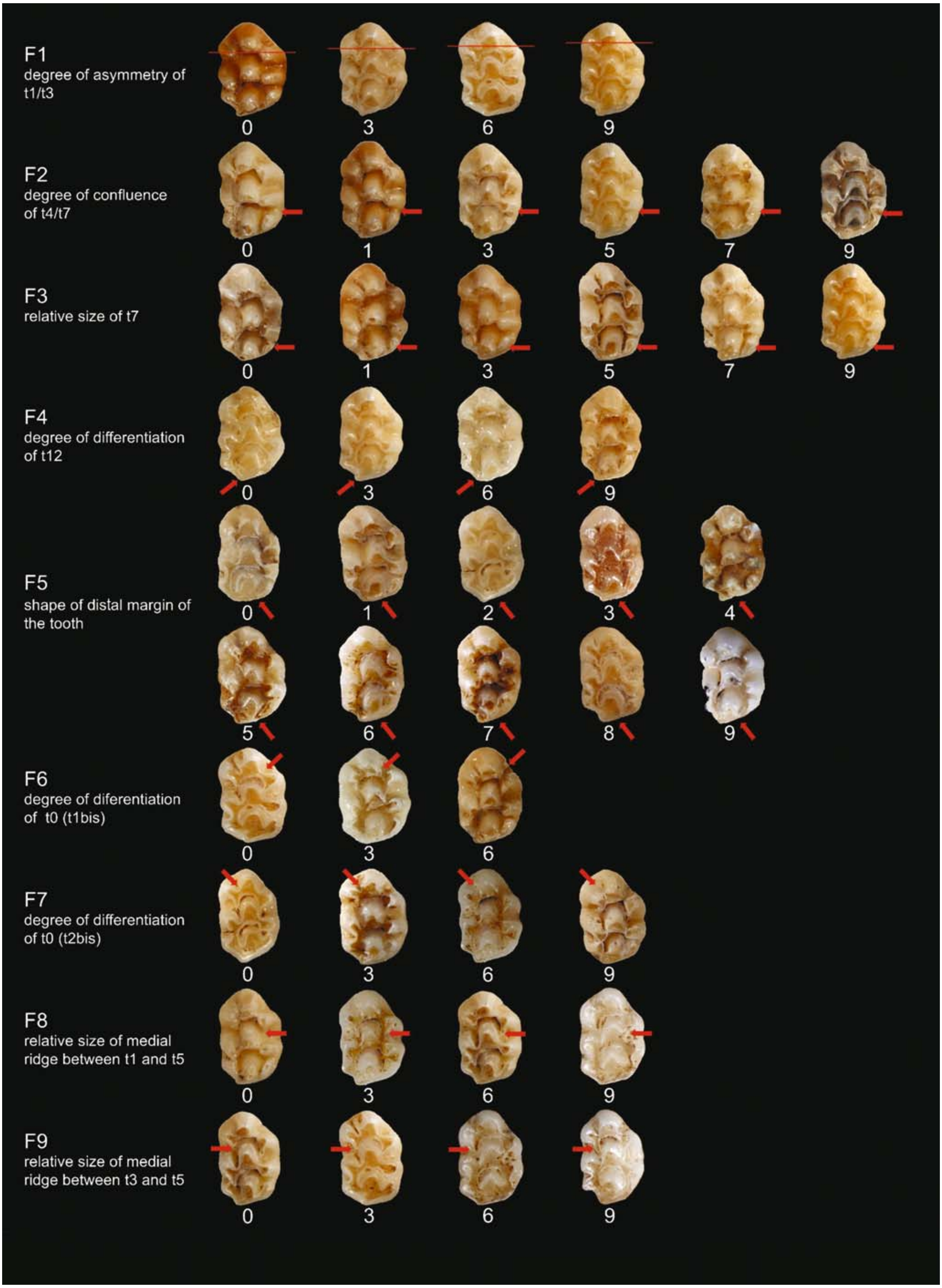
Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M. (2005): Muridae (Rodentia) from the Pliocene of Tollo de Chiclana (Granada, Southern Spain). – Journal of Vertebrate Paleontology, 25: 426–441. https://doi.org/10.1671/0272-4634(2005)025[0426:MRFTPO]2.0.CO;2

Minwer-Barakat, R., Madurell-Malapeira, J., Alba, D. M., Aurell-Garrido, J., De Esteban-Trivigno, S., Moyà-Solà, S. (2011): Pleistocene rodents from the Torrent de Vallparadís section (Terrassa, northeastern Spain) and biochronological implications. – Journal of Vertebrate Paleontology, 31(4): 849–865. https://doi.org/10.1080/02724634.2011.576730

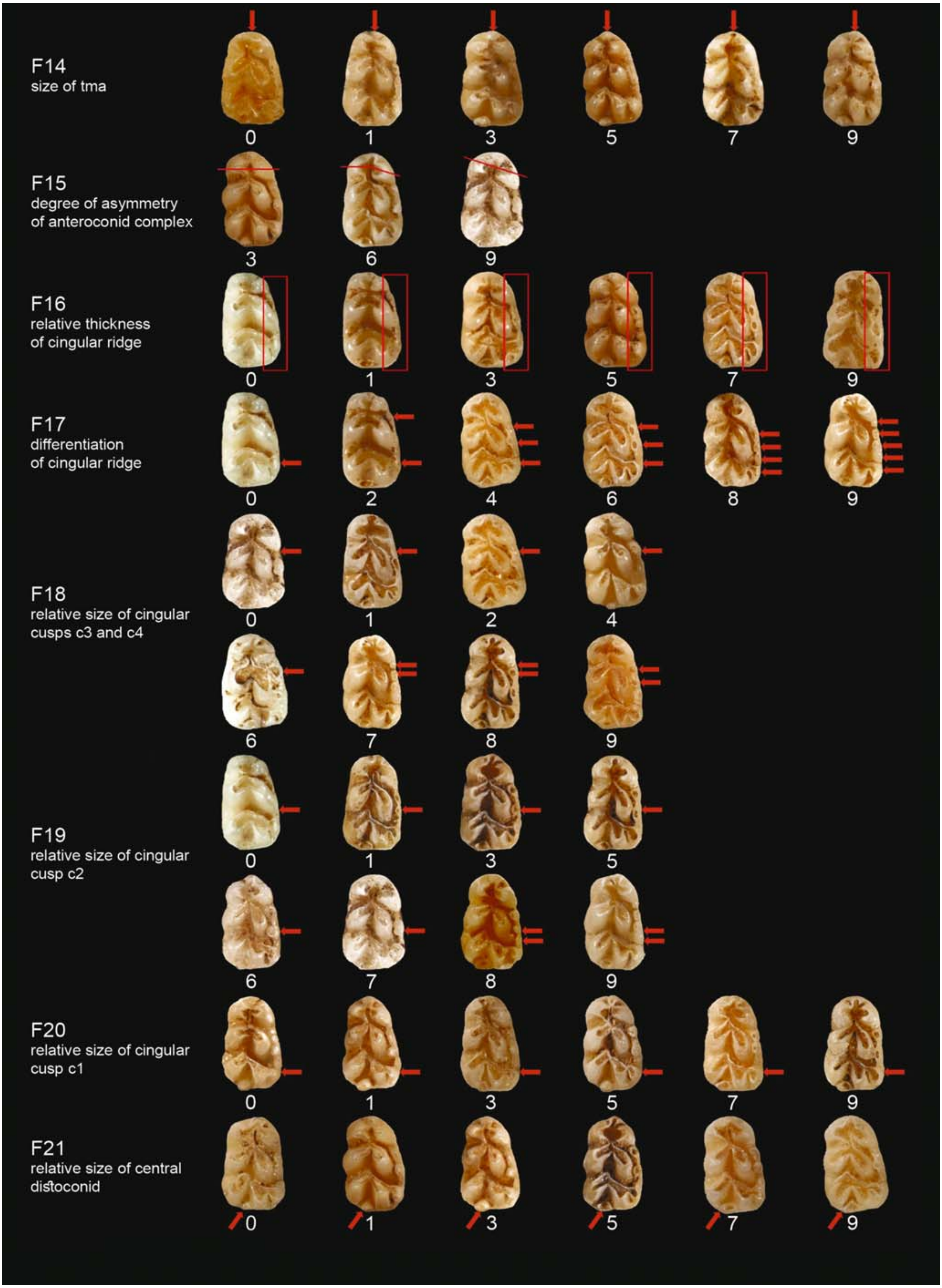
Mörs, T., von Koenigswald, W., von der Hocht, F. (1998): Rodents (Mammalia) from the late Pliocene Reuver Clay

of Hambach (Lower Rhine Embayment, Germany). – Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen, Amsterdam, 60: 135–160.
Musil, R. (ed.) (1995): Stránská skála Hill. Excavation of open-air sediments 1964–1972. – Anthropos, 26(New series 18): 1–213.
Musser, G. G., Brothers, E. M., Carleton, M. D., Hutterer, R. (1996): Taxonomy and distributional records of Oriental and European *Apodemus*, with a review of the *Apodemus-Sylvaemus* problem. – Bonner zoologische Beiträge, 46: 143–190.
Musser, G. G., Carleton, M. D. (2005): Superfamily Muroidea. – In: Wilson, D. E., Reeder, D. M. (eds), Mammal species of the world: a taxonomic and geographic reference. 3rd ed. Johns Hopkins University Press, Baltimore, pp. 894–1531.
Nesin V. A., Storch, G. (2004): Neogene Murinae of Ukraine (Mammalia, Rodentia). – Senckenbergiana lethaea, 84: 351–365.
https://doi.org/10.1007/BF03043476
Niethammer, J. (1978): Genus *Apodemus*. – In: Niethammer, J., Krapp, F. (eds), Handbuch der Säugetiere Europas. Vol. I/1. Akademische Verlagsgesellschaft, Wiesbaden, pp. 305–381.
Pasquier, L. (1974): Dynamique evolutive d'un sous-genre de Muridae, *Apodemus* (*Sylvaemus*). Etude biomètrique des charactères dentaires de populations fossiles et actuelles d'Europe occidentale. – Université des Sciences et Techniques du Languedoc, Académie de Montpellier.
Popov, V. V. (1994): Quaternary small mammals from deposits in Temnata-Prohodna Cave system. – In: Kozlowski, J. K., Luville, H., Ginter, B. (eds), Temnata Cave. Excavations in Karlukovo Karst Area, Bulgaria. 1 (2). Jagellonian University Press, Krakow, pp. 11–53.
Popov, V. V. (2004): Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria). – Geodiversitas, 26: 403–491.
Reutter, B. A., Hausser, J., Vogel, P. (1999): Discriminant analysis of skull morphometric characters in *Apodemus sylvaticus*, *A. flavicollis*, and *A. alpicola* (Mammalia; Rodentia) from the Alps. – Acta Theriologica, 44: 299–308.
https://doi.org/10.4098/AT.arch.99-28
Rietschel, S., Storch, G. (1974): Aussergewöhnlich erhaltene Waldmäuse (*Apodemus atavus* Heller, 1936) aus dem Ober-Pliozän von Willershausen am Harz. – Senckenbergiana Lethaea, 54: 491–519.
Serizawa, K., Suzuki, H., Tsuchiya, K. (2000): A phylogenetic view on species radiation in *Apodemus* inferred from variation of nuclear and mitochondrial genes. – Biochemical Genetics, 38: 27–40.
https://doi.org/10.1023/A:1001828203201
Spitzenberger, F. (2001): Die Säugetierfauna Österreichs. – Grüne Reihe des Bundesministeriums für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien, Bd. 13, 895 pp.
Storch, G. (1974): Die Pleistozän-Holozän-Grenze in der Kleinsäugerfauna Deutschlands. – Zeitschrift für Säugetierkunde, 39: 84–97.
Storch, G. (2004) The fossil history of Muridae (Rodentia), in particular of *Apodemus*. – Terra Nostra, 2004(2): 2 pp.
Storch, G., Dahlmann, T. (1995): 10. Murinae (Rodentia, Mammalia). – In: Schmidt-Kittler, N. (ed.), The vertebrate locality Maramena (Macedonia, Greece) at the Turolian – Ruscinian boundary (Neogene). Münchner Geowissenschaftliche Abhandlungen, A, 28: 121–132.
Suzuki, H., Filippucci, M. G. (2008): A biogeographic view of *Apodemus* in Asia and Europe inferred from nuclear and mitochondrial gene sequences. – Biochemical Genetics, 46: 329–346.
https://doi.org/10.1007/s10528-008-9149-7
Suzuki, H., Sato, J. J., Tsuchiya, K., Luo, J., Zhang, Y. P., Wang, Y. X., Jiang, X. L. (2003): Molecular phylogeny of wood mice (*Apodemus*, Muridae) in East Asia. – Biological Journal of the Linnean Society, 80: 469–481.
https://doi.org/10.1046/j.1095-8312.2003.00253.x
van Dam, J. A. (1997): The small mammals from the upper Miocene of the Teruel-Alfambra region (Spain): palaeobiology and palaeoclimatic recontructions. – Geologica Ultraiectina, Mededelingen van de Faculteit Aardwetenschappen Universiteit Utrecht, 156: 1–205.
van de Weerd, A. (1976): Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. – Utrecht Micropaleontological Bulletins, Special Publication 2: 1–217.
van Kolfschoten, T. (1985): The Middle Pleistocene (Saalian) and Late Pleistocene (Weichselian) mammal fauna from Maastricht-Belvédere (Southern Limburg, the Netherlands). – Mededelingen Rijks Geologische Diens, 39: 45–74.
van Kolfschoten, T., van der Meulen, A. J., Boenigk, W. (1998): The Late Pliocene Rodents (Mammalia) from Frenchen (Lower Rhine Basin, Germany). – Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen, Amsterdam, 60: 161–172.
Vasileiadou, K., Konidaris, G., Koufos, G. D. (2012): New data on the micromammalian locality of Kessani (Thrace, Greece) at the Mio-Pliocene boundary. – Palaeobiodiversity and Palaeoenvironments, 92: 211–237.
https://doi.org/10.1007/s12549-012-0075-7
Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K. (2001): Trends, rhythms, and aberrations in global climate 65 Ma to present. – Science, 292: 686–693.
https://doi.org/10.1126/science.1059412

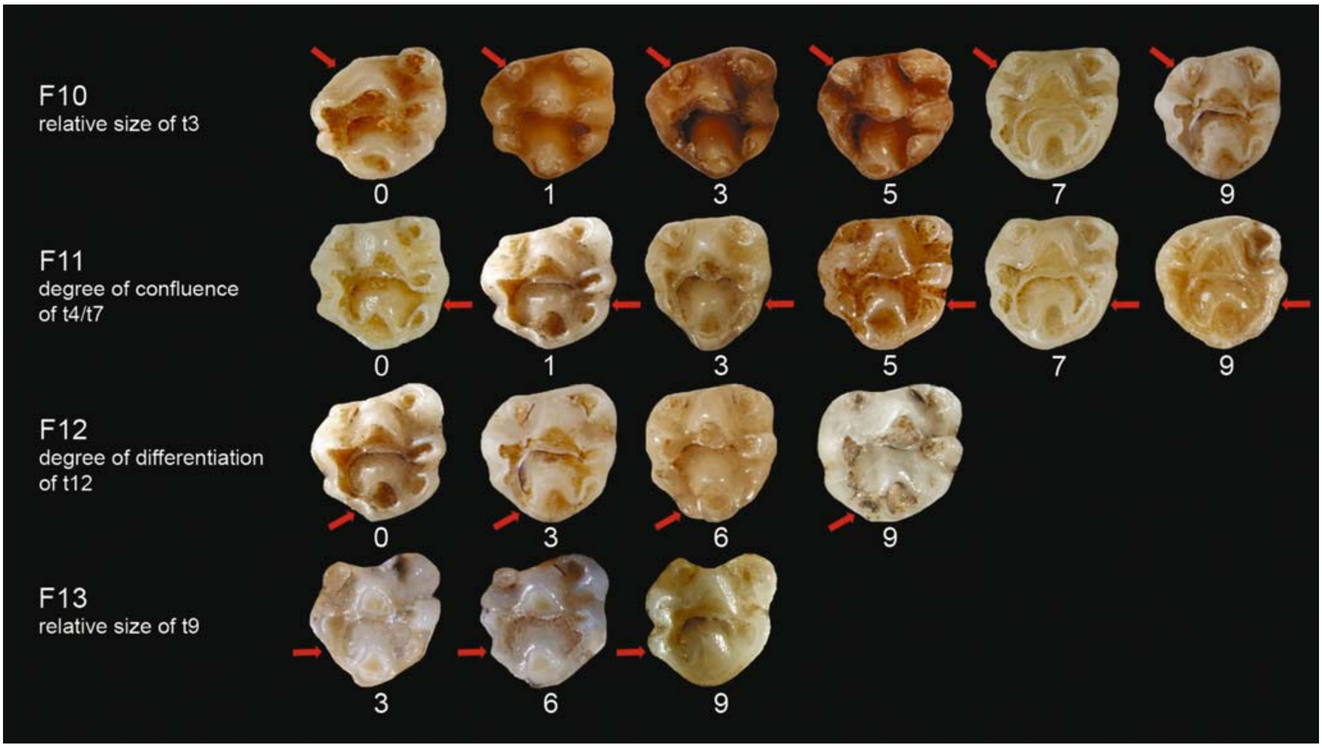
Appendix 1
List of non-metric variables, span of their variation and scoring categories.
(a) The non-metric variables of M1.



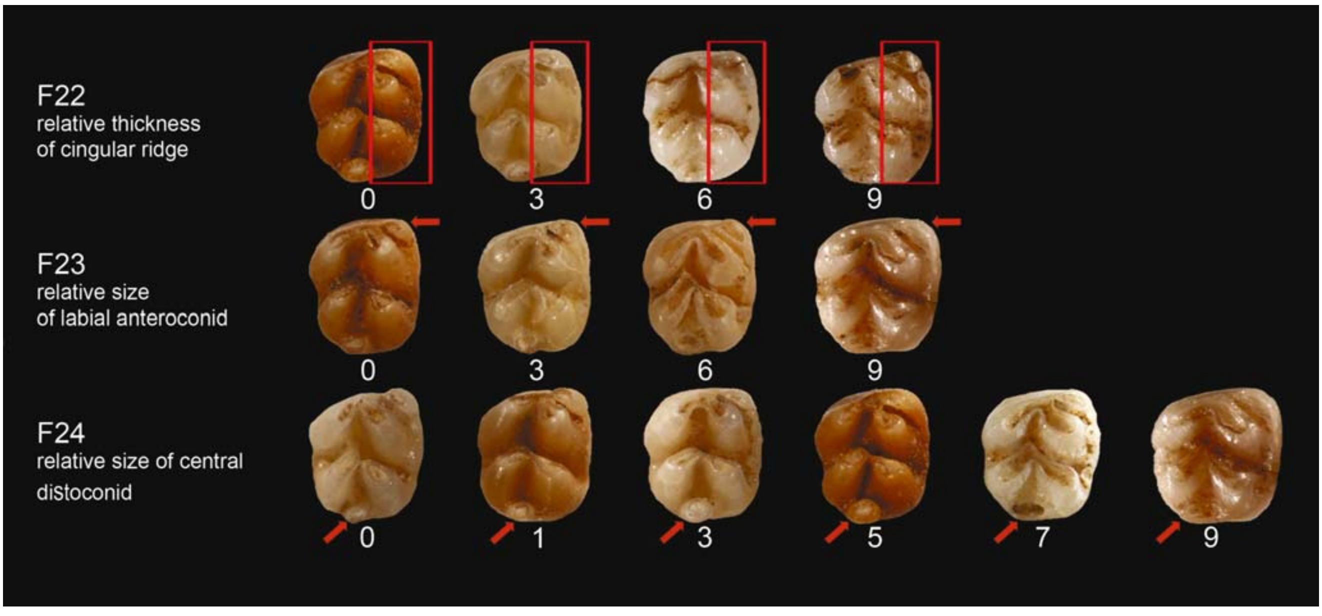
Appendix 1
List of non-metric variables, span of their variation and scoring categories.
(b) The non-metric variables of m1



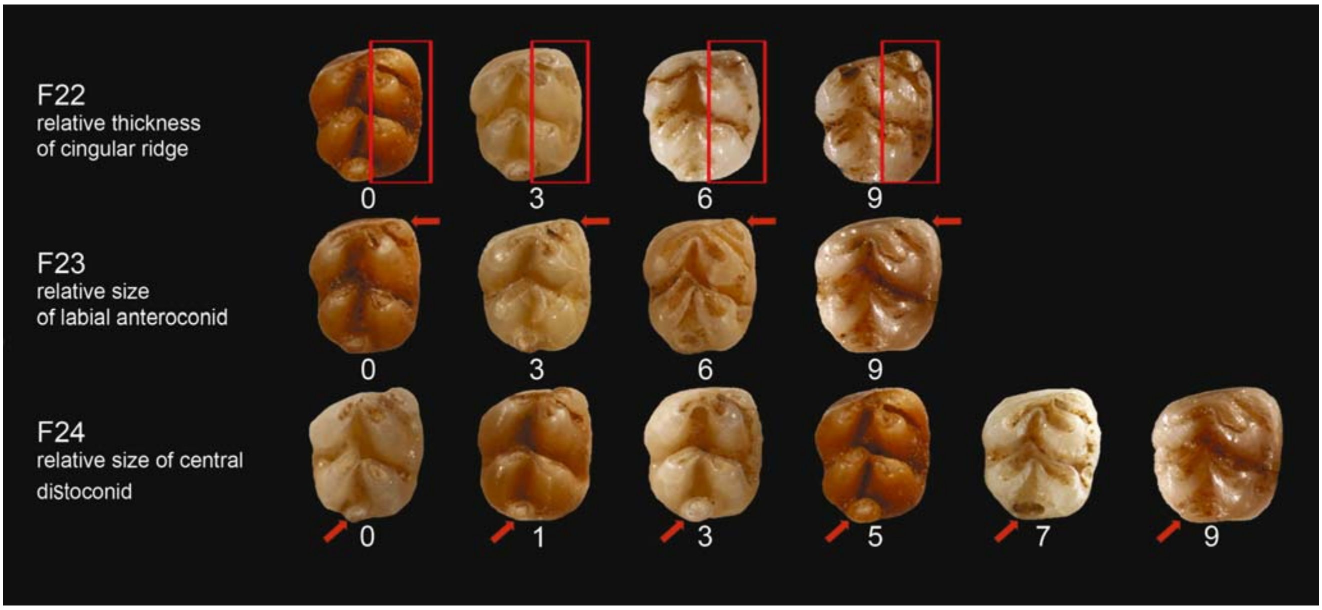
Appendix 1
List of non-metric variables, span of their variation and scoring categories.
(c) The non-metric variables of M2.



Appendix 1
List of non-metric variables, span of their variation and scoring categories.
(d) The non-metric variables of m2.



Appendix 1
List of non-metric variables, span of their variation and scoring categories.
(e) A degree of tooth wear.



Appendix 2
A detailed list of material and representation of particular parataxa in individual fossil samples.

			The total number of molars				*A. uralensis* (Parataxon 1)				*A. ural./sylv.* (Parataxon 2)				*A. sylvaticus* (Parataxon 3)				*A. sylv./flav.* (Parataxon 4)				*A. flavicollis* (Parataxon 5)				*Rhagapodemus* sp.				Number of unidentified teeth			
LOC	**LAY**	**STRA**	**M1**	**M2**	**m1**	**m2**	**M1**	**M2**	**m1**	**m2**	**M1**	**M2**	**m1**	**m2**	**M1**	**M2**	**m1**	**m2**	**M1**	**M2**	**m1**	**m2**	**M1**	**M2**	**m1**	**m2**	**M1**	**M2**	**m1**	**m2**	**M1**	**M2**	**m1**	**m2**
CHLU	4S	Q 2	0	1	–	2	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–
CHLU	4C/3	Q 3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CHLU	4C/4=Y	Q 3	2	1	3	4	1	–	–	–	1	1	–	–	–	–	3	1	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–
CHLU	4C/6	Q 3	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CHLU	4C/6/7	Q 3	–	–	2	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CHLU	4C/ 3 ~6	Q 3	–	2	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	2	1	–
CHLU	4B/10b	Q 2	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–
CHLU	4K/3B	Q 2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
CHLU	4C/“x“	Q 3	–	–	4	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
CHLU	7	Q 3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
KOBY	6	Q 3	–	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	–	–	–
KOBY	9	Q 3	1	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	2	1	–	–	–	–	–	–	–	–
MENA	2	Q 1	1	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CTIN	23	MN 17	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
CTIN	25	MN 17	2	–	1	1	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–
DOBR	II	Q 3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BALC		Q 3	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	–	–	–	–	–	–	–	–	–
STRS	1/6	Q 2	–	1	–	3	–	–	–	–	–	–	–	2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
STRS	1/7	Q 2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
STRJ		Q 3	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–
JAVO	IV	MN 17	–	–	3	2	–	–	–	–	–	–	–	–	–	–	3	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
JAVO	III	MN 17	–	1	2	2	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	2	1	–	–	–	–	–	–	–	–

Appendix 2 – continued.

MLAD	1	Q 1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
MLAD	1B	Q 1	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
MLAD	2	Q 3	6	3	10	6	2	–	1	3	1	–	4	2	1	–	2	–	2	3	3	1	–	–	–	–	–	–	–	–	–	–	–	–
MLAD	2 1m	Q 3	–	–	3	3	–	–	–	–	–	–	2	2	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
MLAD	2 4m	Q 3	20	9	20	8	–	–	2	–	–	–	–	–	–	–	–	–	1	–	1	–	19	9	17	7	–	–	–	–	–	–	–	1
MLAD	2 7/20	Q 3	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
MLAD	2 vrch	Q 3	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
MLAD	3 7/10	Q 3	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SOVI	4	Q 1	1	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
SOVI	4 (353)	Q 1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–
TURO	NE8/1+2	Q 3	1	–	1	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TURO	W1	Q 3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
BZIN	A	Q 2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BZIN	B	Q 2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
BZIN		Q 2	1	1	2	1	–	–	–	–	–	–	–	–	–	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
HONC		Q 1/Q 2	1	2	–	1	–	–	–	–	–	–	–	–	1	1	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–
PLES	A4	MN 17	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	–	–	–	–	–	–	–	–
PLES	E	MN 17	1	2	5	1	–	–	–	–	–	–	–	–	–	–	1	–	1	2	3	1	–	–	1	–	–	–	–	–	–	–	–	–
PLES	6556	MN 17	1	1	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
VCEL	3B/1	Q 1	5	1	2	–	–	–	–	–	–	–	–	–	2	1	1	–	3	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
VCEL	4E	Q 1	–	–	7	4	–	–	–	–	–	–	1	1	–	–	4	1	–	–	1	–	–	–	1	2	–	–	–	–	–	–	–	–
VCEL	5B	Q 1	3	2	4	1	–	–	–	–	1	–	–	–	1	–	1	–	1	2	2	1	–	–	1	–	–	–	–	–	–	–	–	–
VCEL	5 base 90	Q 1	–	2	3	2	–	–	–	–	–	–	2	–	–	1	1	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–
VCEL	4/7	Q 1	1	1	4	–	–	–	–	–	–	–	1	–	1	–	2	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–
VCEL	6/3	Q 1	3	1	3	2	–	–	–	–	–	–	1	–	–	–	2	–	–	1	–	–	2	–	–	2	–	–	–	–	1	–	–	–
VCEL	6/7	Q 1	10	4	10	9	–	–	–	–	3	–	2	1	7	2	8	5	–	2	–	3	–	–	–	–	–	–	–	–	–	–	–	–
VCEL	6/8	Q1	4	4	12	6	–	–	–	–	1	–	2	–	3	1	5	2	–	3	3	2	–	–	2	1	–	–	–	–	–	–	–	1
VCEL	6/1c	MN 17	1	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
VCEL	6/1	MN 17	1	2	2	2	–	–	–	–	–	–	–	–	1	1	2	–	–	1	–	1	–	–	–	1	–	–	–	–	–	–	–	–
VCEL	3	MN 17	1	2	3	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1	–	1	1	1	–	–	–	–	–	–	–	–	–
VCEL	7	MN 17	1	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–
TOTAL			**80**	**52**	**120**	**69**	**5**	**0**	**4**	**3**	**9**	**2**	**18**	**9**	**22**	**9**	**47**	**13**	**13**	**22**	**17**	**22**	**27**	**15**	**31**	**20**	**0**	**0**	**1**	**0**	**4**	**4**	**2**	**2**

Appendix 3
Selected items representing particular taxa under study. a – *Apodemus atavus*.

3a

M1

Včeláre 7; 7vc1; MN 17; 1.88; rootless

Plešivec E; Epl1; MN 17; 2.02; 3 roots

Plešivec A4; A4pl1a; MN 17; 2.02; jaw fragm.

Včeláre 6-1; 6-1vc7a; MN 17; 1.79; jaw fragm.

Včeláre 6-8; 6-8vc1; Q 1; 1.71; 3 roots

Včeláre 6-8; 6-8vc2; Q 1; 1.84; 3 roots

Včeláre 6-8; 6-8vc3; Q 1; 1.85; 3 roots

Včeláre 6-3; 6-3vc1; Q 1; 1.98; rootless

Včeláre 6-3; 6-3vc2; Q 1; 1.99; rootless

Včeláre 3B-1; 3B-1vc4; Q 1; 2.00; rootless

Včeláre 3B-1; 3B-1vc3; Q 1; 1.96; 3 roots

Včeláre 3B-1; 3B-1vc2; Q 1; 1.89; jaw fragm.

Chlum 4C4; 4C4ch2; Q 2; 1.75; 3 roots

Bzince A; Abzi1; Q 2; 1.92; jaw fragm.

Plešivec A4; A4pl2; MN 17

Plešivec A4; A4pl8a; MN 17

Plešivec E; Epl5; MN 17

Plešivec E; Epl6; MN 17

Plešivec E; Epl7; MN 17

Včeláre 3; 3vc6; MN 17

Včeláre 3; 3vc5; MN 17

m1

Včeláre 4/7; 4/7vc6; Q 1

Včeláre 6/3; 6/3vc5; Q 1

Včeláre 5B; vc5B11; Q 1

Včeláre 5B; vc5B12; Q 1

Včeláre 5B; vc5B13; Q 1

Chlum 4C4; 4C4ch6; Q 2

M2

Včeláre 3; 3vc2; MN 17

Včeláre 6-1; 6-1vc7b; MN 17

Včeláre 6-1; 6-1vc1; MN 17

Plešivec A4; A4pl1b; MN 17

Plešivec E; Epl2; MN 17

Javoříčko III; IIIjav5; MN 17

Mladeč 1; 1ml1; Q 1

Včeláre 3B-1; 3B-1vc1b; Q 1

Včeláre 4-7; 4-7vc4; Q 1

Včeláre 6-8; 6-8vc6; Q 1

Včeláre 6-8; 6-8vc8; Q 1

Včeláre 6-8; 6-8vc7; Q 1

Včeláre 6-3; 6-3vc4; Q 1

Včeláre 5B; 5Bvc5; Q 1

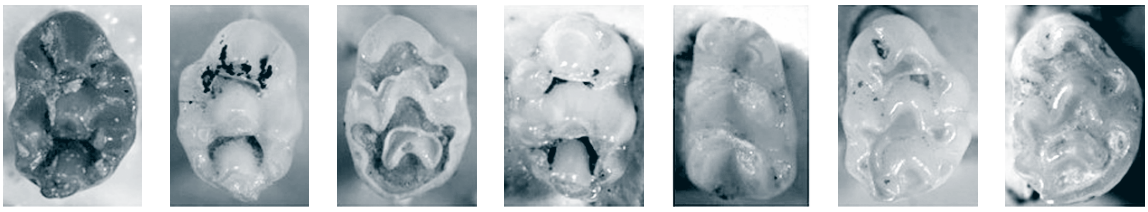
Včeláre 5B; 5Bvc6; Q 1

Bzince; Bzi2; Q 2

Appendix 3
Selected items representing particular taxa under study. b – *A. maastrichtiensis*, c – *A. flavicollis*, d – *A. sylvaticus*, e – *Rhagapodemus* sp.

3b

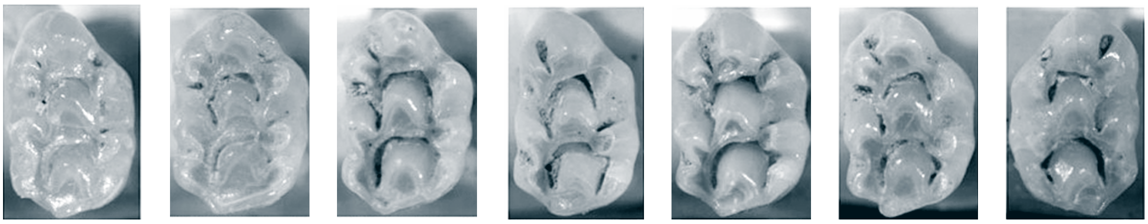
M1



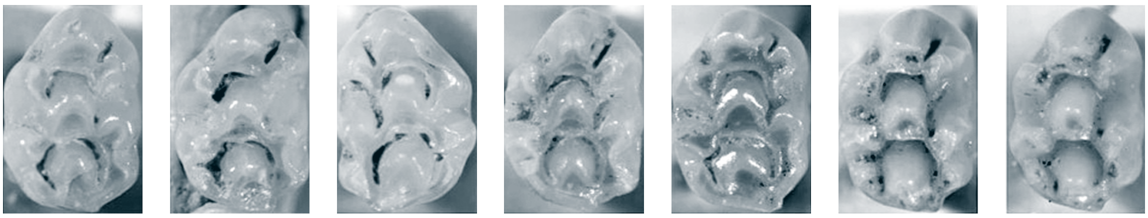
Turold; NE8/1+2tu1; Q 3; 1.72; 3 roots
Mladeč 2; 2ml4; Q 3; 1.59; 3 roots
Mladeč 2; 2ml2; Q 3; 1.66; 3 roots
Mladeč 2 7–20; 2 7–20ml1; Q 3; 1.62; rootless
Mladeč 1B; 1Bml1; Q 1; 1.46
Ctiněves 25; 25cti2; MN 17; 1.80; jaw fragm.
Chlum 4. sluj; 4.sluj ch1; Q 2; 1.65; jaw fragm.

3c

M1



Mladeč 2 4m; 2 4m ml1; Q 3
Mladeč 2 4m; 2 4m ml2; Q 3
Mladeč 2 4m; 2 4m ml11; Q 3
Mladeč 2 4m; 2 4m ml12; Q 3
Mladeč 2 4m; 2 4m ml13; Q 3
Mladeč 2 4m; 2 4m ml15; Q 3
Mladeč 2 4m; 2 4m ml16; Q 3



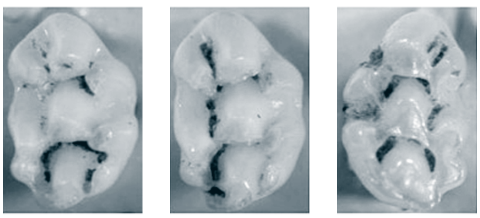
Mladeč 2 4m; 2 4m ml5; Q 3
Mladeč 2 4m; 2 4m ml25a; Q 3
Mladeč 2 4m; 2 4m ml6; Q 3
Mladeč 2 4m; 2 4m ml9; Q 3
Balcarka; b1; Q 4
Balcarka; b2; Q 4
Balcarka; b3; Q 4

M2

Mladeč 2 4m; 2 4m ml19; Q 3
Mladeč 2 4m; 2 4m ml21; Q 3
Mladeč 2 4m; 2 4m ml22; Q 3
Mladeč 2 4m; 2 4m ml23; Q 3
Mladeč 2 4m; 2 4m ml25b; Q 3
Turold; t1; Q 3
Kobyla 9; 9k3; Q 4

3d

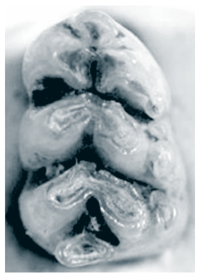
M1



Mladeč 2; 2ml3; Q 3
Mladeč 2; 2ml6; Q 3
Mladeč 2 vrch; 2vrchml1; Q 3

3e

M1



Včeláre 7; 7vc2; MN 17