



SHREWS OF TRIBE NECTOGALINI (MAMMALIA, EULIPOTYPHLA, SORICIDAE) IN THE FOSSIL RECORD OF THE CZECH REPUBLIC AND SLOVAKIA

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Abstract: Shrews of the tribe Nectogalini rank among the rarest items of the late Cenozoic fossil record, and their interpretation is traditionally accompanied by numerous controversies. Here, the data from the Czech Republic and Slovakia covering in total 83 MNI from 45 Pliocene and Quaternary (MN 15 – Q 4 biozones) community samples of 25 sites are reported. A detailed biometric analysis of both *Asoriculus* spp. (MN 15 – Q 1) and *Neomys* spp. (Q 1 – Recent) was undertaken to reveal patterns of phenotype variation in particular samples, and their relations to extant mid-European species *Neomys fodiens* and *N. milleri*. For that purpose, we examined the variation pattern of 239 dental, rostral and mandibular variables in a large set of extant species (n = 135), quantified their discrimination capacity and by forward selection established a set of criteria applicable for identification and comparative analyses of fragmentary fossil specimens.

We found that both extant species occurred in Central Europe with roughly equal number of records both in the Last Glacial and since the beginning of the Holocene.

The late Biharian and early Toringian samples exhibited statistical homogeneity and differences from extant *N. milleri* – they are reported here as *N. newtoni*. Tentatively, we proposed a separate status also for the items of the latest Villanyian – early Biharian age (as *Asoriculus castellarini*). Compared to both extant *Neomys* sp. and MN 15–17 *Asoriculus gibberodon*, the above-mentioned samples seem to be characterized by a broad phenotype variation, particularly in the characters associated with assumed *Asoriculus-Neomys* transition (mandibular unicuspid, distal mandibular structures). Contrary to the hypothesis on parallel appearance of both genera in the Early Pleistocene and the extinction of *Asoriculus* by the end of the Early Biharian, we consider the Early Pleistocene diversity of the clade as a stage of a broad gradual transition subsequently driven by adaptive advances of *Neomys* constitution.

In any case, the morphometric comparisons with the non-European representatives of Nectogalini confirmed close relations between both the European genera and distant divergence of the European clade from the extant Oriental clades.

Key words: shrews, *Neomys*, Quaternary, Pliocene, Europe, phylogeny, paleobiogeography

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Introduction

Tribe Nectogalini ANDERSON, 1879 is a distinct clade of Old-World shrews, mostly of semiaquatic habitat requirements, composed of six extant genera – the W-Palaearctic *Neomys* KAUP, 1829, the Oriental genera *Soriculus* BLYTH, 1854, *Episoriculus* ELLERMANN et MORRISON-SCOTT, 1966, *Chodsigoa* KASTCHENKO, 1907, *Chimarrigale* ANDERSON, 1877 and *Nectogale* MILNE-EDWARDS, 1870, and the extinct genera *Neomysorex* RZEBIK-KOWALSKA, 1981, *Asoriculus* KRETZOI, 1959, *Nesiotites* BATE, 1945, *Macroneomys* FEJFAR, 1966, all described from the European Pliocene or Pleistocene sites.

Among modern authors, Kretzoi (1965) and Repenning (1967) were perhaps the first who proposed the status of a separate tribe for that group, under the names Soriculini and Neomyini, respectively. The diagnosis and taxonomic content of the tribe were further redefined by Reumer (1984, 1998), who stressed a combination of the following characters: mandibular condyle with its articular facets strongly separated by a narrow interarticular area restricted to the lateral side, lingually elongated lower facet, offset of the lower sigmoid notch at its buccal side, lower incisors never tricuspluate, and m1 and m2 with distinct entoconid crests.

The molecular phylogenetic analyses (Dubey et al. 2007) confirmed consistency of the tribe and dated its split from the Nearctic clade Notiosoricini REUMER, 1984 to 13.8 Ma. Together with the later analyses (He et al. 2010, Willows-Munro and Matthee 2011, Fan et al. 2022), they demonstrated a deep split between the Oriental genera and the W-Palaearctic genus *Neomys*.

The earliest record of the tribe in the fossil record comes from three Ukrainian MN 11 sites (Rzebik-Kowalska and Rekovets 2016). In the European sites of the Late Miocene and Early Pliocene age, the clade appears quite regularly; a rich sample from MN 13 site Polgárdi 4, Hungary (Mészáros 1999) is particularly worth mentioning. Taxonomic assignments of all these records (either *Asoriculus* sp. or *A. gibberodon*) refer to the form first described as *Crocidura gibberodon* PETÉNYI, 1964 from MN 16 site Beremend, and then as *Soriculus kubinyii* KORMOS, 1934, from MN 17 Villány 3 (both Hungary). Kretzoi (1956), in his large-scale revision of the Hungarian Early Pleistocene fossil record, suggested identity of both forms, and synonymized them under the name *Soriculus gibberodon* (PETÉNYI, 1864). Reporting the same form from MN 15 site Csarnóta, he separated it in a subgenus *Asoriculus* KRETZOI, 1959, for which he later (Kretzoi 1962) proposed a generic status. Nevertheless, Repenning (1967) suggested affinity of the European fossils to the extant genus *Episoriculus* in his authoritative monograph, and included the form *gibberodon* in it. That proposal was followed by all further authors until Hutterer (1994) – after a detailed re-examination of diagnostic characters of extant forms – demonstrated distinct differences between *A. gibberodon* and extant *Episoriculus*, supporting an independent generic status of *Asoriculus*.

Except for the large-sized forms described from the Quaternary sites of the Mediterranean region (*Episoriculus thenii* MALEZ et RABEDER, 1984 from Q 1 Podumci (Croatia), *Asoriculus burgioi* MASINI et SARÀ, 1998 from Sicily, and *A. maghrebiensis* RZEBIK-KOWALSKA, 1988 from MN 17

Irhoud Ocre (Morocco)), the vast majority of all records of the genus are attributed to *A. gibberodon*. This is also true for the new species described from MN 15 sites Osztramos 13 and 1 (Hungary) as *Episoriculus tornensis* JÁNOSSY, 1973 and *E. borsodensis* JÁNOSSY, 1973 by Jánossy (1973), whose taxonomic relevance was doubted by Rzebik-Kowalska (1981), and a detailed analyses by Reumer (1984) convincingly identified them as elements of a broad intraspecific variation of *A. gibberodon*.

In contrast to regular appearance of *Asoriculus* in the Pliocene fossil record, the Quaternary records of Nectogalini are surprisingly scarce, and this holds true also for the sole extant W-Palaearctic genus *Neomys* (Tab. 1).

The genus *Neomys* is composed of four extant species: *Neomys fodiens* (PENNANT, 1771), occupying a large eupalaearctic range covering most regions of Europe, including N. Iberia, Italy, Balkans, England, and northernmost Scandinavia up to central Siberia and Far East; *N. teres* MILLER, 1908, restricted to Transcaucasia and N. Turkey; *N. anomalus* CABRERA, 1907, endemic to Iberia; and *N. milleri* MOTTAZ, 1907, distributed in S. France, Italy, Balkans, most of Central Europe and Ukraine, with recent records from N. Poland and Baltic countries. The separate species status of the latter two was proposed quite recently, based on a distinct genetic divergence between the Iberian (*N. anomalus* s. str.) and mainland clade (*N. milleri*). Castiglia et al. (2007), who demonstrated it, also showed a sister relation of *anomalus-milleri* clade to *N. teres*, and deep divergence between that clade and *N. fodiens*, which they dated by molecular clocks to 6.9 Ma. A multilocus analysis by Igea et al. (2015) confirmed this topology of the *Neomys* tree, but refined datings of the divergences: 1.14 (0.86–1.52) Ma for split of *N. fodiens* and *teres-anomalus* clades, 0.46 (0.32–0.62) for that of *teres/anomalus*, and 0.27 (0.19–0.4) Ma for that of *anomalus/milleri*.

Unfortunately, neither molecular phylogeography nor the fossil record provide a reliable picture of early history and paleobiogeography of the genus *Neomys*, including

Table 1. Tabular survey of literary data on European fossil record of *Asoriculus* and *Neomys* taxa reported for specific biozones: number of sites (those reported in present paper, mostly also included in total number of literary records, in brackets).

Species/Biozone	MN 11–13	MN 14	MN 15	MN 16	MN 17	Q 1	Q 2	Q 3	Q 4
<i>Asoriculus</i> (aff., cf.) <i>gibberodon</i>	13	17	16 (2)	15 (2)	13 (2)	16			
<i>Asoriculus thenii</i>						2			
<i>Asoriculus burgioi</i>					1				
<i>Asoriculus maghrebiensis</i>					2				
<i>Asoriculus</i> sp.	5		1	1					
<i>Asoriculus</i> (cf.) <i>castellarini</i>					1	3 (5)			
<i>Neomys</i> (aff., cf.) <i>newtoni</i>						4	12 (3)	4 (1)	
<i>Neomys browni</i>								2	
<i>Neomys intermedius</i>								2	
<i>Neomys hintoni</i>								2	
<i>Neomys</i> (aff., cf.) <i>fodiens</i>								6	59 (4)
<i>Neomys anomalus</i>									3
<i>Neomys</i> (cf.) <i>milleri</i>								1	13 (6)
<i>Neomys teres</i>									1
<i>Neomys</i> sp.								9	11 (6)

the immediate history of its extant species. Compared to other small mammals, remains of *Neomys* are rather rare in the fossil record, since most sites where it was recorded yielded only a single or a few jaw fragments. As demonstrated in Table 1 and Supplementary material (SM:SF III), the vast majority of available records are of the Late Pleistocene or Holocene age, mostly identified as *Neomys fodiens* or *Neomys* sp. (81.4% of sites), while only 16 references (18.6%) reported *N. anomalus/milleri*. The striking discrepancy in the fossil record of both clades indicates that *N. milleri*, whose range is centred in southern Europe, appeared in Central Europe rather exceptionally, supposedly in warm interglacial stages. Supported by the currently demonstrated northward range extension of *N. milleri* to N. Poland, Lithuania, and Estonia (Balčiauskas et al. 2016), this might suggest its Late Holocene spread in Central Europe, contrasting to continuous presence of *N. fodiens* (Anděra and Hanzal 2022). The earliest records unambiguously attributed to the genus *Neomys* come from 14 late Biharian (Q 2) sites (Hinton 1911, Fejfar 1964, Bishop 1982, Maul 1990, Rzebik-Kowalska 1991, 1994, Zaitsev and Baryshnikov 2002, Agadjanian and Kondrashov 2007, Maul and Parfitt 2010, Rzebik-Kowalska and Rekovets 2016, Pazonyi et al. 2018). Similarly to the earliest records of that type (Q 1, Żabia cave in Poland; Rzebik-Kowalska 2013), they are mostly co-identified with *N. newtoni* HINTON, 1911. This taxon was described from type locality of Cromerian, Upper Freshwater Bed of West Runton, and Hinton (1911) diagnoses it as a distinctly smaller form than *fodiens*, differing in shape of condylar process (very narrow interarticular area, distal position of the upper facet) and possessing lower coronoid process, in comparison with the extant taxon.

Regarding metric characters, *N. newtoni* obviously falls into the variation range of extant *milleri*, yet further differences between these taxa have not been analysed in detail until now.

The information on roots of *Neomys* radiation and ancestry of that clade are even more fragmentary and confusing. It is generally expected that the genus originated from the Pliocene European *Asoriculus*, yet such a scenario has been questioned by Rofes and Cuenca-Bescós (2006). The form described as *Neomys castellarini* PASA, 1947 from Q 1 Soave Cava Sud (Italy) and later reported from other three European sites (mostly as *Asoriculus castellarini*), is particularly worth of interest here, despite the doubts regarding its taxonomic status (Reumer 1984, Rzebik-Kowalska 2000, Rofes and Cuenca-Bescós 2006).

Beside these taxa, the mid-European record of Nectogalini is further supplemented by the largest form of the group: *Macroneomys brachygnathus* FEJFAR, 1966, described from the Q 2 sites Koněprusy C718 and JK (the Czech Republic), and further reported from 11 European sites of the late Q 2 and early Q 3 sites (Jammot 1975, Clot et al. 1976, Jánossy 1986, Maul 1990, Fanfani 1998, Maul and Rzebik-Kowalska 1998, Rzebik-Kowalska 1998, Masini et al. 2005, Bona et al. 2008, Parfitt and Harrison 2011). This topic is omitted here and will be analysed elsewhere. The account of European Nectogalini is further complemented by the genus *Nesiotites*, endemic in the Balearic Islands from the Early Pliocene to the

Late Holocene (Rofes et al. 2012), recently identified with aid of aDNA analyses as a sister clade of extant Oriental genus *Soriculus* (Bover et al. 2018).

Even without references to the latter two genera, the above survey demonstrates that current view on history of the mid-European Nectogalini is accompanied by several open questions not yet satisfactorily settled. Namely: (i) Are all the Late Pleistocene and Holocene records properly identified? Do they support scenario of climate specific distribution of the extant species (*fodiens* – glacials, *milleri* – interglacials only)? How frequent were sympatric occurrences and how did they affect patterns of phenotype variation? (ii) What were actual relations of the Early and early Middle Pleistocene records to the extant species? Can they be directly co-identified with either one or both? Did they represent a single or more species? (iii) Is there any real support for possible transition from *Asoriculus* to *Neomys*? When did it occur? (iv) Do *Asoriculus* and *Neomys* indeed represent a single clade distant from non-European members of the tribe?

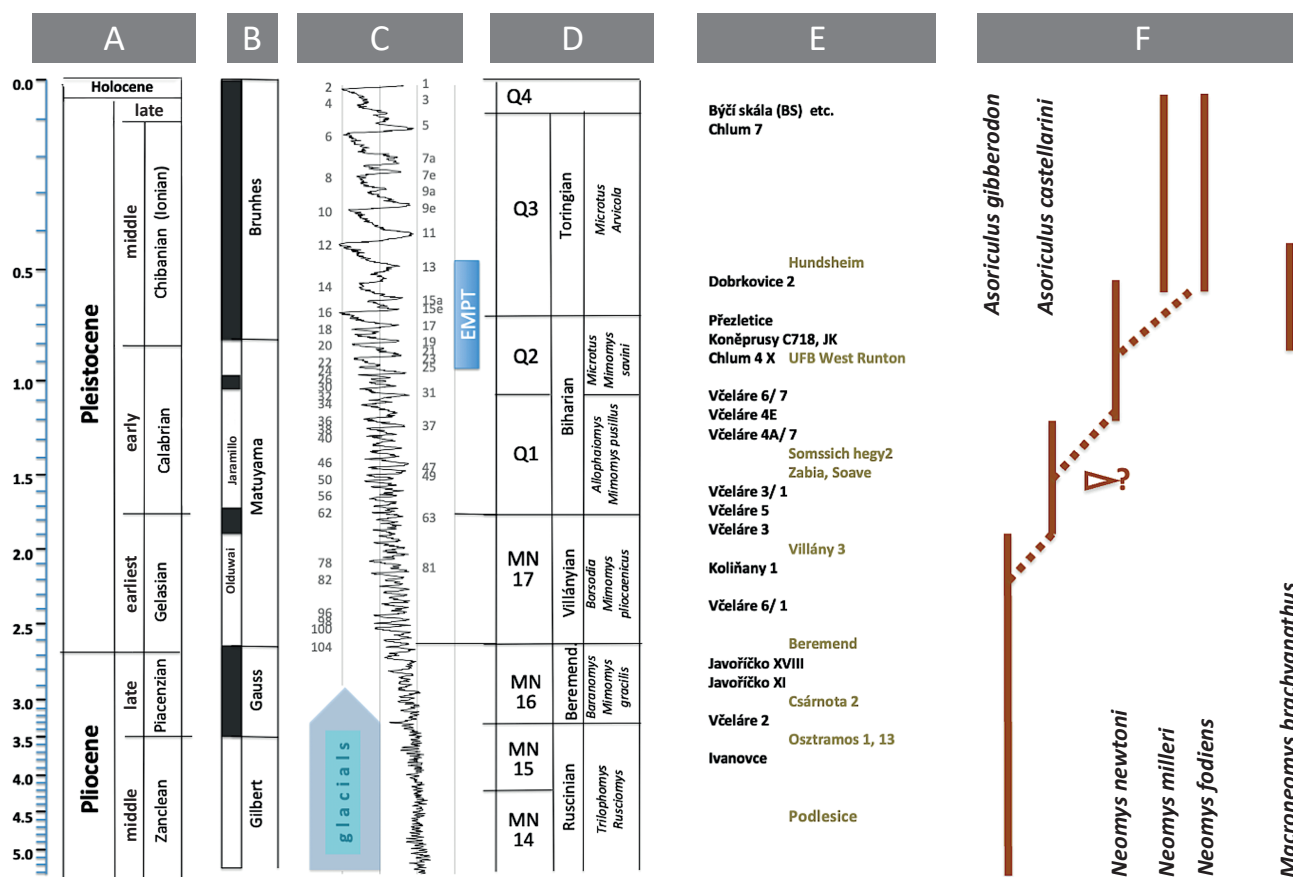
Based on a survey of the fossil record of the tribe from the Pliocene and Quaternary sites of the Czech Republic and Slovakia, the present paper is intended to contribute to these issues with results of biometric comparisons particularly focused on relations of individual fossil items to the extant taxa.

Unfortunately, the topic of variation patterns in extant species is obviously underestimated in paleontological literature, and it cannot be excluded that the above-mentioned striking discrepancy in the fossil record of both extant mid-European species might partly result from this.

In any case, *N. fodiens* and *N. anomalus-milleri* differ quite distinctly in external characters, yet their differences in skull and dental features are far from being so clear (Spitzenberger 1980, 1990, Spitzenberger and Bauer 2001, Kryštufek and Quadracci 2008, Popov and Zidarova 2008, Balčiauskas et al. 2014, Zidarova and Popov 2018). All authors dealing with these topics demonstrated that despite obvious size differences, significant in both mean and extreme values of most dimensions (*N. fodiens* being the larger species), the zones of between-species overlaps may take a considerable part of their variation span. There is no categorical variable that would provide absolute discrimination, while at the same time, both size and non-metric characters reveal a broad span of geographic within-species variation, notwithstanding the locally diversified effects of character displacements (Rácz and Demeter 1998, Rychlik et al. 2006, Kryštufek and Quadracci 2008, Popov and Zidarova 2008, Nováková and Vohralík 2019).

Besides a general rule suggesting body enlargements in *milleri-anomalus* towards the South (Kryštufek and Quadracci 2008), there are considerable local variations in all expected effects (including supposed character displacements etc.), which show a confused picture offering a series of alternative explanations, rather than distinct rules (Rychlik et al. 2006).

Consequently, a careful re-examination of patterns of character variation and their discrimination capacity in the extant clades comprised the first step for our study on Nectogalini fossils.



Text-fig. 1. Stratigraphic context of topics. A: Chronology (Ma) and global stratigraphic subdivision. B: Magnetostratigraphic scale. C: Climatostratigraphic record (after global benthic $\delta^{18}\text{O}$ record by Lisiecki and Raymo 2005) and sequence of MIS units. D: Biostratigraphic subdivision and mammal biozones (MN, Q) applied in present paper (after Fejfar et al. 1997, Horáček and Ložek 1988). E: List and assumed stratigraphic positions of sites covered in present survey (in bold) and important reference sites abroad (in colour). F: Tentative summary of stratigraphic distribution of discussed taxa and their assumed relations.

Material and methods

The material

For input comparative analyses, the material was subdivided into the following operation taxonomic units (OTUs):

- (I) *Neomys fodiens*, Recent population (the Czech Republic) – 55 complete skulls.
- (II) *Neomys milleri*, Recent population (the Czech Republic) – 80 complete skulls.
- (III) Q 4 samples (of the Vistulian and Holocene age), mostly coming from multilayered stratigraphic sections (Býčí skála, Peskö, Chlum 7, Maštalná, Skalice, Soví převis, Srbsko, Červeného muže, Zazděná, Holštejnská) – MNI = 52.
- (IV) Q 2 samples (of the late Biharian and early Toringian age): Chlum 4/X2, Koněprusy C718, JK, Dobrkovice 2 – MNI = 13.
- (V) Late MN 17 – Q 1 samples (of terminal Villanyian and early Biharian age): Včeláře 3B, Včeláře 5, Včeláře 4/7, Včeláře, 4E, Včeláře 6/7 – MNI = 11.
- (VI) MN 15 – MN 17 (of the Pliocene and early Villanyian age): MN 15: Ivanovce, Včeláře 2B (the site supposedly related to the macrofauna site Včeláře 2 dated by Sabol et al. 2008 to MN 16; comp. Horáček 1985); MN 16: Javoříčko 11, 18; MN 17: Koliňany 1, Včeláře 6/1 – MNI = 7.

- (VII) *Soriculus nigrescens* (GRAY, 1842), Recent sample of 10 mandibles + 5 skulls.
- (VIII) *Episoriculus macrurus* (BLANFORD, 1888), Recent sample of 11 mandibles + 5 skulls.
- (IX) *Episoriculus leucops* (HORSFIELD, 1855), Recent sample of 11 mandibles + 5 skulls.

All the material is deposited in the collection of Dept. Zoology, Charles University Prague and/or National Museum, Prague.

The assessment of the stratigraphic position of individual fossil record following the proposals by Fejfar and Heinrich (1983), Fejfar et al. (1997), and Horáček and Ložek (1988) and referring to major units of hierarchical biostratigraphic system (i.e., Villanyian, Biharian, Toringian – comp. Text-fig. 1) was preferably expressed in terms of the Neogene mammalian biozones (MN) after Mein (1975) and Quaternary zones (Q 1 – Q 4) by Horáček and Ložek (1988) – see Text-fig. 1 for details. Alternatively, where relevant, reference to units of global climatostratigraphic scale (MIS zones) is also applied. For the present glacial cycle (Q 4 biozone), the following scheme was applied: Q 4w1 – early Vistulian (MIS 5d–4), Q 4w2 – middle Vistulian (MIS 3), Q 4w3 – the late Vistulian pleniglacial (LGM: MIS 2), Q 4h1 – the post-LGM Vistulian and the earliest Holocene (Preboreal to Boreal), Q 4h2 – Middle and Late Holocene.

The geographic position, faunal composition and further details of the sites are available from Horáček and Ložek (1988), Fejfar and Horáček (1990), Horáček (1990), Knitlová and Horáček (2017) or Horáček and Lebedová (2022).

Biometric analyses

Detailed analyses of morphometric variations in extant species were taken as the basic prerequisite of the comparative analyses. We took in account the extensive literary references on that subject (Spitzenberger 1980, Rácz and Demeter 1998, Spitzenberger and Bauer 2001, Kryštufek and Quadracci 2008, Popov and Zidarova 2008, Balčiauskas and Balčiauskienė 2012, Balčiauskas et al. 2014, Zidarova and Popov 2018, Nováková and Vohralík 2019, Thier et al. 2020), and first turned our attention to the character proposed there as discrimination criteria among the extant W-Palaearctic species. Of course, in most instances, they included the linear measurements in complete skulls and jaws, which are only rarely available in fossil record, notwithstanding extensive between-species overlaps in most of these variables. Regarding that, more authors proposed an application of multivariate discrimination functions and geometric morphometry as the approaches promising the most robust discriminative capacity (Popov and Zidarova 2018, Nováková and Vohralík 2019). Yet possibilities to apply these approaches in identification of fragmentary fossil material are even more limited.

It is because for both geometric morphometry and related multivariate comparisons, a complete availability of the whole set of landmarks/variables in all specimens under study is an indispensable prerequisite. Unfortunately, this precondition obviously contradicts the real properties of the actual fossil record, which is composed mostly of isolated teeth or incomplete jaw fragments, each providing often quite a different set of available characters. In response to these constraints, we developed a technique that might partly resolve the dilemma. We predefined a large set of landmarks available within a set of diverse fossil items (including isolated teeth etc.) and analysed the variation patterns,

between-species overlaps, and discriminative capacity for each of the linear measurements defined by the respective landmarks in a large comparative series of extant species, then applied the results as a blueprint discrimination matrix for comparative analyses of fossil items.

The landmarks and 230 linear measurements applied in the present study are listed in detail (including their abbreviations used in the text) in Appendix; the corresponding biometric data for individual OTUs are available in SM:SF II. The individual variables were grouped into 10 classes representing cranial, rostral, mandibular, and dental structures, supplemented with variables expressing proportions of specific dental elements and those quantifying extent of teeth pigmentation (see Appendix for details). The number of variables available for particular classes in individual OTUs and total amounts of corresponding input data are listed in Table 2.

We performed a post hoc forward selection of the dimensions available in relevant parts of the fossil items, and by using diverse combinations of them, we established input variables for a series of discriminant analyses alternatively applied in species identification and comparative analyses (the most productive of them are summarized in SM:SF I).

The quantitative assessments of metric correspondences among all compared cases (corresponding to multivariate outputs of geometric analyses) are presented as instant summaries of particular between-OTUs comparisons (Tabs 6, 9, 10).

All fossil and recent items were photographed in a standardised way with the aid of Optica C-B3 digital microscope. Position of landmarks and associated linear dimensions were fixed using the TpsDig software (Rohlf 2015) and stored in a database.

SEM microphotographs were taken by JEOL 6380 LV in the Laboratory of electron microscopy, Faculty of Science, Charles University, Prague.

The morphological terms follow the standards proposed by Repenning (1967) or Reumer (1984), the elements of

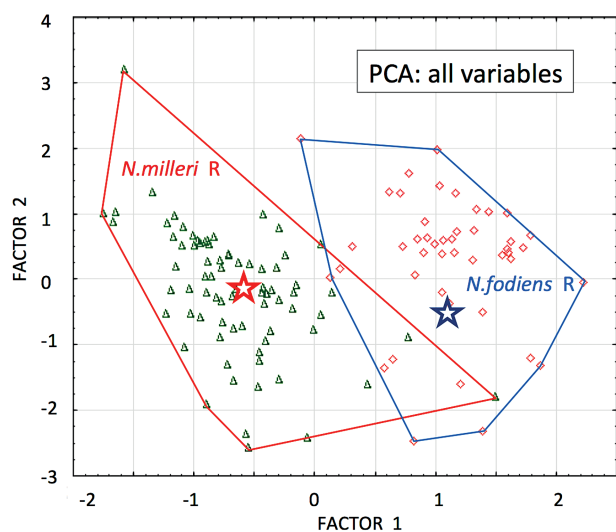
Table 2. List of metric data available for extant and fossil populations of genus *Neomys*. A: n – number of variables measured in particular character classes. B: n – number of analysed individuals (MNI). C: n* – number of cases (basic input data obtained for variables of class) from particular OTUs. NF – extant *N. fodiens*, NM – extant *N. milleri*, Q 4 – samples of present glacial cycle (Vistulian + Holocene), Q 2 – samples of late Biharian age (= *N. newtoni*).

Group (structure)		A	B				C			
			NF	NM	Q 4	Q 2	NF	NM	Q 4	Q 2
		n	n	n	n	n	n*	n*	n*	n*
cranial		2	53	24	0	0	106	48	0	0
rostral		24	54	79	0	0	1262	1340	0	0
mandibular		62	55	80	46	13	1319	4829	1348	397
dental	maxillary unicuspid	27	55	27	2	1	1350	580	6	1
	maxillary molariforms	35	48	78	5	2	1641	1334	97	31
	mandibular unicuspid	19	54	79	21	15	964	1495	155	54
	mandibular molariforms	32	54	80	35	10	1619	2543	628	150
proportions	maxillary	8	54	79	0	1	413	386	0	1
	mandibular	17	55	80	34	12	802	1338	247	72
pigment	maxillary	3	54	20	0	0	189	445	0	0
	mandibular	10	53	80	39	11	445	768	170	38

maxillary dentition are denoted by the upper case (I, Z, P, M), those of the mandibular dentition by the lower case (i, z, p, m).

Data analyses

We computed basic statistics of each variable (n, mean, min, max, SD, CV, skewness, kurtosis) for all OTUs, particular species and site subsets and we tested the normality of distribution using the Shapiro-Wilk test. For all dimensions, the differences between compared OTUs (and/or further subsets) were tested by t-test, zones of metric overlap between the compared sets were computed and expressed in terms of a percentage of the total variation



Text-fig. 2. Results of PCA based on all metric variables in sample of extant *N. fodiens* and *N. milleri*, F1 vs. F2, centroids indicated by stars.

span. The dimensions with overlap zones under 25% of the variation span were considered to have top discrimination capacity and were used in the following identification procedures.

The identification procedure was based on the comparison between the percentages of cases corresponding to non-overlapping zones of either *N. fodiens* or *N. milleri*. The items with more than 75% correspondence were identified with respective extant species; those whose correspondence appeared within limits from 50% to 75% were denoted as “cf.” (confer); those falling in the overlap zone were denoted as “intermediate”.

The multivariate approach included PCA analyses of the sample of extant items, and a series of discriminant analyses operating with the variables properly represented in the fossil record.

The database operations and statistical analyses were undertaken in Microsoft Excel, Statistica 8.0, Past 4.11 (Hammer et al. 2001) or IBM SPSS.

Results

Phenotype variation in the extant populations (OTUs I, II), the discrimination criteria applicable to fossil record

Pls 1–3

A summary of biometric comparisons of two extant species, *N. fodiens* and *N. milleri*, in Table 3 illustrates significant differences in mean values of 84.1% of 239 metric variables, *N. fodiens* is distinctly larger on average. Yet, for the vast majority of 230 primary metric variables, more than half of individuals (58.5%) exhibit the values falling in the overlap zone of the compared species. A smaller rate of overlap

Table 3. Results of biometric comparisons of extant species I. A: Total number of metric variables in particular classes of characters. B: Number of variables in which mean values of compared species differ significantly (t-test, n = number of variables, % = percentage of total number of variables in class). C: Those with significantly reduced between-species overlap (<0.25). D: Mean overlap within class. E: Variables in which mean value for *N. milleri* exceeds that of *N. fodiens*. F, G: Number of variables showing significant sex differences in mean values (t-test) in *N. fodiens* (F), and *N. milleri* (G).

Group (structure)		Between species comparison							Sex dimorphism				
		A	B		C		D	E		F		G	
		n	t test(NM/NF)<0.05		overlap < 0.25		mean overlap	avgNM>avgNF		f/m NF p<0.05		f/m NM p<0.05	
		n	%	n	%	%	n	%	n	%	n	%	
cranial		2	2	100.0	0	0.0	73.6	0	0.0	0	0.0	0	0.0
rostral		24	24	100.0	10	41.7	33.3	0	0.0	0	0.0	1	4.2
mandibular		62	52	83.9	17	27.4	67.3	2	3.2	0	0.0	15	24.2
dental	maxillary unicuspid	27	27	100.0	6	22.2	60.0	1	3.7	0	0.0	1	3.7
	maxillary molariforms	35	30	85.7	5	14.3	54.6	1	2.9	0	0.0	0	0.0
	mandibular unicuspid	19	18	94.7	1	5.2	55.5	0	0.0	3	15.8	4	21.1
	mandibular molariforms	32	31	96.9	0	0.0	65.9	1	3.1	1	3.1	1	3.1
proportions	maxillary	8	7	87.5	0	0.0	82.4	3	37.5	0	0.0	0	0.0
	mandibular	17	5	29.4	0	0.0	100.0	4	23.5	1	6.3	0	0.0
pigment	maxillary	3	2	66.7	1	33.3	62.9	0	0.0	0	0.0	0	0.0
	mandibular	10	3	33.3	0	0.0	100.0	1	10.0	2	20.0	0	0.0

Table 4. Results of factor analyses of mandibular (incl. dental) variables in sample of extant populations of *Neomys fodiens* and *N. milleri* (PCA, varimax normalized). List of factor loadings arranged according to discrimination capacity of particular variables (those >0.5 in bold).

Factor 1		Factor 2		Factor 3	
Lzp	0.906	TalLm2	0.850	m2W	0.861
CorH	0.832	i1L	0.761	m1W	0.851
Lzp/m1m3	0.813	m2L	0.645	TrWm1	0.787
Cd1Cd2	0.811	i1L	0.626	TrWm2	0.754
Cd4Cd5	0.810	TalLm1	0.596	TalWm1	0.681
Cd1Cd3	0.809	m1L	0.557	TalWm2	0.658
z1L	0.791	m1m3	0.536	m3W	0.553
Cd1Cd10	0.759	TalLm3	0.468	pL	0.535
pW	0.753	m3W	0.383	m1m3	0.367
z1W	0.684	TrWm3	0.316	CorH	0.351
i1L	0.613	z1W	0.297	z1W	0.350
m1L	0.562	m3L	0.260	m1L	0.342
TrLm1	0.495	TrLm1	0.255	TrLm1	0.333
TalLm1	0.478	Cd1Cd3	0.219	pW	0.324
m3L	0.478	Cd1Cd10	0.182	m3L	0.321
m3W	0.445	pW	0.167	Cd1Cd3	0.271
m2L	0.426	Lzp	0.157	Lzp	0.251
TalWm1	0.410	Cd4Cd5	0.150	z1L	0.250
m1m3	0.379	z1L	0.140	Cd1Cd2	0.230
TrWm2	0.340	TalWm2	0.133	TrLm2	0.227
m2W	0.269	CorH	0.122	Cd4Cd5	0.224
m1W	0.263	TalWm3	0.114	i1L	0.214
TrLm2	0.231	Cd1Cd2	0.113	Cd1Cd10	0.190
TalLm2	0.213	m2W	0.111	m2L	0.153
TalWm2	0.208	TalWm1	0.101	TalLm1	0.130
TrWm1	0.196	TrWm2	0.040	TrLm3	0.087
i1L	0.195	TrWm1	0.030	i1L	0.054
pL	0.120	m1W	-0.014	Lzp/m1m3	0.021
TalWm3	0.029	TrLm3	-0.063	TalLm2	0.006
TrLm3	0.023	TrLm2	-0.084	TalWm3	-0.038
TrWm3	-0.142	pL	-0.124	TalLm3	-0.046
TalLm3	-0.187	Lzp/m1m3	-0.211	TrWm3	-0.085
Eigenvalue	14.534	Eigenvalue	3.434	Eigenvalue	2.470
% Total	45.417	% Total	10.732	% Total	7.720
Cumulative%	45.417	Cumulative%	56.149	Cumulative%	63.869

(33.3%) was found in the class of rostral dimensions, in ten of them even smaller than 25% of individuals. Such kind of characters, promising application in discrimination praxis of isolated items, appeared also in the classes of mandibular dimensions, maxillary unicuspid and maxillary molars. Among dental variables, excessively larger dimensions in *Neomys fodiens* are particularly apparent in the prolonged unicuspidal part of dentition, wider molariforms together with robust distal part of mandible related to strengthened mastication. In contrast, *Neomys milleri* exceeds otherwise larger *Neomys fodiens* in several characteristics of the molar upper (M2MeL) and lower (TalLm3) dentition and especially their proportions (M3L/M1M3, M3L/M1L, m2L/m1m3, m3L/m1m3), all related to lesser degree of M3L/

m3L (and talonid m3) reduction. Besides that, it possesses wider last upper unicuspid (WZ4). However, significant overlaps between the two species were detected in the class of mandibular proportions, where the two species overlap completely.

The Principal Component Analysis (PCA) operating with all variables considerably reduced the overlap zone (Text-fig. 2) between *N. fodiens* and *N. milleri*, the variables most significantly contributing to species discrimination are in Table 4. A summary survey of basic statistics of these variables in particular OTUs is in Table 5.

Summing up: Based on our results, the most suitable variables for practical identification of the fragmentary fossil items are the following: i1L (incisor length, labial view), Lzp

Table 5. continued

	Q 2 <i>Neomys</i>					MN 15–17 <i>Asoriculus</i>					Q 1 <i>Asoriculus</i>				
	n	avg	min	max	sd	n	avg	min	max	sd	n	avg	min	max	sd
zlw															
iL(occ)	1	3.12	3.12	3.12	0.000	1	0.65	0.65	0.65	0.000					
m1L(occ)	7	1.53	1.34	1.64	0.116	4	1.51	1.44	1.60	0.075					
m2L(occ)	4	1.37	1.15	1.52	0.155	3	1.33	1.28	1.39	0.055	1	1.30	1.30	1.30	0.000
TalLm1	8	0.65	0.53	0.79	0.093	4	0.62	0.54	0.76	0.100					
m1m3	2	4.19	4.13	4.25	0.085	3	3.89	3.81	3.99	0.093					
m2w	4	0.73	0.66	0.78	0.055	3	0.72	0.54	0.86	0.163	1	0.80	0.80	0.80	0.000
m1w	7	0.74	0.65	0.84	0.064	4	0.69	0.53	0.81	0.118					
TrWm1	8	0.74	0.68	0.81	0.056	4	0.78	0.69	0.89	0.090					
TrWm2	5	0.73	0.67	0.77	0.038	3	0.80	0.72	0.91	0.098	1	0.77	0.77	0.77	0.000
TalWm2	5	0.82	0.75	0.93	0.069	3	0.84	0.76	0.94	0.091	1	0.83	0.83	0.83	0.000
m3w	3	0.59	0.56	0.63	0.038	3	0.63	0.52	0.73	0.106	1	0.57	0.57	0.57	0.000
pL	3	1.05	1	1.11	0.057	2	0.80	0.75	0.84	0.064					

(total length of the lower unicuspid and premolar), m1m3 (lower molar row length), Lzp/m1m3, CorH (height of the coronoid process), Cd1Cd2 (distance between upper and lower facet), Cd4Cd5 (lower facet width), Cd1Cd10 (upper facet width), i1L (incisor length, occlusal view), z1L (z1 length, occlusal view), pL (premolar length, occlusal view), m1L (m1 length, occlusal view), pW (premolar width, occlusal view), m2W (m2 width, occlusal view), m3W (m3 width, occlusal view), TrWm1 (width of the trigonid of the m1), TalWm1 (width of the talonid of the m1), TrWm2 (width of the trigonid of the m2), TalWm2 (width of the talonid of the m2) TalLm1 (length of the talonid of the m1), TalLm2 (length of the talonid of the m2).

For the upper jaw it concerned particularly in the following variables: Z1Z1 (distance Z1-Z1), Z2Z2, Z3Z3, P4P4, M1M1, M2M2, IP4 (distance incisor – premolar), IM1, IM2, IM3, P4M3, LP4 (premolar length), LM1 (M1 length), LM2 (M2 length) and their relations to M3L: M3L/M1M3, M3L/M1L.

The biometric analyses of extant species split the variation range of each metric variable into three distinct categories: NF – the non-overlap zone of *N. fodiens*, NM – the non-overlap zone of *N. milleri*, and “intermediate” – the zone of between-species overlap. The identification approach applied onto fragmentary fossil specimens operated with it in the following way: (i) identifying correspondence of the measured value to above-mentioned categories of variation span in extant samples, performed separately for each variable available in the studied specimen, (ii) summing appearances of particular categories within the set of variables available in the studied specimen, and (iii) assuming the final identification as *N. fodiens* when frequency of NF > 75%, *N. cf. fodiens* when NF frequency was between 50% and 75%, *N. milleri* when NM > 75%, *N. cf. milleri* when NM is 50–75%, and *Neomys* sp. when intermediate > 50% or when frequencies of both NF and NM appeared in roughly equal proportions.

OTU III: Q 4 samples

Pl. 4

A group of the Vistulian and Holocene specimens included 54 items from 29 community samples of 10 sites, mostly the multilayered stratigraphic series covering period after LGM (comp., e.g., Horáček and Ložek 1988). Considering the total amount of material available from these sites (MNI > 29,000, 880 community samples, 135 sites), *Neomys* occurred in 3.3% of samples only, with a relative total abundance 0.18%. The most frequent records were obtained from the stratigraphic sequence of Býčí skála (BS), 12.5–8.4 ka BP, where *Neomys* represented 1.5% of the total MNI of small ground mammals (= 2,345).

Biometric characteristics of the Q 4 samples are in SM:SF II and Table 5, their comparison with the sample of Recent populations is summarized in Table 6. The Q 4 sample shows an extensive overlap with variation range of both species, yet in more variables it even exceeded it, including the maximum values of extant *N. fodiens* (comp., e.g., Text-figs 4, 5). The parallel determination procedures covering both partial discrimination functions established based on sample of Recent species, and the comparative

Table 6. Summary of biometric comparisons of Q 4 sample of *Neomys* to samples of extant species. n* – number of cases (basic metric data obtained for particular character class), % – percentage of cases corresponding to non-overlap values in extant *N. milleri* (NM), *N. fodiens* (NF) and to a zone of between-species overlap (intermediate).

Group (structure)		Recent	Q 4 <i>Neomys</i>			
		n*	n*	NM	intermediate	NF
				%	%	%
cranial		154	0	0.0	0.0	0.0
rostral		2602	0	0.0	0.0	0.0
mandibular		6148	1348	25.4	60.5	14.2
dental	maxillary unicuspid	1930	6	0.0	16.7	83.3
	maxillary molariforms	2975	97	2.1	54.6	43.3
	mandibular unicuspid	2459	155	4.5	68.4	27.1
	mandibular molariforms	4162	627	13.7	74.8	11.5
proportions	maxillary	799	0	0.0	0.0	0.0
	mandibular	2140	247	20.2	77.7	2.0
pigment	maxillary	634	0	0.0	0.0	0.0
	mandibular	1213	170	2.4	91.2	6.5

Table 7. Number of variables in which specimens from particular Q 4 stages corresponded to either *N. fodiens* (F), *N. milleri* (M) or intermediate position (i). PCA refers to comparison with partial PCA analyses operating on sample of extant species with reduced number of variables available in fossil record.

Period	disc. functions			dent max mol			md			md dent uni			md dent mol		
	F	i	M	F	i	M	F	i	M	F	i	M	F	i	M
Q 4w1	0	0	1	0	0	0	0	4	1	0	0	0	0	4	0
Q 4w2	1	0	0	0	0	0	2	3	0	0	0	0	0	5	0
Q 4w3	1	0	1	0	0	0	6	5	1	2	1	0	0	11	9
Q 4h1 exc. BS	2	0	2	0	0	0	3	11	6	0	0	0	5	19	5
BS Dryas	2	0	1	0	0	0	4	7	5	3	2	0	4	20	0
BS Preboreal	5	0	7	18	4	0	16	38	26	7	11	2	15	94	13
BS Boreal	0	0	2	0	0	0	0	2	7	0	6	0	2	27	12
Q 4h2	2	0	1	4	2	0	5	14	4	0	3	0	0	18	6

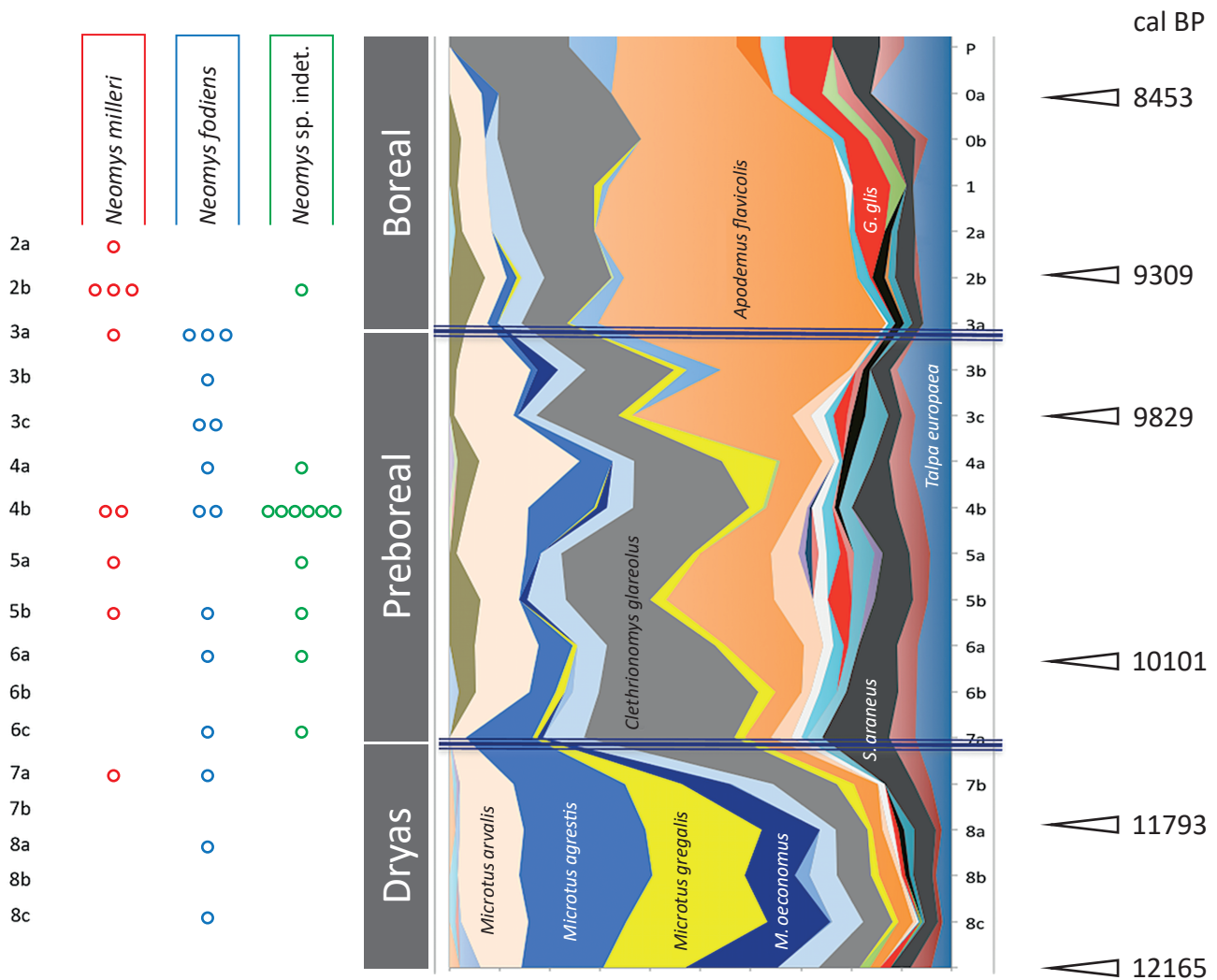
Table 8. Summary of species identification in set of Q 4 samples (MNI).

Period / Taxon	<i>N. fodiens</i>	<i>N. cf. fodiens</i>	intermediate	<i>N. cf. milleri</i>	<i>N. milleri</i>
Q 4w1	0	0	0	1	0
Q 4w2	0	1	0	0	0
Q 4w3	2	0	2	0	1
Q 4h1 exc. BS	0	1	3	0	1
BS Dryas	1	2	0	1	0
BS Preboreal	11	1	10	2	4
BS Boreal	0	0	1	1	3
Q 4h2	1	0	3	2	0

approach described in the previous paragraph enabled identification of most Q 4 items (Tabs 7, 8).

A detailed record from late Glacial and Preboreal was obtained from the profile Býčí skála (Text-fig. 3). It is obvious that *Neomys fodiens* appears in Býčí skála before the beginning of Holocene, as implied by two samples from

layers 8c and 8a. It is then continuously recorded mainly from the early Preboreal (layers 6a, 5b, 4b, 4a, 3c, 3b and 3a). During the late Vistulian (7a) and Preboreal (5b, 5a, 4b), *Neomys milleri* is present as well. It seems that *N. milleri* reaches its peak in the late Boreal. Earlier (2b, 3a – late Preboreal), *N. milleri* is more abundant than *N. fodiens*.



Text-fig. 3. Appearance of *N. fodiens* (F), *N. milleri* (M) and *Neomys* sp. indet. (i) in the Late Pleistocene – early Holocene stratigraphic series in Býčí skála with survey of small mammal communities of particular layers and their ¹⁴C cal. BP dating.

However, it probably appears later than *N. fodiens* at Býčí skála. It is possible that both species lived there in sympatry and inhabited this particular locality either before or since the very beginning of Holocene. However, it is important to point out that the oldest samples do not express strict characteristics of one species, and most of the variables belong to the category of “undetermined”.

The Slovakian locality Peskő provides evidence of both species as well. A mandible from Peskő /12 (Q 4w2) was identified as *N. fodiens*; the sample from Peskő /8 (Q 4w3) showed even more significant characteristics of this species. Considering its length, the lower incisor from Peskő /7P (Q 4w3) also belongs to *N. fodiens*. Two samples from Peskő /6 (Q 4w3) were available, one of them undoubtedly showing characteristics of *N. milleri*, the other was impossible to identify, as also was the case the mandible from Peskő /7L (Q 4w3).

Our only record from the oldest unit of Vistulian glacial (Q 4w1 = early Glacial) is the mandible from Chlum near Srbsko (Chlum 7, chimney of Srbské Cave), whose identification is complicated due to the absence of teeth. According to the discrimination function and measurements of the condylar process, it most probably represents *N. milleri*.

We also identified as *N. milleri* an almost complete mandible from Srbsko-stěna (SS1), representing the assemblage from the late Vistulian. In this case, the identification is clear. Unfortunately, material from other localities of a similar age (Maštalná /9, Soví převis /83) could not be identified. One specimen from LGM assemblage Skalice /7 could not be determined for sure, the other was identified as *N. fodiens*.

Records from Q 4h2 are mostly problematic in terms of identification. A maxillary fragment (M1 and M2) from Zazděná /1 positively determined as *Neomys fodiens* is an exception. The sample from Červeného muže /5 seems to represent *N. milleri*, the items from Červeného muže /1, Soví převis /34, /36 and /83 could not be identified.

In terms of systematic paleontology, the Q 4 OTU III can be characterized as follows:

Neomys fodiens PENNANT, 1771

Q 4w3 Peskő /7P: right i1. Peskő /8: right md with z1–m3. **Q 4w2** Peskő /12: right md with m1. **Q 4h2** Zazděná /1: max with M1+M2. **Q 4h1** Skalice /7: right md with m2, fragment of right md with p4–m1. **Býčí skála (BS) /3a**: left md with m1–m2, left i1. **BS /3b**: right md with p4–m1.

BS /3c: rostrum with Z2–Z3+M1–M3, rostrum with Z3–Z4+M1–M2. BS /4a: right i1. BS /4b: right i1, right md with i1+m1. BS /5b: max with M1+M2. BS /6a: left i1. BS /6c: left md with i1–m1. BS /7a: left md with i1+p4–m2. BS /8a: left md with p4. BS /8c: right md with m1.

Neomys milleri MORTAZ, 1907

Q 4w1 Chlum 7: left md without dentition. **Q 4w3 Peskö /6**: fragment of left md (corpus md) with m1–m3. **Q 4h1 Býčí skála (BS) /2a**: right md with p4–m2. **BS /2b**: left md with m1–m2, fragment of left md (corpus md) with z1–m2, fragment of right md (corpus md) with m2–m3. **BS /3a**: left md with p4–m1, **BS /4b**: right md with p4, left md with m1–m3. **BS /5a**: fragment of right ramus md. **BS /5b**: right md with m1. **BS /7a**: right md with m1–m2. **Srbsko ss1**: right md with m1–m2 and broken i1. **Q 4h2 Červeného muže /5**: left md with damaged m3. **Holštejnská /2**: fragment of right md (corpus md) with p4–m2.

Neomys sp.

Q4w3 Peskö /6: md without dentition. **Peskö /7L**: ramus mandibulae. **Q4h1 Býčí skála (BS) /2b**: md with z1–m1. **BS /4b**: md with i1–m2, md with m1–m3, md with m2, ramus mandibulae (broken), md with m1–m3, md without dentition. **BS /5a**: ramus mandibulae. **BS /5b**: md with m1–m2. **BS /6a**: md with m1. **BS /6c**: md with m1–m3. **Skalice /7**: md with m2. **Maštalná /9**: md with m1–m2. **Soví převis /83**: md with m1. **Q4h2 Červeného muže /4a**: md with m1–m3. **Soví převis /34**: ramus mandibulae. **Soví převis /36**: md with m1. **Holštejnská /2**: i1.

Conclusions. Though we did not succeed in species determination of all items, a considerable part of the Q4 record was identified. It showed the appearance of both *N. fodiens* and *N. milleri* not only in the Late Holocene, but also in Late Pleistocene and Early Holocene communities (Text-fig. 3), as well as those of Vistulian age.

OTU IV: Q 2 samples – *Neomys newtoni* HINTON, 1911

Pl. 5, Figs 1–4

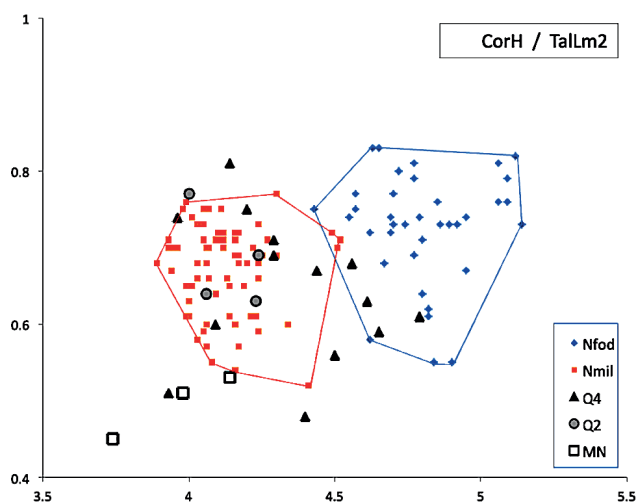
Measurements. See SM:SF II and Tabs 5–6.

Material. Q 2: Chlum 4S-K: md., **Koněprusy C718/H3**: 2 i1, md with p4–m3. **C718/H4**: md with m1–m3. **C718/H5**: md with m1. **C718/f5**: max with P4–M2, max with Z4, 2 i1, M1. **Koněprusy JK 2** (coll. Fejfar; Fejfar 1956, 1961, 1966, Horáček 1985 – as *N. newtoni*): md with m1, md with m1–m2, md with i1+p4+m1. **JK 3**: md with m2. **Q3/1: Dobrkovice 2** (Fejfar 1965): md with m3 (damaged).

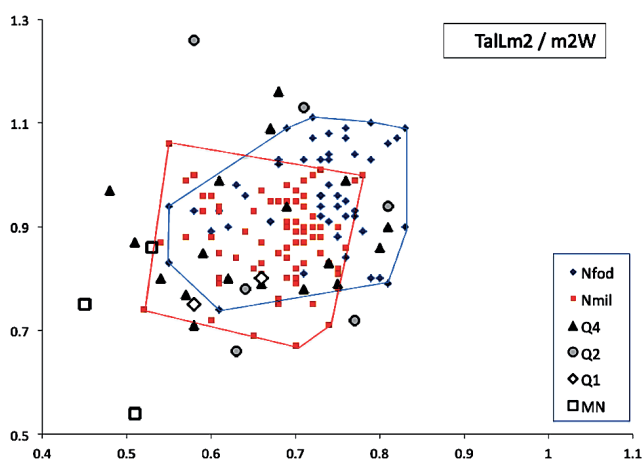
Description and comparisons. In general size as well as in height of the coronoid process (4.00–4.53 mm), all Q 2 specimens are distinctly smaller than *N. fodiens*. At first glance, they correspond well to extant *N. milleri*. Hence, our comparison was first focused on possible identity of both OTUs and/or differences between them. We found out the following: (i) mean values in Q 2 samples are mostly larger and often fall in the range of the overlap of the Recent species (Tab. 9), (ii) the length of the lower incisor invariably exceeded maximum values of *milleri* in all Q 2 specimens, (iii) the interarticular area is significantly narrowed: this concerns not only absolute values of the variable (Cd8Cd9), but also relative ratio to the height of the condylar process (Cd8Cd9/Cd1Cd2), (iv) height of horizontal ramus is smaller, (v) the upper sigmoid notch (CdL) is significantly shorter, (vi) m3 is less reduced (m3L, TalLm3 significantly longer), (vii) upper condylar facet is situated in notably distal position: differences, especially from *N. fodiens*, are visible (RM1, Cd1Cd2, Cd1Cd3). The values in Q 2 sample remarkably exceed both mean and extreme values of *N. milleri* and *N. fodiens* (regardless of size differences), (viii) in some variables, a span of variation exceeds those in extant samples: this concerns, e.g., the apical width of the coronoid process (Cr1). Similarly, the factor 1 and 2 scores in PCA 4 and 5 analyses (combinations of the variables related to proportions of ascending ramus and proportions of molars) indicate the intermediate position between the two recent

Table 9. Summary of biometric comparisons of Q 2 sample of *Neomys* to samples of extant species. n* – number of cases (basic metric data obtained for particular character class), % – percentage of cases corresponding to non-overlap values in extant *N. milleri* (NM), *N. fodiens* (NF) and to a zone of between-species overlap (intermediate), probability values (p) for normal distribution in Q 4 sample (Shapiro-Wilk – 1).

Group (structure)		Recent	Q 2 <i>Neomys</i>				
		n*	n*	NM	intermediate	NF	normality
				%	%	%	p
cranial		154	0	0.0	0.0	0.0	
rostral		2602	0	0.0	0.0	0.0	
mandibular		6148	397	51.9	41.1	7.1	0.914
dental	maxillary unicuspsids	1930	1	0.0	0.0	100.0	
	maxillary molariforms	2975	31	48.4	51.6	0.0	1
	mandibular unicuspsids	2459	54	9.3	74.1	16.7	0.869
	mandibular molariforms	4162	150	26.7	71.3	2.0	0.924
proportions	maxillary	799	1	100.0	0.0	0.0	
	mandibular	2140	72	19.4	76.4	4.2	0.955
pigment	maxillary	634	0	0.0	0.0	0.0	
	mandibular	1213	38	5.3	92.1	2.6	0.903



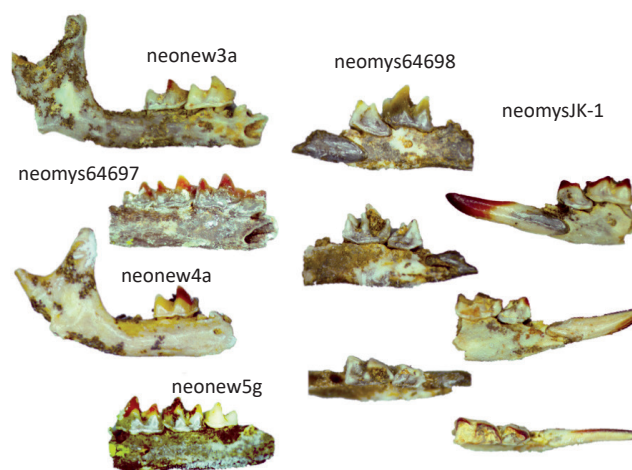
Text-fig. 4. Bivariate plot of coronoid height (CorH, abscissa) and m2 talonid length (TaLm2, ordinata), in particular OTUs.



Text-fig. 5. Bivariate plot of m2 talonid length (TaLm2, abscissa) and m2 width (m2W, ordinata), in particular OTUs.

taxa, (ix) in PCA6 (measurements of the condylar process and CdL), Q 2 specimens exhibit a wide spectrum of variance that exceeds *N. milleri* and shows tendencies to shape and size characteristics of *N. fodiensis*, (x) compared to *milleri*, p4 was relatively large with a high and well developed distal cusp, (xi) unlike in the Recent species, we observed an extreme variability in pigmentation of teeth. Both intensity and extent of teeth colouration varied from the state corresponding with a dark red pigmentation to recent taxa (in a single specimen – *neomysJK1* – Text-fig. 6) to nearly an absence or very light pigmentation limited just to apex of protoconids and hypoconids of m1 and m2. Most specimens exhibited a light orange colouration with diffuse pigmentation edges.

Comments. Despite overall correspondence between the Q 2 sample and *milleri* in biometric characteristics, especially regarding measurements of condylar process, values exceeding the maximum of *milleri* were recorded in 16 cases (6 individuals, 6 variables – e.g., i1L, length of distal unicuspid tooth), values under the minimum of *milleri* occurred in 16 cases as well (5 individuals, 12 variables – e.g., horizontal ramus height). A



Text-fig. 6. Specimens of Q 2 *Neomys newtoni* (five from Koněprusy C718, one from Koněprusy JK-1) illustrating variation in tooth pigmentation.

remarkable deviation from *Neomys milleri* was observed in the length of a lower incisor – the maximum value of *N. milleri* was exceeded in every Q 2 specimen. Compared to the Q 4 sample, the Q 2 specimens were smaller on average.

Summing up the comparisons, we can conclude that the Q 2 material generally resembles recent *Neomys milleri*, yet in many ways it differs from the extant taxon. At the same time, results of the factor analysis as well as comparison with other OTUs showed relative homogeneity of the Q 2 sample, which was then also strongly supported by the Shapiro-Wilk test: 88 out of 98 variables ($p = 0.05$) showed normal distribution. This suggests that despite a broad variation in some characters, all Q 2 (incl. Q 3/1) specimens can be considered a single species.

Overall, our material corresponds to the original diagnosis of *Neomys newtoni* in the following characteristics: small size and relatively low coronoid process, significantly narrowed interarticular area, distal position of the upper condylar facet (Hinton 1911). In both metric and non-metric characters, it corresponds to those reported for *Neomys newtoni* from other European Q 2 sites such as Voigstedt (Maul 1990, Maul and Parfitt 2010), Zalesiaky 1A and Kozi Grzbiet (Rzebik-Kowalska 1991, 1994), Somssichhegy 2 (Pazonyi et al. 2018), Kuznetsovka (Agadjanian and Kondrashov 2007) or Q 3 Schöningen (van Kolfschoten 2014), Medzybozh (= Medzhybizh 1; Rzebik-Kowalska and Rekovets 2016, Stefaniak et al. 2022).

Even though we observed extensive overlap with *N. milleri*, our fossil material demonstrated significant differences (e.g., variability of teeth pigmentation), which together with the results of the factor analysis and Shapiro-Wilk test strongly supports taxonomic homogeneity and a separate status of *Neomys newtoni*.

OTUs V–VI: MN 15 – Q 1 samples – *Asoriculus* KRETZOL, 1959

Pls 5, 6

The specimens of the Pliocene (MN 15–16) and earliest Pleistocene (MN 17 – Q 1) sites differ from the above-

surveyed representatives of the genus *Neomys* in characters conforming the diagnosis of the genus *Asoriculus*, sometimes considered an ancestor of the extant genus. Among others, the differences are a smaller size, lesser height of the coronoid process, a higher degree of m3 and m3 talonid reduction, lesser relative distance between the upper and lower articulation condyle, shortened i1 and its mesial part in front of the dorsal cuspid and carrying distinct distal cingulid, compressed p4 with distally tapered labial margin, absence of teeth pigmentation, etc. The specimens from MN 15, 16 and early MN 17 sites (OTU VI) fit the diagnosis perfectly – we identified them as *Asoriculus gibberodon*, while those from the late MN 17 and Q 1 sites (OTU V), denoted here as *Asoriculus castellarini*, exhibited certain differences, which are reported in detail below.

Biometric data are surveyed in SM:SF II and Table 5, a summary of biometric comparisons is in Table 10.

Asoriculus gibberodon (PETÉNYI, 1864)

Pl. 6, Figs 1–5

Material. MN 15: Včeláre 2B: fragment of left md (ramus md), M1. Ivanovce: right md with p4–m3 (as *Asoriculus gibberodon* in Fejfar and Sabol 2005). MN 16: Javoříčko XI: complete left md except for the angular process. Javoříčko XVIII: right md without dentition. MN 17: Včeláre 6/1: fragment of right md without dentition. Koliňany 1: fragment of md without dentition (condylar process + part of corpus md preserved).

Description and comparison. Overall, our material corresponds to the original diagnosis of *Asoriculus gibberodon* (absence or reduction of pigment, robust jaws, low coronoid process, pronounced spiculum, shallow upper sigmoid notch, compression of the unicuspid dentition, short i1 with visible cingulum, compact m3 with shortened talonid).

We consider the significantly shorter distance between the condylar process and the ascending ramus (CdL) than in extant *Neomys milleri* to be an important diagnostic feature of *Asoriculus gibberodon*. Another notable difference is observed in the height of the condyle (Cd1Cd2), which is lower in our MN 15 – MN 17 material; it also possesses a narrower upper facet compared to *N. milleri*. The last lower molar is also often slenderer than in the extant species. Apart from metric characteristics, differences in non-metric traits were observed as well, such as closer position of the teeth row to the ascending ramus, prolonged bean-shaped mandibular foramen (which is usually round and small in recent taxa) and strongly pronounced spiculum of the coronoid process in the Plio-Pleistocene form. The cingulum is, in agreement with the recent species, present on both labial and lingual side. In the specimen from Javoříčko XI, it is also present on the lower incisor (unfortunately this specimen is the only one in our collection that possesses the lower incisor), which represents another difference from *N. milleri*. A faint light orange tooth pigmentation is present in various amounts; in samples of MN 15–16 age it is completely absent.

The diagnosis (established at the description of *Soriculus kubinyii* KORMOS, 1934) emphasized “the bicuspid lower incisor with insignificant cusps and weak pigmentation

limited to the apical part of the teeth”. Regarding the European fossil record, the following features are often mentioned: (i) the lower incisor is short and bicuspid (Reumer 1984, Koufos et al. 2001, Rofes and Cuenca-Bescós 2006, Minwer-Barakat et al. 2010, Angelone et al. 2011, Vasileaidou et al. 2012, Rzebik-Kowalska 2013, Joniak et al. 2017, Moya-Costa et al. 2023) with (ii) a well-developed cingulum (Reumer 1984, Dahlmann and Storch 1996, Furió and Angelone 2010, Minwer-Barakat et al. 2010, Rzebik-Kowalska 2013). (iii) Molars possess a rather weak cingulum (Rofes and Cuenca-Bescós 2006, Botka and Mészáros 2017, Joniak et al. 2017), (iv) the entoconid is pronounced (Rofes and Cuenca-Bescós 2006, Minwer-Barakat et al. 2010, Vasileaidou et al. 2012, Botka and Mészáros 2017). (v) Pigment is usually present only slightly, usually limited to tips of trigonid and talonid (Reumer 1984, Popov 2003, Rofes and Cuenca-Bescós 2006, Botka and Mészáros 2017, Moya-Costa et al. 2023). (vi) The terminal part of the coronoid process is round (Popov 2003, Rofes and Cuenca-Bescós 2006, Moya-Costa et al. 2023). (vii) The condylar process carries a wide but low upper facet of cylindrical shape, the lower facet is often bent lingually. The two facets are separated by long and extremely narrow interarticular area (Rofes and Cuenca-Bescós 2006, Rzebik-Kowalska 2013, Moya-Costa et al. 2023). (viii) The horizontal ramus is low (Rofes and Cuenca-Bescós 2006).

Compared to it, our material shows a high level of variability. It conforms to the above characters in a narrow upper facet (Včeláre 2B – MN 15, Včeláre 6/1 – MN 17, Včeláre 3 – MN 17, Včeláre 4E – Q 1), low horizontal ramus (Včeláre 6/1 – MN 17, Včeláre 3 – MN 17, Včeláre 3/1 – MN 17), narrow tip of coronoid process (Včeláre 6/1 – MN 17), significant entoconid (Ivanovce – MN 15, Javoříčko XI – MN 16, Včeláre 3/1 – MN 17, Včeláre 4/7 – Q 1), and absence or reduction of pigment (Ivanovce – MN 15, Javoříčko XI – MN 16, Včeláre 4/7 – Q 1). In contrast, some of our samples possess a high horizontal ramus (Ivanovce – MN 15), wide tip of coronoid process (Ivanovce – MN 15, Včeláre 3 – MN 17, Včeláre 4E – Q 1) or fuller pigmentation (Včeláre /upper molar/ – MN 15, Včeláre 3/1 – MN 17).

Asoriculus castellarini (PASA, 1947)

Pl. 5, Fig. 4, Pl. 6, Fig. 3

Material. MN 17: Včeláre 3: right md with m1–m3 (as *Episoriculus* cf. *castellarini* in Fejfar and Horáček 1983), 4 fragments of left md (3 ramus md, 1 corpus md without dentition). MN 17/Q 1: Včeláre 3/1: 1 part of ramus mandibulae (coronoid process), 1 part of md (corpus mandibulae) with molar tooth. Včeláre 5: fragment of left md (coronoid process). Q 1: Včeláre 4E: fragment of right md (ramus md). Včeláre 4A/7: fragment of left md (corpus md) with m2–m3 (as *Episoriculus* cf. *castellarini* in Fejfar and Horáček 1983). Q 1/Q 2: Včeláre 6/7: right md with p4–m1 (alternatively as *Neomys newtoni* HINTON, 1911).

Description and comparison. Smaller size, more gracile teeth than *Asoriculus gibberodon*. Slight pigmentation of teeth, limited to the apical parts of the crown present in all specimens. Upper sigmoid notch not as shallow as in *Asoriculus gibberodon*, CdL in samples from Včeláre 3/1

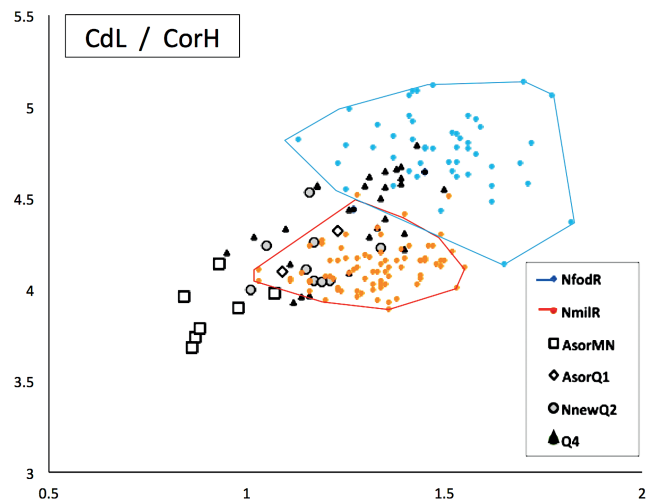
Table 10. Summary of biometric comparisons of *Asoriculus* samples of MN 15 – MN 17 age to those of late MN 17 – Q 1 age (*castellarini*), to samples of extant *Neomys milleri* (Rec NM) and Q 2 sample of *N. newtoni*. n* – number of cases (basic metric data obtained for particular character class), % – percentages of cases falling into variation range of compared OTUs and those which exceed it (>) or fall under lower variation margin of them (<).

Group (structure)	Rec NM	Q 2 NN	<i>Asoriculus</i> MN 15–17						<i>Asoriculus</i> late MN 17 – Q 1										
			<i>milleri</i>		<i>newtoni</i>		n*	<i>milleri</i>		<i>newtoni</i>		<i>Asoriculus</i> MN 15–17							
			<	>	<	>		<	>	<	>	<	>						
cranial	n*	48	0	0.0	0.0	0.0	0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0				
		1340	0	0.0	0.0	0.0	0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0				
		4829	397	31.6	64.2	4.2	285	12.3	79.4	8.4	31.6	62.6	5.8	11.0	65.2	23.2			
dental		580	1	0.0	0.0	0.0	0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0			
		1334	31	22.2	77.8	0.0	9	22.2	11.1	66.7	0	0.0	0.0	0.0	0.0	0.0			
		1495	54	26.1	69.6	4.3	23	43.5	26.1	4.3	66.7	33.3	0.0	0.0	66.7	33.3			
		2543	150	8.2	87.8	4.1	49	18.4	65.3	24.5	71	29.6	70.4	2.8	64.8	15.5	19.7		
proportions		386	1	0.0	0.0	0.0	0	0.0	0.0	0.0	0	0.0	0.0	0.0	0.0	0.0	0.0		
		1338	72	14.6	79.2	6.3	48	25.0	47.9	20.8	30	13.3	80	6.7	26.7	56.7	16.7	36.7	
pigment		445	0	0.0	0.0	0.0	0	0.0	0.0	0.0	8	0.0	0.0	0.0	0.0	0	0	0	0
		768	38	100	0.0	0.0	1	100	0.0	0.0	8	0.0	100	0.0	62.5	12.5	0.0	0	0

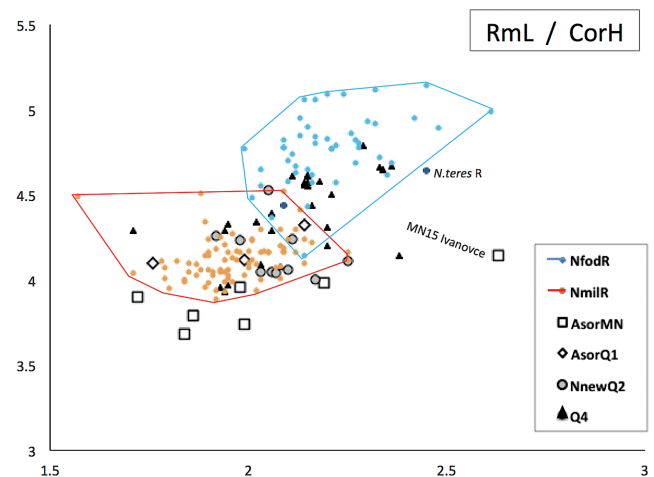
and Včeláre 6/7 significantly exceeds variance span of *A. gibberodon*, as former corresponds to smallest individual of *N. milleri*, and latter to mean value of this species. Coronoid process leans in mesial direction, similarly to *Neomys*.

We were able to obtain biometric comparative information for 88 mandibular measurements (n = 3–12) of *A. castellarini* and *A. gibberodon*, for which the Shapiro-Wilk test showed normal distribution in 80 variables. Deviance from this state (p = 0.003–0.05) was observed in the following variables: Cr3, Cr5, RM1, RM2, mdLm2, Cd1Cd10, TrLm1, TalLm3. In five of them, values of the Q 1 and MN specimens differ distinctly: Cr3, Cr5, TalLm3 (Q 1 > MN) and RM1, RM2 (Q 1 < MN). The difference was also indicated by the results of PCA4.

Until the late MN 17, our material is homogenous and comprised the original form *A. gibberodon*, and similarly to the European fossil record (Rzebik-Kowalska 1998, 2002), this taxon represents the vast majority of our material. In



Text-fig. 7. Bivariate plot of length of upper condylar process, from deepest point of incisura sigmoidea to distal margin of condyle (CdL, abscissa) and coronoid height (CorH, ordinata), in particular OTUs.



Text-fig. 8. Bivariate plot of length of ramus mandibulae (RmL, abscissa) and coronoid height (CorH, ordinata), in particular OTUs.

contrast to our expectations, our samples did not follow the trend of enlarging body size throughout the MN 15 – Q 1 period. In most of the measurements, specimens from MN 15 exceeded the samples from MN 16 and MN 17 and reached values similar to the Q 1 material. Yet when the MN 15 specimens were excluded, the expected trend is confirmed. Similarly to our results, Popov (2003) also reported bimodality while comparing large sample of *A. gibberodon* from MN 17 Varshets, Bulgaria with other localities (MN 14 – Q 1).

As expected, our results showed a smaller size of *Asoriculus* in comparison with Q 2 and Q 4 *Neomys*, as well as extant *N. milleri*. Sometimes an overlap with *N. milleri* was recorded. However, some samples exceeded the maximum of *N. milleri*. A wide terminal part of the coronoid process was observed in samples from Ivanovce (MN 15), Včeláre 3 (MN 17) and Včeláre 4E (Q 1). The specimen from Ivanovce also exceeds the recent species in other aspects (pW, RmL), yet the distance between tip of upper facet and centre of upper sigmoid notch (lingual view, CdL) is shorter. This trend is observed in another 9 specimens (out of 11), and thus could be considered a significant distinguishing criterion between *Asoriculus* and *Neomys*. Similarly to *Neomys*, the width of the talonid of the first two lower molars exceeds the width of the trigonid, yet the m3 in *Asoriculus* is more reduced (comp. smaller length and width of talonid).

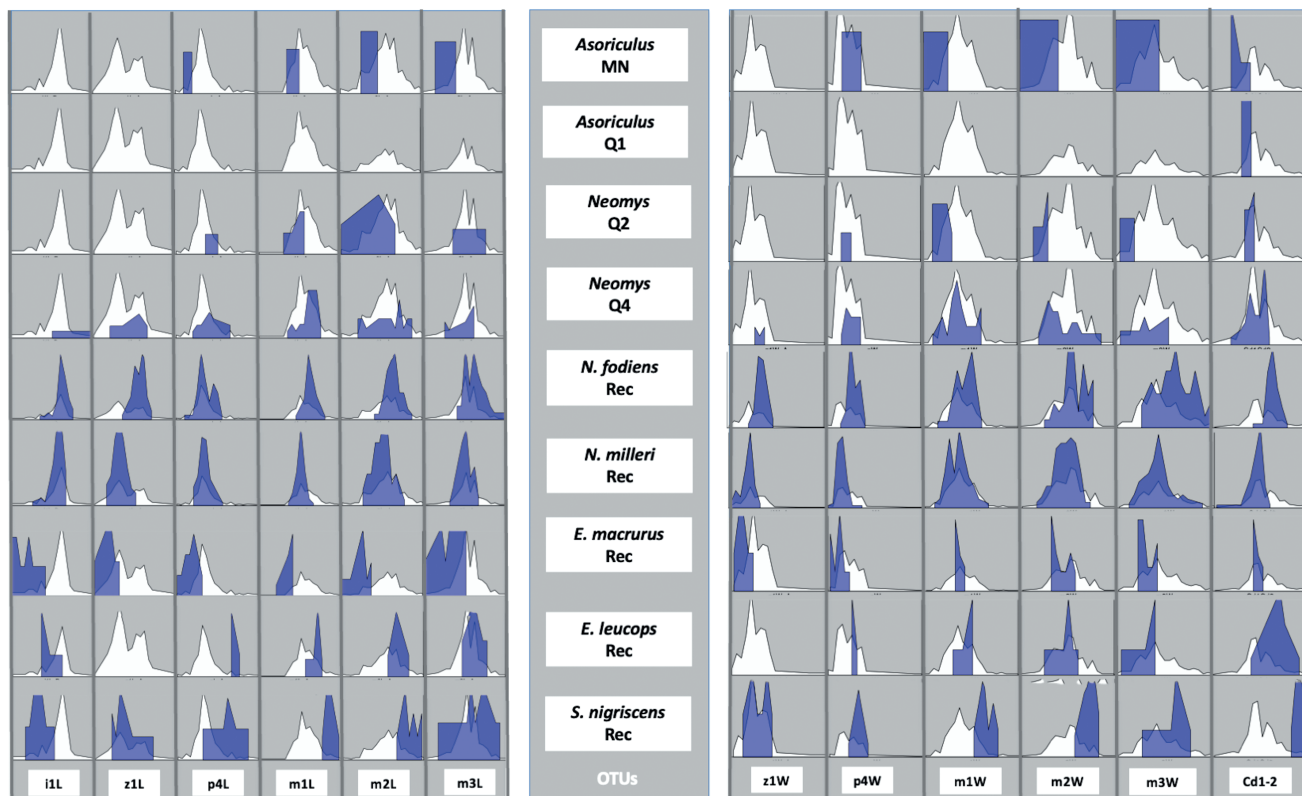
The sample from Včeláre 3/1 (the earliest Q 1) possesses a combination of characteristics mentioned above. There is not an enhanced gap between the molar row and ascending ramus, the coronoid process points almost straight upwards

(without leaning forwards, as is typical for *Neomys*) and its spiculum is pronounced. The talonid of the last molar is small; the entoconid is relatively low in all molars. In terms of metric variables, this specimen is one of the largest, especially regarding the CdL. It corresponds well to the diagnosis and redescrptions of *A. castellarini* by van der Meulen (1973).

In contrast, the specimen from Včeláre 6/7 (late Q 1) shares more characteristics with *Neomys* than *Asoriculus*. Even though the spiculum is pronounced, and according to the position of alveoli, the last molar was positioned closely to the ascending ramus, based on the value of CdL and the high coronoid process pointing dorsally, it could alternatively be assigned to *Neomys newtoni*.

Apparently, *Asoriculus gibberodon* differs from *Neomys newtoni* significantly by the shape of the lower premolar (massive unicuspid with pronounced distal prolonging of the labial cingulum in *Asoriculus*, and wide bicuspid with significant occlusion edges of the cusps in *Neomys*). Unfortunately, not a single specimen from all of the European Q 1 fossil record possesses this particular tooth, except for those from Atapuerca, Trinchera del Elephante, Spain (Rofes and Cuenca-Bescos 2006), in which it corresponds clearly to the state in *A. gibberodon*, while at the same time, it differs from it by a dorsally tapered coronoid process and distinctly pronounced high position of the upper articulation condyle.

Comments. Unfortunately, our material is not sufficient to test the relevance of the hypothesis that *A. castellarini* represents a transient form between *A. gibberodon* and *N. newtoni*, nor to prove the trend of enlarging body size during the period of MN 17 – Q 1.



Text-fig. 9. Survey of frequency distribution of basic dental variables in all OTUs under study, plotted against overall distribution in whole set of all OTUs.

A similar issue stands behind the sceptical view on the validity of other forms described from various European Pliocene and Early Pleistocene sites: *Soriculus kubinyii* KORMOS, 1934, *Episoriculus tornensis* JÁNOSSY, 1973 and *Episoriculus borsodensis* JÁNOSSY, 1973. Considering the wide variability of *Asoriculus gibberodon*, these taxa are usually synonymised with this form (Reumer 1984, Rzebik-Kowalska 1998).

Nevertheless, at least considering the span of variation among our OTU IV specimens, the tendencies conforming to expected transitional state between the *Asoriculus* and *Neomys* phenotypes seems to be clearly marked. Hence, we tentatively propose, as a provisional solution, to separate the late MN 17 – Q 1 populations as a distinct taxonomic unit, for which a prior name *A. castellarini* (PASA, 1947) is available.

Mid-European Nectogalini vs. Asiatic clades

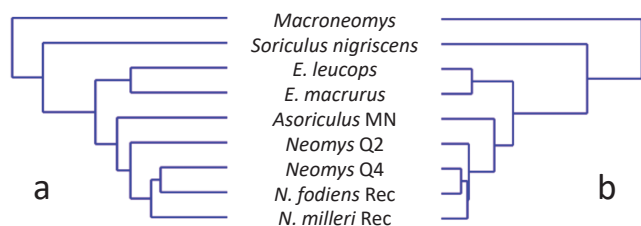
Pl. 7

In addition to the above performed comparisons, we analysed the phenotype relations between the studied mid-European taxa and a set of items representing the extant Oriental clades, namely *Soriculus nigrescens*, *Episoriculus macrurus*, *E. leucops*, *Chimarrogale platycephalus* (TEMMINCK, 1842), and *Anourosorex* sp. (Anourosoricini ANDERSON, 1879, formerly part of Neomyini MATSCHIE, 1909).

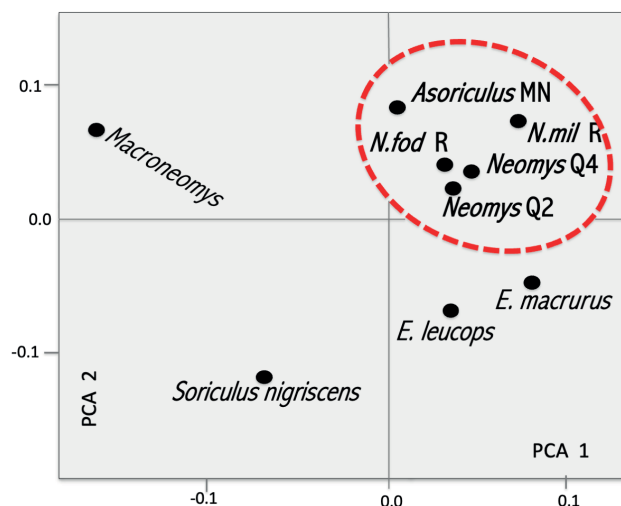
In contrast to the latter two genera, which exhibit distinct differences, the representatives of *Soriculus* and *Episoriculus* reveal obvious similarities in cranial and dental characters to the European Pliocene *gibberodon*, for which that species was included in these extant genera (e.g., Ellermann and Morrison-Scott 1951, Repenning 1967), until Hutterer (1994) demonstrated the differences validating the concept of an independent genus *Asoriculus*, proposed by Kretzoi (1962).

We examined the samples of these extant species using the biometric technique applied in other OTUs, and quantified the differences in form of Euclidean distances of 42 metric variables represented in the majority of the OTUs (unfortunately except for OTU V), normalized by filtering off their size differences, and further evaluated by PCA and cluster analyses.

The comparison of frequency distributions for basic dental dimensions in particular OTUs is summarized in Text-fig. 9. The results of multivariate analyses demonstrating similarity relations among particular OTUs are visualized in Text-figs. 10 and 11. They show close relations among



Text-fig. 10. UPGMA cluster analyses of phenotype characteristics of OTUs based on multivariate Euclidean distances of 88 metric variables, normalized by filtering off size differences (a) and Factor 1 of PCA operating with mean values of 41 mandibular variables (b).



Text-fig. 11. Results of PCA analysis operating with mean values of 41 mandibular variables, normalized by filtering off size differences: plot of factors 1 and 2. Note clustered position of European OTUs.

the W-Palaearctic clades (*Asoriculus-Neomys*) and distinct differences from both *Episoriculus* and *Soriculus* samples. The results thus strongly support the stand of Kretzoi (1962) and Hutterer (1994) against alternative synonymisation of *Asoriculus*, *Soriculus* and *Episoriculus* (e.g., Ellermann and Morrison-Scott 1951, Repenning 1967). The case of *Macroneomys brachygnathus* (Q 2/Q 3 border, 11 European sites) occupying the most distant position will be discussed elsewhere.

European radiation is characterized by successive enlarging of body size and arrangements of horizontal ramus (including strengthening of the distal position of coronoid process) in the sequence AsorQ1-NeomQ2, later followed by divergence to the morphotypes of *Neomys milleri* and *Neomys fodiens* during the Middle Pleistocene. *Episoriculus macrurus* BLANDFORD, 1888 is smaller in comparison with the extant European species, and there is occasional overlap with *Neomys milleri*. Its size is comparable to *Asoriculus* or Q 2 *Neomys*, while *Episoriculus leucops* HORSFIELD, 1855 is approximately of *Neomys fodiens* size (or exceeding it in some dimensions – e.g., pL, Cd1Cd2). Therefore, it exceeds all the fossil forms in terms of size, similarly to *Soriculus nigrescens*. Overall, even though we witnessed some overlap in particular measurements (esp. *E. macrurus* with *Asoriculus*), they differ considerably in combinations of characters.

We noticed several characteristics that are shared by all examined Asian species: (i) the upper sigmoid notch is shallow and round, (ii) the coronoid process is robust, especially in *Soriculus* but with the exception of *E. macrurus*, (iii) the entoconid is long (especially in *Soriculus*), but in *Episoriculus* it is not very significant, (iv) there are only three unicuspid teeth in the rostral part of the upper dentition (however, *Soriculus* carries a tiny residual Z4 on the palatal edge of the P, (v) the first two upper molars possess a peculiarly shaped hypocone with strengthened cingulum, which is notably distanced from protocone. Even though we do not have access to the upper dentition of *Asoriculus*, according to Reumer (1984), this is a trait clearly distinguishing *Asoriculus* from *Episoriculus* and *Soriculus*.

Discussion

Neomys during the Last Glacial Cycle

The scarcity of European fossil material together with the absence of reliable determination criteria represent a major setback, as it has often led to troubles with identification. Therefore, most of the specimens have been ascribed to *Neomys* sp. or very often *Neomys* cf. *fodiens*. However, relevant discrimination of most of the material is lacking, and the aspects of variability, especially the overlap between the two species, are barely considered.

As a result of the issues mentioned above, knowledge of the most recent history of genus *Neomys* is limited. Regarding the outcomes of our survey of extant populations, we analysed 58 Q 4 specimens from Czech and Slovak fossil sites. Our material showed extreme variability, especially regarding size and shape of the condylar process and both condylar facets (comp. Text-figs 6, 7, 10). We also observed differences in the shape of the coronoid process apex. Considering that most of our material was collected from taphocenoses by accumulation of owl pellets, it is possible that such differences are taphonomic artefacts. Besides that, our Q 4 material shows general similarities with the extant populations regarding basic dental characteristics.

In Europe, genus *Neomys* has been reported from 83 Holocene and Late Pleistocene (Q 4, Q 3/Q 4) localities of 18 countries (see SM:SF III for details). The earliest records are from the Q 3 biozone in Spain (Moya-Costa et al. 2023), three localities in France (Jammot 1977, Reumer 1996), one locality in Italy (Bartolomei and di Broglio 1964), Netherlands (van Kolfschoten 1990), Romania (Rădulescu and Samson 1992) (*N. fodiens*) and Austria (Rabeder 1972) (*N. milleri*). Generally, *Neomys fodiens* is considered a resident species in Central Europe since the Middle Pleistocene, while *anomalous-milleri* clade is expected to be distributed primarily in southern Europe, and to invade Central Europe only during few interglacial stages, including the Holocene (Rzebik-Kowalska 1998, Kryštufek et al. 2000, Castiglia et al. 2007, Anděra and Hanzal 2022).

A significant number of samples followed by detailed descriptions are presented in Rzebik-Kowalska (2006) from Komarowa Cave in Poland (*Neomys* cf. *fodiens* MNI = 16, *Neomys* sp. MNI = 2). While the specimens ascribed to *Neomys fodiens* seem to be more robust in comparison to our Q 4 material (even though their variance ranges overlap in all cases), the specimens identified as *Neomys* sp. are smaller: one mandible corresponds well to our Q 4 *N. fodiens* (p4L, m1L, CorH), the other fragment of a lower jaw presents similar metric characteristics to our recent and fossil *N. milleri*. Material from Ightham Fissures, Dogholes (Late Pleistocene) and Leasowe (Holocene) (both UK; Hinton 1911), all of them described as *Neomys fodiens*, are smaller than our Q 4 *Neomys fodiens* regarding height of the coronoid process and length of the molar row. A mandible from Bois Roche (France, MIS 4–5) described as *Neomys* cf. *fodiens* (Sesé and Villa 2008) possesses a longer premolar than our Q 4 *Neomys fodiens*. On the contrary, its width is moderate compared to our samples. The first two molars with small deviations correspond to our material in their lengths and widths. Both species were reported (as *N. cf. fodiens* and

N. cf. anomalous) from Grotta Maggiore di San Bernardino in Italy (MIS 3–7) (López-García et al. 2017), Höhle Fels in Germany (MIS 3–5; *N. cf. fodiens*, *N. cf. milleri*, *Neomys* sp.) (Luzi et al. 2022) and Grotta della Ferrovia in Italy (LGM; *N. cf. anomalous*, *N. fodiens*) (Ceregatti et al. 2023).

As seen from previous paragraphs, knowledge of the most recent history of genus *Neomys* is limited, mostly due to the absence of reliable determination criteria and fragmentary state of the record. However, by application of combined determination technique based on results of the biometric analysis of extant populations, we were able to identify 41% of the 58 Q 4 records with high degree of reliability. Even though fossil material of *Neomys* from this period is generally rare, so that it is not possible to make detailed conclusions, our survey denies the possibility that *Neomys milleri* represents an apochoric element invading Central Europe during the Late Holocene. Instead, we managed to prove the presence of both species in Central Europe during the Vistulian, in early units probably with higher abundance of *N. fodiens*, but even before the beginning of Holocene, *Neomys milleri* is also recorded, and becomes at least locally more abundant by the end of the Preboreal. We believe the two species coexisted in sympatry or parapatry during whole glacial cycle, even though their presence was probably mosaic-like in terms of both time and space. The significantly enlarged span of phenotype variation demonstrated for our Q 4 sample can be tentatively ascribed to the effects of character displacements accompanying the stages of sympatric occurrence.

Genus *Neomys* during the Early and Middle Pleistocene

Most of the European fossil record from late Biharian (Q 2) and early Toringian (Q 3) (Fejfar 1961, 1966, Maul 1990, Rzebik-Kowalska 1991, Rzebik-Kowalska 1994, Zaitsev and Baryshnikov 2002, Agadjanian and Kondrashov 2007, Maul and Parfitt 2010, Rzebik-Kowalska 2013, van Kolfschoten 2014, Rzebik-Kowalska and Rekovets 2016, Pazonyi et al. 2018) is ascribed to *Neomys newtoni*, a fossil species described from Upper Freshwater Beds at West Runton, type locality of the Cromerian fauna (Q 2). The chronological span of these records and the *Neomys newtoni* stage of the *Neomys* history can be estimated by the interval 1.2–0.4 Ma (MIS 28–12). In any case, *Neomys newtoni* represents the oldest form clearly affiliated to *Neomys*. After a detailed analysis of material from the Austrian Q 3 locality Hundsheim, Rabeder (1972) highlights the resemblance of this taxon with extant *N. anomalous/milleri*, even suggesting putative identity of *newtoni* and *N. anomalous/milleri*. Examining that (at first sight quite robustly supported) alternative, we confirmed that despite the overall resemblance, *N. newtoni* differs from *milleri* in more respects. A particularly broad phenotype variation seems to be a quite characteristic feature of this form. Demonstrating a normal statistical distribution in almost all characters in the entire set of respective specimens, we consider that all the items belong to a single clade, different from the extant *milleri*, i.e., *N. newtoni*. The span of phenotype variation suggests that *Neomys newtoni* may represent the source taxon of all recent species. The phylogenetic morphocline of *N. anomalous/milleri* would then be characterized by

stabilization of phenotype of the ancestor species, while that of *N. fodiens* was driven by enlarging of skull and dentition, extension of molariform teeth and strengthening of the distal part of the mandible.

Apart from *N. newtoni*, further three fossil species of the genus *Neomys* were reported from biozones Q 2 and Q 3: *N. intermedius* BRUNER, 1952, *N. hintoni* ZAITSEV et BARYSHNIKOV, 2002, and *N. browni* HINTON, 1911. *Neomys intermedius* is reported from two localities in Germany (Breitenberghöhle – Q 3 (Bruner 1957), Markgrabenhöhle – Q 3 (Bruner 1952)) and followed by an uninformative description that is not sufficient for exact diagnosis. *Neomys hintoni* is reported from three localities from Caucasus: Treugolnaya Cave – Q 3 (Zaitsev a Baryshnikov 2002), Mezmaiskaya Cave – Q 3 (Zaitsev a Osipova 2004), Haykadzor – Q 2 (Tesakov et al. 2019). Even though the description is detailed and exactly defines the traits of this taxon, its taxonomic relevance should be further confronted with detailed information on phenotype variation of related species and dynamics of their local divergences, which are unfortunately still not available in a proper extent. The same can be said about *Neomys browni*, reported from two localities in the United Kingdom (Grays Thurrock – Q 3 (Hinton 1911), Cudmore – Q 3 (Roe et al. 2009)), and diagnosed by a narrow and low coronoid process. With regards to a broad phenotype variation (also demonstrated in the present paper) as a characteristic feature of *N. newtoni*, we tend to consider *N. hintoni*, *N. intermedius* as the local forms of *Neomys newtoni*, alternatively *Neomys milleri* (pertinent in the case of *N. browni*).

Numerous hypotheses regarding history and range dynamics of *Neomys* were proposed based on methods of molecular phylogenetics and phylogeography, palaeontology and morphological similarities. Molecular phylogenetics establishes the interval of divergence of the extant species between 0.4 and 1.6 Ma.

According to Igea et al. (2015), *Neomys fodiens* was the first species to diverge (around 1.22 Ma), being the sister group of the rest of the species. Colonization of Europe during the Early Pleistocene followed by rapid expansion to northern and central European regions is presumed by Rzebik-Kowalska (1998) and Castiglia et al. (2007). According to Igea et al. (2015), *Neomys teres* separated from the common ancestor of *N. milleri* and *N. anomalus* 0.56 Ma. *N. teres* and *N. anomalus/milleri* could represent two lineages that survived Quaternary climatic oscillations in southern refugia: *N. teres* in Anatolia and *N. anomalus* on the Iberian Peninsula (Castiglia et al. 2007). This agrees with one of the hypotheses presented by Kryštufek et al. (2000), who assume that the common ancestor of *Neomys milleri* and *Neomys anomalus* crossed the Bosphorus and colonized Anatolia during one of the glacials. Part of the population stayed in the region south from the Black Sea and later evolved in *Neomys teres*. An alternative hypothesis assumes expansion of *Neomys fodiens* during a cold period southwards across Balkan-Anatolian bridge, followed by a return northward during an interglacial. The authors presume that one population was isolated in the Pontic mountains, where it evolved into *N. teres*. The population living along the land bridge evolved into the ancestor of *N. milleri/teres* (Kryštufek et al. 2000). Based on morphologic features, the

same authors present a third hypothesis: the possibility of expansion of *N. fodiens* along the shore of the Black Sea to Caucasus and the Pontic mountains, where as a result of allopatric speciation, it evolves into *N. teres*. However, this hypothesis does not correspond to the results of molecular genetics, hence Kryštufek et al. (2000) as well as Castiglia et al. (2007) and Igea et al. (2015) consider the possibility of *N. fodiens* diverging first and being the sister taxon of the rest of the species the most probable. On the contrary, *Neomys milleri* would be a relatively recent taxon.

According to Castiglia et al. (2007), expansion of *Neomys fodiens* was faster in comparison to *Neomys anomalus/milleri*, due to *N. fodiens* possessing more developed adaptations to a challenging environment. Climatic oscillations would have had a more serious impact on the latter species. According to Castiglia et al. (2007), the *N. anomalus-milleri* clade shows a considerably higher degree of divergence. According to mitochondrial phylogenetics, *N. anomalus* comprises the population inhabiting the central region of the Iberian Peninsula, and *N. milleri* the rest of European population, including northeast of the Iberian Peninsula. These two lineages would have diverged 0.4 Ma, with a deviation 0.26–0.86 million years – in other words, during the Middle or Late Pleistocene (Igea et al. 2015). According to the authors, it is probable that *N. anomalus* evolved on the Iberian Peninsula during one of the Middle Pleistocene glacials, while *N. milleri* colonized the Pyrenees only during the latest Pleistocene or Holocene.

The fossil record does not support hypotheses about older origins of *N. fodiens* and later divergence of *N. milleri*. The presence of *N. fodiens* in Europe is not proved until the Middle Pleistocene age (a few records, biozone Q 3); most of the records are dated to the present cycle (biozone Q 4). The hypothesis by Rzebik-Kowalska (1998) assuming colonization of Europe by *N. fodiens* during the Early Pleistocene still lacks any support from the actual fossil record. Considering its phenotype constitution, *N. milleri* can undoubtedly be regarded as the form retaining plesiomorphic patterns of the genus (comp. e.g., less reduced distal molars), while *N. fodiens* exhibits a derived state in most of the phenotype variables.

It cannot be ruled out that the increase of *N. fodiens* size was related to the disappearance of another large shrew, *Macroneomys brachygnathus*, during early Toringian. The earliest records positively representing *Neomys fodiens* are reported from the Iberian Peninsula (TD10 in Atapuerca, 370 ka; Moya-Costa et al. 2023). The respective specimens exceed the limits of our extant samples, particularly with the specimens (from the same layer) identified as “*Neomyini* cf. *Macroneomys*”. These extremely large phenotypes correspond to the extant Iberian form, *Neomys fodiens niethammeri*, which shows – against expectancy – only shallow genetic differences from other extant populations of the species (Balmori-de La Puente et al. 2019).

Between-genera relations of mid-European Nectogalini

Genus *Asoriculus*, the ancestral taxon of European Nectogalini, has previously been frequently synonymized with genera *Soriculus* and *Episoriculus* (Repenning 1967). In agreement with conclusions by Hutterer (1994), our

analyses supported close relations between *Asoriculus* and *Neomys*, and the distant position of that European clade from the extant Oriental genera. Despite overlaps in some of the dimensions (especially concerning *Episoriculus macrurus* and *Asoriculus*), bivariate comparison of the variables shows clear differences between the OTUs. Moreover, representatives of the Oriental group express clear differences from the European taxa in various non-metric traits (absence or reduction of Z4, shape of hypocone and modification of its cingulum). All these differences demonstrate *Asoriculus-Neomys* as a single clade of the European radiation, distinctly separated from phylogenetic dynamics of the Oriental clades (notwithstanding *Nesiotites* and *Macroneomys*, both showing relations to extant *Soriculus*).

Asoriculus appeared in the European fossil record since the earliest Late Miocene (MN 11), and was reported from many sites until Early Pleistocene (Q 1). The oldest specimens come from two localities in Ukraine (Rzebik-Kowalska and Rekovets 2016), and despite several differences from Pliocene representatives (double foramen mentale etc.), are assigned to the genus *Asoriculus*. As *A. gibberodon*, the genus is reported almost from all Pliocene small mammal communities throughout Europe. Yet in those of the earliest Pleistocene age, its records are rather rare, obviously due to its range retreat during glacial stages. The scarce records of that time suggest its survival in the southern European region (Jammot 1977, Koufos et al. 2001, Kotsakis et al. 2003, Rofes and Cuenca-Bescós 2006, Agustí et al. 2010, Furió and Angelone 2010, Siori et al. 2014, Moya-Costa et al. 2023), including, at least temporarily, also the southern areas of Central Europe (Fejfar and Horáček 1983, Reumer 1984, Jánossy 1986, Botka and Mészáros 2017, Pazonyi et al. 2018).

The last occurrences of *Asoriculus* s. str. are dated to time of the Q 1/Q 2 boundary, with the latest individuals recorded from the Hungarian site Somssich Hill (Somssichhegy) (Botka and Mészáros 2017, Reumer 1984) and in Spanish Atapuerca cave, Gran Dolina TD5-6, 0.73–0.9 Ma (Cuenca-Bescós et al. 2010, Moya-Costa et al. 2023). Similarly to Żabia Cave (middle Q 1) in Poland (Rzebik-Kowalska 2013), in all these sites, the remains assigned to *Asoriculus* appeared simultaneously with those identified as *Neomys newtoni*. Perhaps in reference to the expected early ancestry of *Neomys*, supported by predictions of molecular phylogenetics, the above-cited authors tend to emphasize a hypothesis on a long-lasting parallel occurrence of both clades.

Rzebik-Kowalska (2013) proposed as discrimination criteria (i) a narrow interarticular facet in *Asoriculus gibberodon*, (ii) absence of tooth pigmentation in *Asoriculus*, and (iii) different shape of the lower incisor, particularly the ratio between total length and the distance from apex to primary cuspid (*Asoriculus* 2.72–3.38, *Neomys* under 2.5). However, our material suggests a broad overlap between *Asoriculus* and *Neomys* in all these characters (see Text-fig. 10; numerous extant *N. fodiens* with the index > 2.5, etc). The specimens from Q 1 Atapuerca, Trincheras del Elephante (Rofes and Cuenca-Bescós 2006) are also worth mentioning in this context. They exhibit, compared to *A. gibberodon*, a dorsally tapered coronoid process and distinctly pronounced high position of the upper articulation condyle. Both these arrangements are obviously related to the enlarged biting

force of incisor occlusion, the phenotype shift which seems to be quite a characteristic component of the *Asoriculus-Neomys* transition.

In short, we found little support for the hypothesis on long lasting parallel occurrence of *Asoriculus* and *Neomys*, terminated by the extinction of *Asoriculus* in the end of biozone Q 1 (as expected, e.g., by Rofes and Cuenca-Bescós 2006).

A pronounced disposition of the Early Pleistocene *Asoriculus* to enlarged phenotype variation (indicated, e.g., by appearance of novel local forms in the Mediterranean region – *A. thenii*, *A. burgioi*, *A. maghrebiensis*) suggests rather a possibility of a dynamic rearrangements, attaining with the *Neomys*-like phenotype an adaptive response to the environmental changes accompanying that period. Taking into account that phenotype differences between *Asoriculus* and *Neomys* are, in general, rather of a stochastic than categorical nature, and a mosaic pattern in the state of concerned characters observed in specimens of the Early Pleistocene age (besides a few of those which can be directly identified either with *Asoriculus* or *Neomys*), it seems reasonable to consider the Nectogalini populations of that time as belonging to a single transitional clade. Unfortunately, the European fossil record is still too fragmentary to allow testing similar hypotheses by reliable empirical evidence.

This also applies for real phenotype characteristics of individual fragmentary items, including type of *Neomys castellarini* PASA, 1947, otherwise *Asoriculus castellarini* after van der Meulen (1973) or Fejfar and Horáček (1983), the form providing a priority name for the presumed transient taxon.

Tentatively, our conclusions can be summarized as follows. (i) The ancestral clade of the W-Palearctic radiation, *Asoriculus gibberodon*, representing a constant element of the European Pliocene communities, bears all main apomorphies of the tribe, and was disposed to a broad phenotype variation (Reumer 1984, Popov 2003, a.o.), well-marked particularly in its MN 17 – Q 1 record. (ii) In that time, a tendency to strengthen biting force at incisor occlusion (cf. prolongation of the mandibular incisor) and mastication versatility (with higher position of dorsal articulation condyle), both associated with dorsal tapering of coronoid process, become particularly pronounced. (iii) It marked a transitional state from *Asoriculus* to *Neomys* phenotypes, which was supposedly retained together with a broad phenotype variation throughout the whole Early Pleistocene. (iv) The early stage, with prevalence of plesiomorphic constitutions can be taxonomically separated as *Asoriculus castellarini*; the later stage, in which the *Neomys*-like phenotype predominated can be then co-identified with a Q 2 taxon, *Neomys newtoni*. (v) The divergence of extant clades, i.e., *Neomys anomalus-milleri* and *Neomys fodiens* is supposed to have arisen from that transitional stage. Yet to hypothesize on the background paleogeographic and ecological factors that did actually drive the divergences is still, due to a lack of real records, considerably beyond scope of this study.

In any case, in central Europe, both extant species probably occurred during the Middle Pleistocene, and certainly throughout the Late Pleistocene and Holocene, in sympatry, at least temporarily.

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Supplementary material

- SM:SF I: List of the variables and corresponding factor loadings included in PCA analyses 2–6.
- SM:SF II: Detailed account of biometric data of particular OTUs.
- SM:SF III: Survey of European fossil records of Nectogalini (except for *Macroneomys* and *Nesiotites*), based on literary resources.

Explanations of the plates

PLATE 1

Neomys fodiens, Recent, Czech Republic, upper dentition

1. Occlusal view.
2. Lateral view.
3. Mesial view of incisors.

Neomys fodiens, Recent, Czech Republic, mandible

4. Lateral view.
5. Lingual view.
6. Occlusal view.

PLATE 2

Neomys milleri, Recent, Czech Republic, upper dentition

1. Occlusal view.
2. Lateral view.
3. Mesial view of incisors.

Neomys milleri, Recent, Czech Republic, mandible

4. Lateral view.
5. Lingual view.
6. Occlusal view.

PLATE 3

Neomys teres, Recent, Turkey, upper dentitions

1. Occlusal view.
2. Lateral view.
3. Mesial view of incisors.

Neomys teres, Recent, mandibles

4. Lateral view.
5. Lingual view.
6. Occlusal view.

PLATE 4

Neomys samples from current glacial cycle (Q 4)

1. *N. milleri*, Peskö 6. a: lateral view, b: lingual view, c: occlusal view.
2. *N. fodiens*, Peskö 8. a: lateral view, b: condylar process.
3. *N. cf. fodiens*, Peskö 12. a: lateral view, b: lingual view, c: condylar process.
4. *N. fodiens*, Býčí skála /D5b (“Býčí 8”). a: lateral view, b: lingual view, c: condylar process.
5. *N. fodiens*, Červeného muže /5. a: lateral view, b: condylar process.

PLATE 5

Our oldest record of *N. milleri* (Q 4w1), *N. newtoni* (Q 2) and *Asoriculus castellarini/Neomys newtoni* (Q 1)

1. *N. milleri*, Chlum 7. a: lateral view, b: lingual view, c: condylar process.
2. *N. newtoni*, Dobrkovice 2. a: lateral view, b: lingual view, c: condylar process.
3. *N. newtoni*, Koněprusy C718. a: lateral view, b: lingual view, c: occlusal view, d: condylar process.
4. *A. castellarini/N. newtoni*, Včeláře 6/7. a: lingual view, b: condylar process.

PLATE 6

Nectogalini of the Early Pleistocene age, MN 17 – Q 1

1. *Asoriculus gibberodon*, Koliňany. a: lateral view, b: lingual view, c: condylar process.
2. *A. gibberodon*, Včeláře 6/1. a: lateral view, b: lingual view, c: condylar process.
3. *A. castellarini*, Včeláře 3. a: lateral view, b: lingual view, c: occlusal view, d: condylar process.

Nectogalini of Pliocene age, MN 15 – MN 16

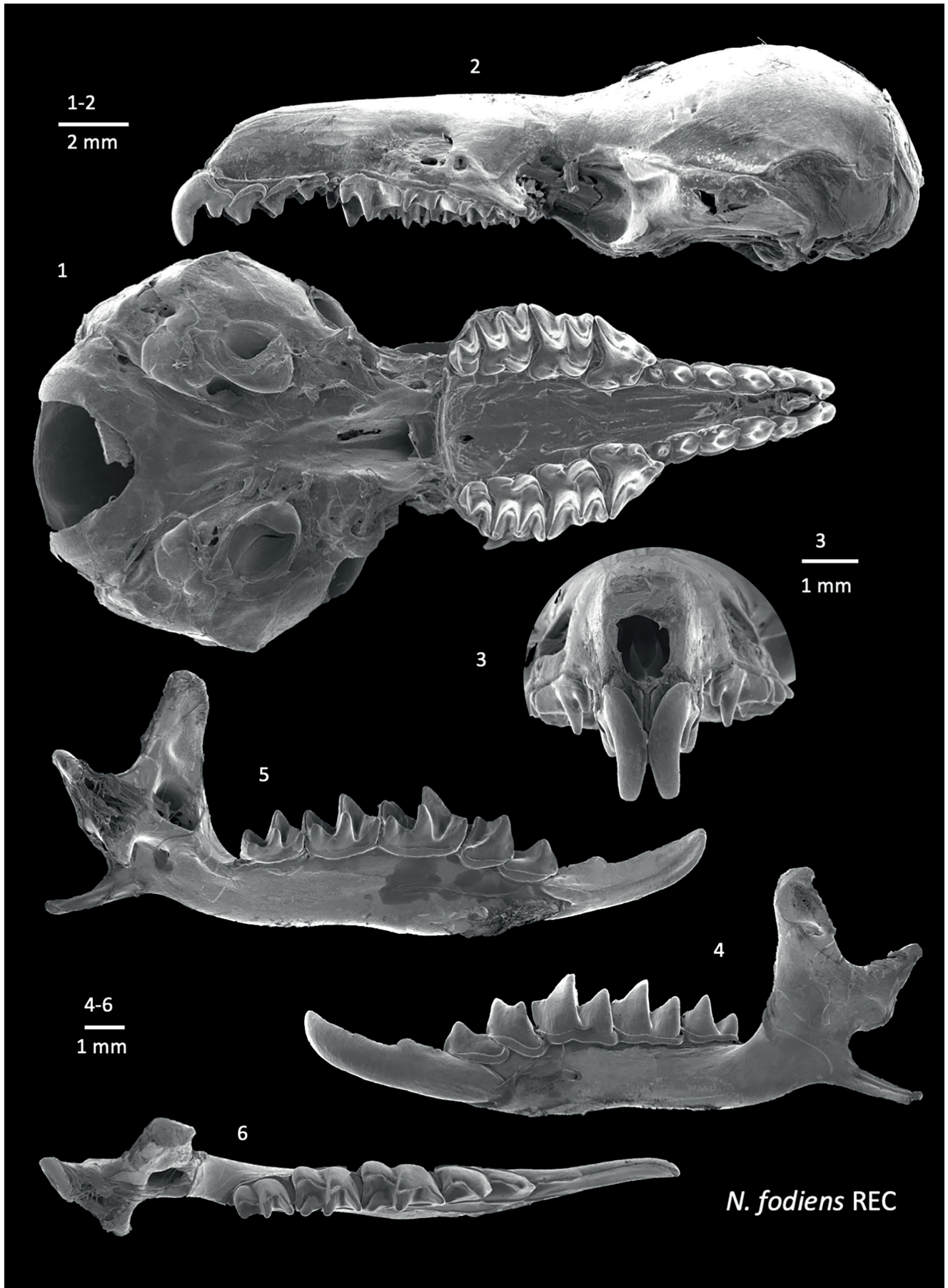
4. *A. gibberodon*, Javoříčko 11. a: lateral view, b: lingual view, c: occlusal view, d: condylar process.
5. *A. gibberodon*, Ivanovce. a: lateral view, b: lingual view, c: occlusal view.

PLATE 7

Representatives of Oriental genera *Episoriculus* and *Soriculus*

1. *Episoriculus leucops*, Nepal. a: lateral view, b: lingual view, c: occlusal view, d: condylar process.
2. *Episoriculus macrurus*, Nepal. a: lateral view, b: lingual view, c: occlusal view, d: condylar process.
3. *Soriculus nigrescens*, Nepal. a: lateral view, b: lingual view, c: occlusal view, d: condylar process.

PLATE 1



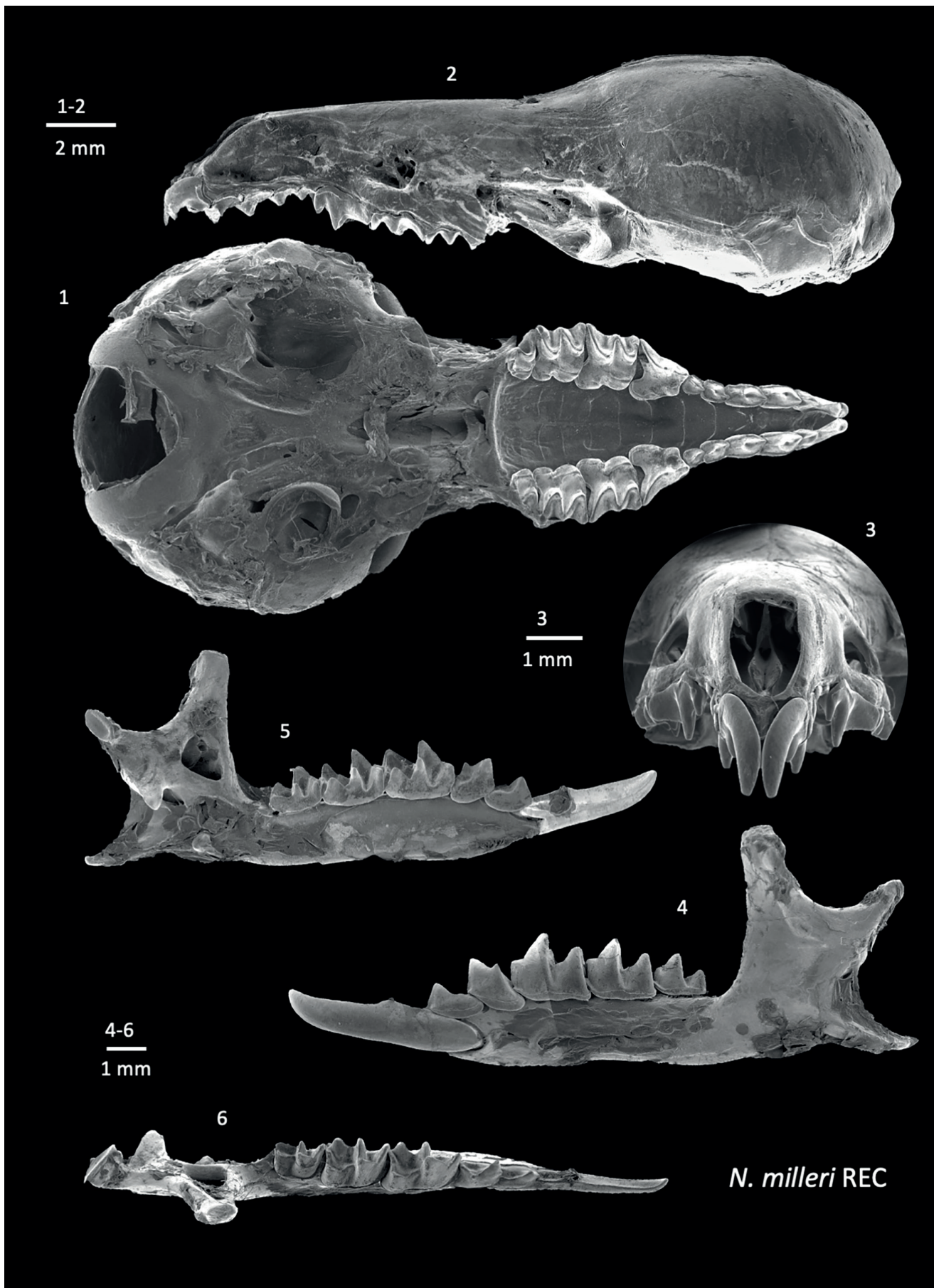


PLATE 3

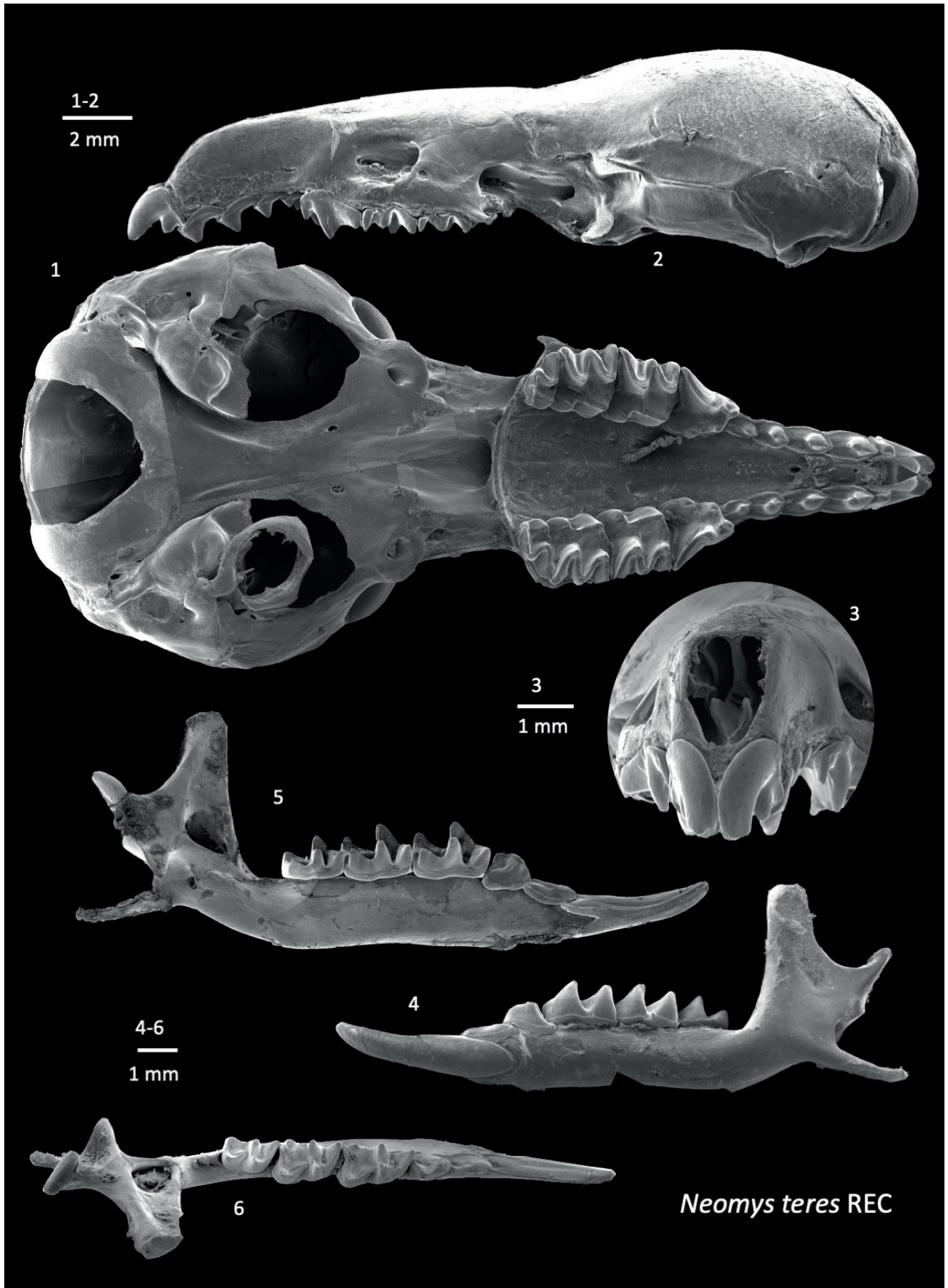
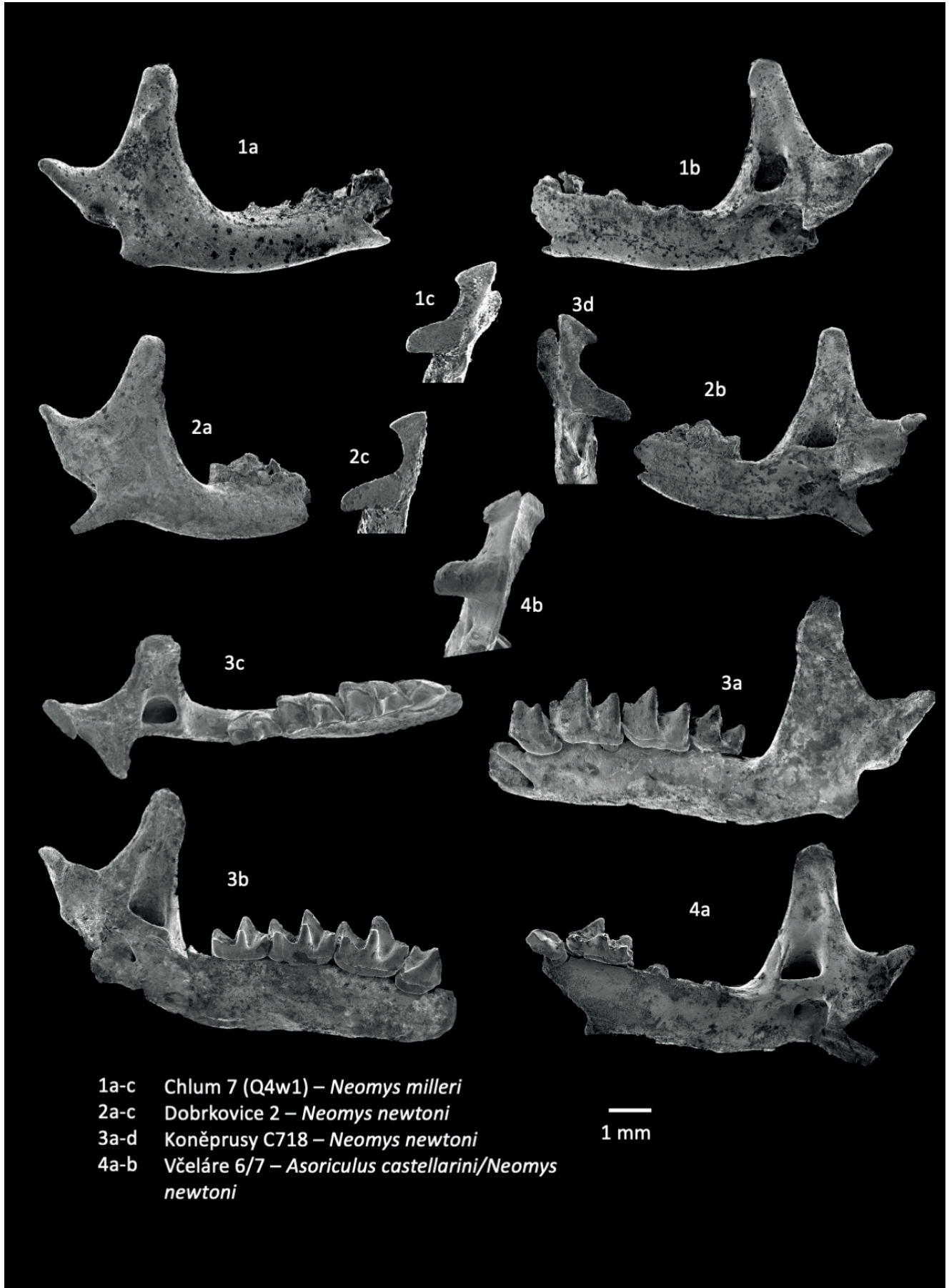




PLATE 5



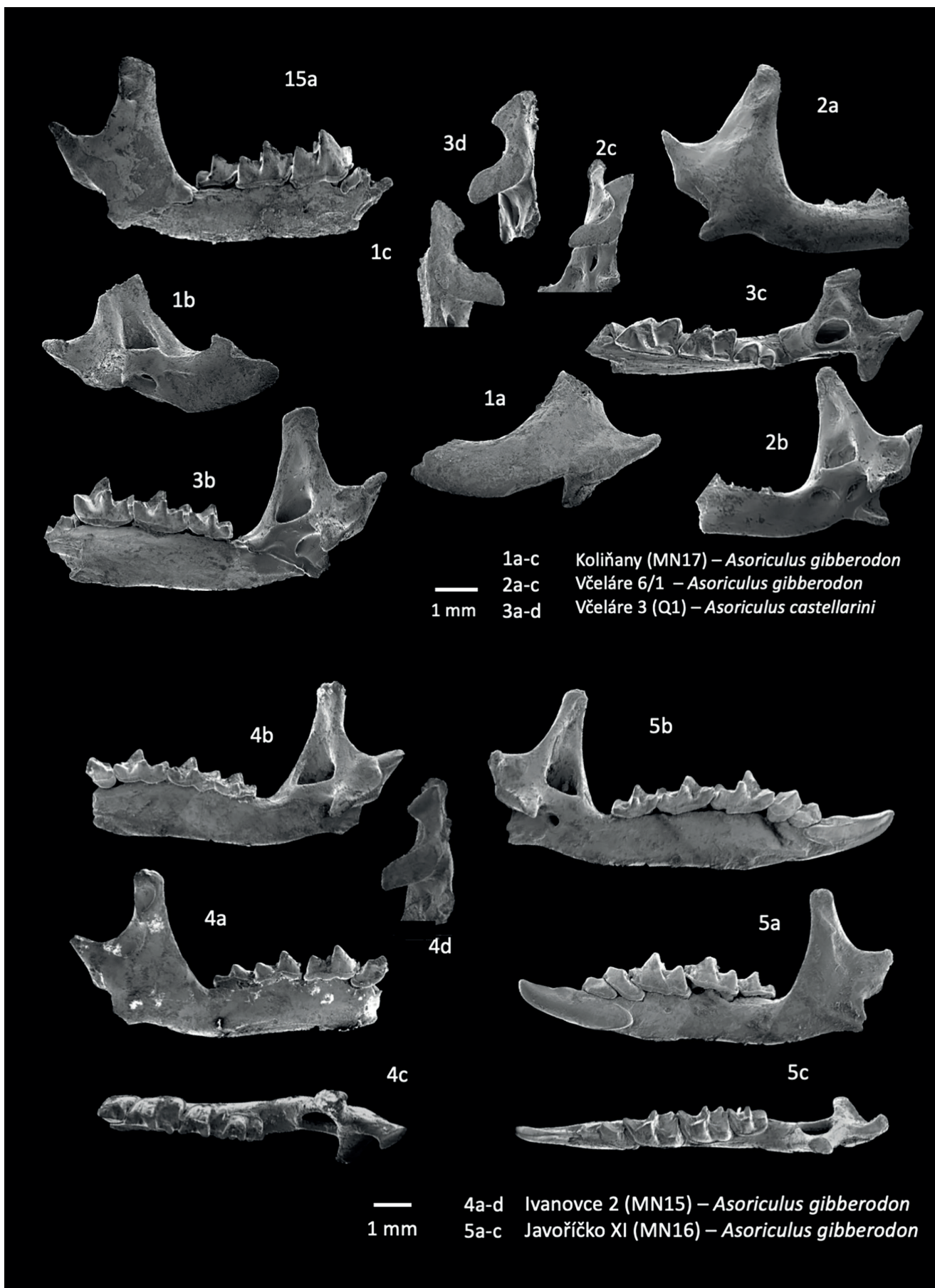
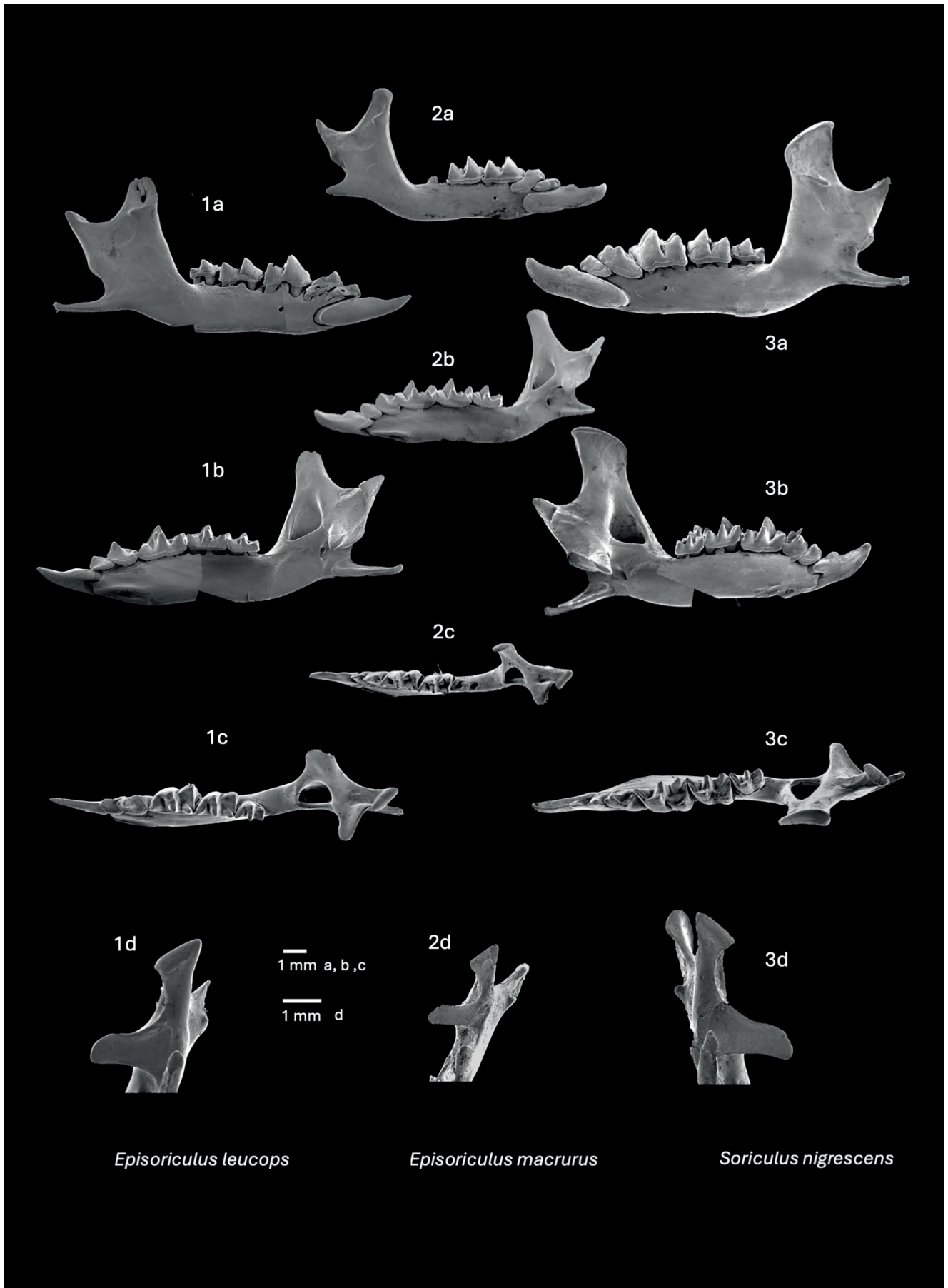


PLATE 7



Appendix

Landmarks and metric dimensions applied in the present study

Positions of landmarks are demonstrated below in Text-figs A1–A5. The following list provides a brief account of the linear dimensions applied in this study (in terms of distances between landmarks denoted by the numbers, as in the Text-figs A1–A5). The landmarks 1–4 refer to cranial characters not available in fossil record.

A: Rostral variables (Text-fig. A1)

I1I1: width incisor-incisor: 5-6 * Z1Z1: width unicuspl-unicusp1: 7-8 * Z2Z2: width unicuspl2-unicusp2: 9-10 * Z3Z3: width unicuspl3-unicusp3: 11-12 * Z4Z4: width unicuspl4-unicusp4: 13-14 * P4P4: width premolar-premolar: 15-16 * M1M1: width m1-m1: 17-18 * M2M2: width m2-m2: 19-20 * M3M3: width m3-m3: 21-22 * LPal1: palatal length (short, up to the boarder of Z1Z2, perpendicular to W1): 23-24 * LPal2: palatal length (long, up to the boarder of Z1Z2, perpendicular to W2): 23-25 * LpalI1: palatal length up to the cusp of I1: 24-26 * IP4: incisor-premolar: 26-27 * IM1: mesial margin of the incisor to bucco-distal margin of M1: 26-28 * IM2: mesial margin of the incisor to bucco-distal margin of M2: 26-29 * IM3: mesial margin of the incisor to bucco-distal margin of M3: 26-30 * P4M1: P4 to M1: 31-28 * P4M2: P4 to M2: 31-29 * P4M3: P4 to M3: 31-30 * M1M2: 1st-2nd molar: 27-29 * M1M3: 1st-3rd molar: 27-30 * M2M3: 2nd-3rd molar: 28-30 * LUni: length of the unicuspid row (I1-Z4): 26-32 * Lmol: length of the molariform row (P4-M3): 31-30 *

B: Mandibular variables (Text-fig. A1)

Cr1: coronoid process: width of the tip: 33-34 * Cr2: coronoid process: tip: 33-35 * Cr3: coronoid process: tip: 33-36 * Cr4: coronoid process-spicule: 33-37 * Cr5: coronoid process-level of the spicule: 33-38 * CdL (lat): condyle length: 39-40 * CdH1: condyle height: 39-41 * CdH2: condyle height: 40-41 * AngL: length of the angular process: 42-43 * RmL: length of the horizontal ramus (from the lower sigmoid notch): 43-44 * CorH: of the coronoid process: 42-33 * FM: Base of the coronoid and angular process to mental foramen: 42-45 * Lz1-m3: z1-m3 length: 46-47 * Hmd: height of the mandible (level of the m2): 48-49 * Lzp: length z1+p4: 46-50 * m1m3: length of the molar row: 50-47 * CdL(ling): length of the condylar process: 51-52 * CdH: upper condylar facet to angular process base: 52-53 * RM1: Ascending ramus width (up to the upper cond. facet): 54-52 * RM2: ascending ramus width (up to the lower cond. facet): 54-55 * RM3: ascending ramus width (up to the lower sigmoid notch): 54-56 * CrH1: height of the coronoid process (base of PAng to tallest point of PCor): 53-57 * CrH2: height of PCor from the base of PAng: 53-58 * CrH3: height of PCor from the base of PAng: 53-51 * CrH4: height of PCor from the level of the tooth row: 54-57 * CrH5: height of PCor from the level of the tooth row: 54-58 * CrH6: height of PCor from the level of the tooth row: 54-51 * mdL1: length i1-point1 (upper facet): 59-52 * mdL2: length i1-point2 (lower facet): 59-55 * mdL3: length i1-point3 (upper sigmoid notch): 59-51 * mdL4: length i1-

point4: 59-54 * mdL5: length i1-point5 (base of PAng): 59-53 * mdL1m1: length m1-1: 60-52 * mdL2m1: length m1-2: 60-55 * mdL3m1: length m1-3: 60-51 * mdL4m1: length m1-4: 60-54 * mdL5m1: length m1-5: 60-53 * mdL1m2: length m2-1: 61-52 * mdL2m2: length m2-2: 61-55 * mdL3m2: length m2-3: 61-51 * mdL4m2: length m2-4: 61-54 * mdL5m2: length m2-5: 61-53 * mdL1m3: length m3-1: 62-52 * mdL2m3: length m3-2: 62-55 * mdL3m3: length m3-3: 62-51 * mdL4m3: length m3-4: 62-54 * mdL5m3: length m3-5: 62-53 * symfL: length of the symphysis: 63-59 * symfW: width of the symphysis: 64-65 * CrW1: PCor width: 57-58 * CrW2: PCor width: 66-67 * fpL: length of the pterygoid fossa: 68-69 * fpH: height of the pterygoid fossa: 70-71 * mdH1: Mandible height (m1): 72-73 * mdH2: Mandible height (m2): 74-75 * mdH3: Mandible height (m3): 76-77 * Cd1Cd2: height of the condyle: 78-79 * Cd1Cd3: height of the condyle: 78-80 * Cd1Cd10: width of the upper facet: 78-87 * Cd4Cd5: width of the lower facet: 81-82 * Cd6Cd7: height of the lower facet: 83-84 * Cd8Cd9: width of the interarticular area: 85-86 *

C: Maxillary unicuspid (Text-fig. A2)

I1I1: length of I1: 88-89 * LZ1: length of Z1: 89-90 * LZ2: length of Z2: 90-91 * LZ3: length of Z3: 91-92 * LZ4: length of Z4: 92-93 * I1W1: I1 width: 94-95 * I1W2: I1 width: 96-97 * I1W3: I1 width: 98-99 * Z1W: Z1 width: 100-101 * Z2W: Z2 width: 102-103 * Z3W: Z3 width: 104-105 * Z4W: Z4 width: 106-107 * Z1Lx: Z1 diagonal: 108-109 * Z2Lx: Z2 diagonal: 110-111 * Z3Lx: Z3 diagonal: 112-113 * I1_2: I1: length of the apex: 114-115 * I1_3: I1: length of the distal apex (talon): 114-116 * I1_4: length I1 up to the contact point with z1: 114-117 * I1dist_1: apex of the talon to contact point of the cusps: 118-116 * I1dist_2: apex of the talon to contact point with z1: 116-117 * I1dist_3: width of the secondary apex (talon): 118-117 * WZ1: width of Z1: 117-119 * WZ2: width of Z2: 119-120 * WZ3: width of Z3: 120-121 * WZ4: width of Z4: 121-122 * H1I: incisor height: 127-128 * W1I: incisor width: 129-130 *

D: Maxillary molars (Text-figs A2, A3)

P4: width of P4: 122-123 * WM1: width of M1: 123-124 * WM2: width of M2: 124-125 * WM3: width of M3: 125-126 * LP4: length of the premolar: 133-134 * LM1: length of M1: 134-135 * LM2: length of M2: 135-136 * LM3: length of M3: 137-138 * P4W1: P4 width (parastyle+protocone): 133-139 * P4W1x: P4 width (parastyle+hypocone): 133-140 * P4W2x: P4 width (parastyle-distal edge of the hypocone): 133-141 * P4Wdi: Posterior emargination to distal tip of the paracone: 134-142 * P4W2: P4 width: 134-140 * P4Lc: Paracone: distal tip to cusp: 134-143 * P4Lx: P4 length (posterior emargination-parastyle): 142-133 * M1W1: M1 width: parastyle-protocone: 134-144 * M2W1: M2 width: parastyle-protocone: 135-145 * M1W2: M1 width: metastyle-hypocone: 135-146 * M2W2: M2 width: metastyle-hypocone: 136-147 * M1W1x: M1: parastyle-metaloph: 134-148 * M2W1x: M2: parastyle-metaloph: 135-149 * M1W2x: M1: parastyle to hypoconal edge of the molar: 134-150 * M2W2x: M2: parastyle to hypoconal edge of the molar: 135-151 * M1Lx: M1 length (level of the posterior emargination): 152-153 * M2Lx: M2 length (level of the posterior emargination): 154-155 * M1PaL: parastyle-

mesostyle M1: 156-157 * M2PaL: parastyle-mesostyle M2: 158-159 * M1MeL: mesostyle-metastyle M1: 157-158 * M2MeL: mesostyle-metastyle M2: 159-160 * M1PaC: mesostyle-paracone M1: 157-161 * M2PaC: mesostyle-paracone M2: 159-163 * M1MeC: mesostyle-metacone M1: 158-162 * M2MeC: mesostyle-metacone M2: 160-164 * M3W1: M3 width: 136-165 * M3Lx: length of M3 buccal margin: 136-138 *

E: Mandibular unicuspid (Text-figs A3, A4)

i1Lx: i1: tip of the incisor to lower notch (under the secondary cusp): 166-167 * i1L: i1 length: 166-168 * i1Lprim: i1: length of the primary cusp: 166-169 * i1Lsek: i1: length of the secondary cusp (from the connection point with the primary cusp to the tip of the secondary cusp): 169-170 * z1L: z1 length: 171-172 * pL: Premolar length: 173-174 * i1Lc: length i1 base to cusp: 168-170 * i1H1: i1 height: 170-167 * i1H2: i1 height: 171-175 * z1H1: Z1 height (cusp): 176-177 * z1H2: z1 height: 173-178 * pH: Premolar height: 179-172 * Hcingz1: z1: cingulum height: 180-181 * Hcingp: p4: cingulum height: 172-182 * i1L (occ): i1 length: 183-184 * z1L (occ): z1 length: 184-185 * pL (occ): p4 length: 185-186 * z1W (occ): z1 width: 187-188 * pW (occ): p4 width: 189-190 *

F: Mandibular molars (Text-figs A3, A4)

m1L: m1 length: 174-191 * m2L: m2 length: 191-192 * m3L: m3 length: 192-193 * HCingm1: height of the cingulum of m1: 194-195 * HCingm2: height of the cingulum of m2: 196-197 * HCingm3: height of the cingulum of m3: 198-199 * HTrm1: m1: height of trigonid: 200-201 * HTal1: m1: height of talonid: 202-203 * HTrm2: m2: height of trigonid: 204-205 * HTal2: m2: height of talonid: 206-207 * HTrm3: m3: height of trigonid: 208-209 * HTal3: m3: height of talonid: 210-211 * TrLm1: length of the trigonid of m1: 212-213 * TalLm1: length of the talonid of m1: 213-214 * TrWm1: width of the trigonid of m1: 213-215 * TalWm1: width of the talonid of m1: 214-216 * TrLm2: length of the trigonid of m2: 217-218 * TalLm2: length of the talonid of m2: 218-219 * TrWm2: width of the trigonid of m2: 218-220 * TalWm2: width of the talonid of m2: 219-221 * TrLm3: length of the trigonid of m1: 222-223 * TalLm3: length of the talonid of m1: 223-224 * TrWm3: width of the trigonid of m3: 223-225 * TalWm3: width of the talonid of m3: 224-226 * Wm1Tal: talonid width: entostylid to buccal cingulum of m1: 214-227 * Wm2Tal: talonid width: entostylid to buccal cingulum of m2: 219-228 * m1l (occ): m1 length: 212-214 * m2L (occ): m2 length: 217-219 * m3L (occ): m3 length: 222-224 * m1W (occ): m1 width: 213-229 * m2W (occ): m2 width: 218-230 * m3W (occ): m3 width: 223-231 *

G: Pigmentation of maxillary dentition (Text-fig. A5)

I1_1: length of I1 from upper base down to the upper edge of the pigment: 232-233 * I1pigm: distance between the upper edge of the pigment and tip of the incisor (buccal view): 233-234 * HI1pigm: distance between the upper edge of the pigment and tip of the incisor (front view) *

H: Pigmentation of mandibular dentition (Text-fig. A5)

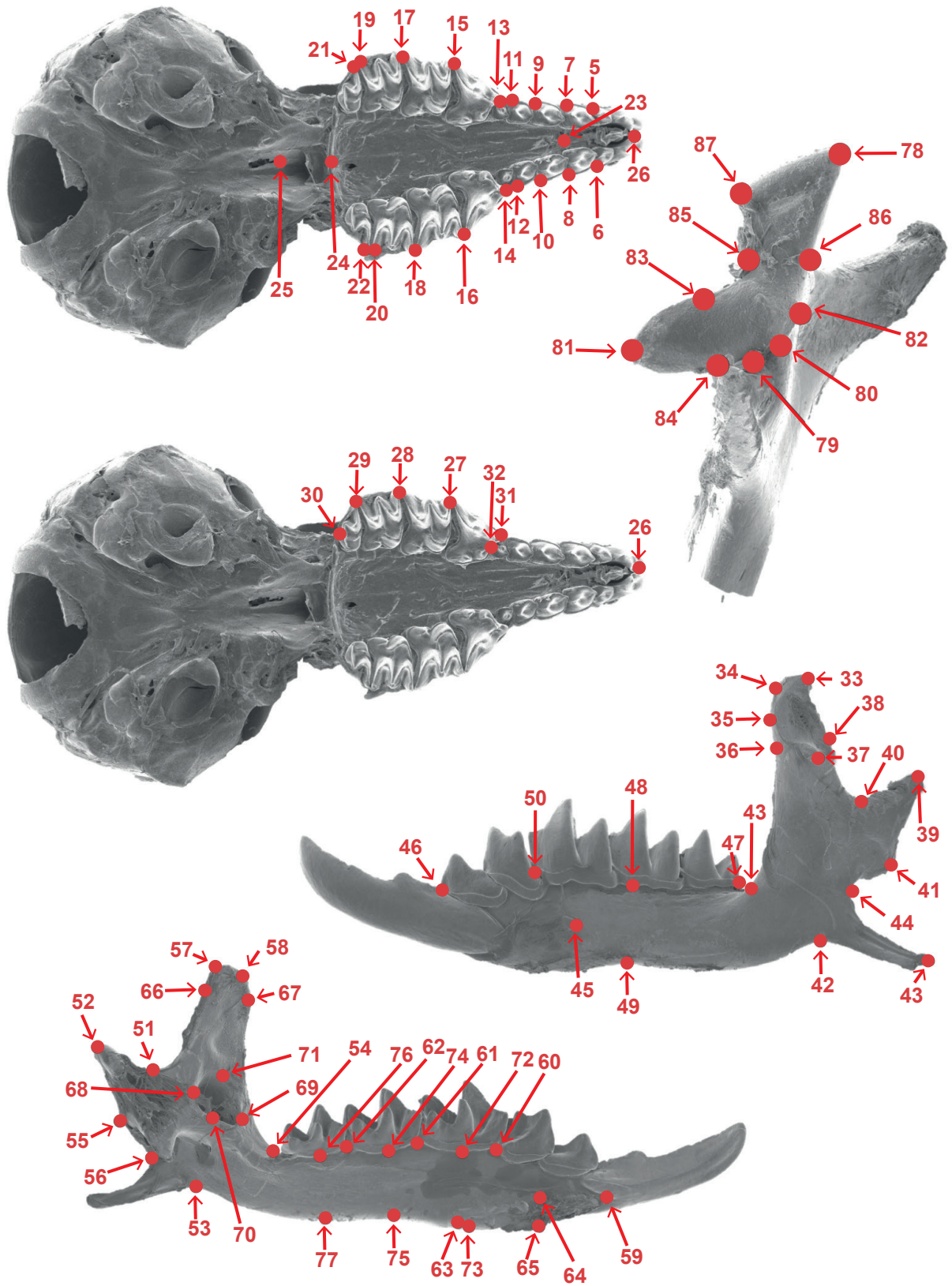
I1RPigm: tip of the i1 – connecting point of the ridge and pigment: 237-238 * pigmpH1: premolar pigment height

(front tip): 239-240 * pigmpH2: premolar pigment height (caudal tip): 240-241 * HPigmTrm1: pigmentation of the trigonid of m1 * HPigmTalm1: pigmentation of the talonid of m1: 244-245 * HPigmTrm2: pigmentation of the trigonid of m2: 246-247 * HPigmTalm2: pigmentation of the talonid of m2: 248-249 * HPigmTrm3: pigmentation of the trigonid of m3: 250-251 * PigmTalm1: width of pigmentation on the hypoconid edge (m1, occlusal view): 252-253 * PigmTalm2: width of pigmentation on the hypoconid edge (m2, occlusal view) 254-255 *

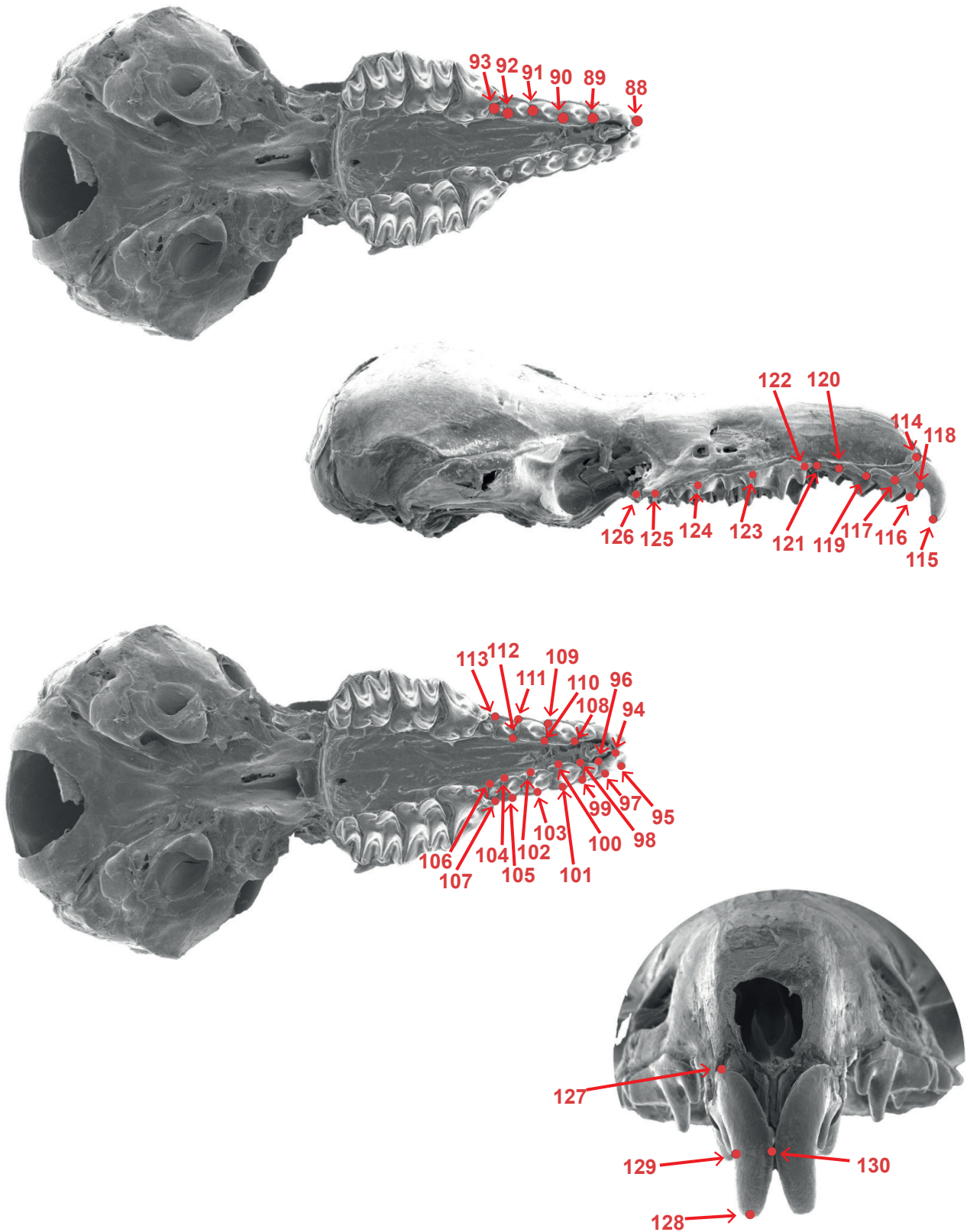
Metric proportions (not demonstrated in the figures)

Maxillary: LUni/Lmol: length of the unicuspid row/length of the molar row: 26-32/30-31 * M1/M13: length of M1/length of the molar row: 134-135/30-31 * M2/M13: length of M2/length of the molar row: 135-136/30-31 * M3/M13: length of M3/length of the molar row: 137-138/30-31 * M3L/M1L: length of M3/length of M1: 137-138/134-135 * P4L/M2L: length of P4/length of M2: 133-134/135-136 * M22/M13: distance M2-M2/length of the molar row: 19-20/30-31 * M22/M3L: distance M2-M2/length of M3: 19-20/137-138 *

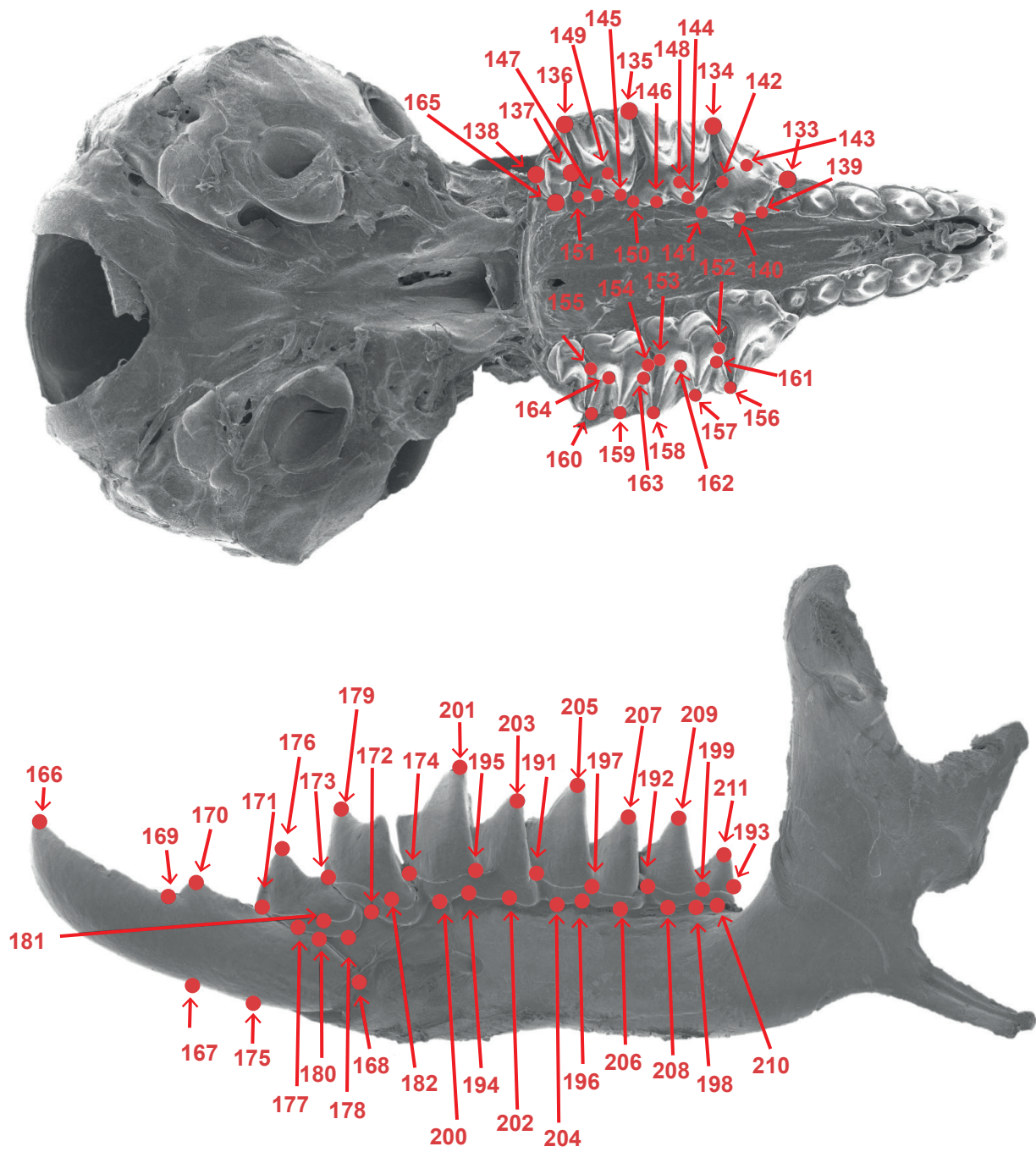
Mandibular: Lzp/mlm3: length f z1+p4/length of the molar row: 46-50/47-50 * m1/m13: length of m1/length of the molar row: 174-191/47-50 * m2/m13: length of m2/length of the molar row: 191-192/47-50 * m3/m13: length of m3/length of the molar row: 192-193/47-50 * tr/talLm1: trigonid/talonid length of m1: 212-213/213-214 * tr/talLm3: trigonid/talonid length of m3: 222-223/223-224 * talW/m1L: m1 talonid width/length of m1: 214-216/212-214 * talW/m2L: m2 talonid width/length of m2: 219-221/217-219 * talW/m3L: m3 talonid width/length of m3: 224-226/222-224 * talWm3/talWm1: m3 talonid width/m1 talonid width: 224-226/214-216 * pL/m1L: premolar length/length of m1: 185-186/212-214 * pL/m3L: premolar length/length of m3: 185-186/222-224 * CrH/m13: height of the coronoid process/length of the molar row: 33-42/47-50 * RM1/CrH: ascending ramus width up to the upper facet/height of the coronoid process: 52-54/33-42 * Cd12/CrH: condyle height/height of the coronoid process: 78-79/33-42 * Cd45/CrH: lower facet width/height of the coronoid process: 81-82/33-42 * Cd1cd10/Cd45: upper facet width/lower facet width: 78-87/81-82 *



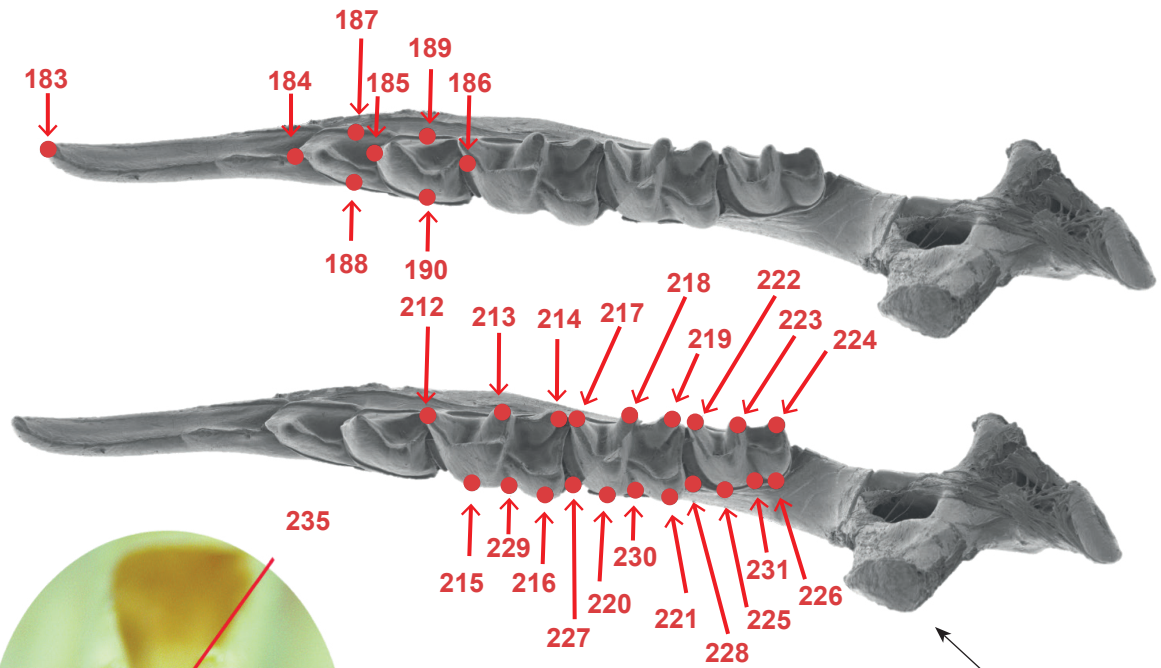
Text-fig. A1. Position of landmarks: A rostral 5–32, B mandibular 33–87.



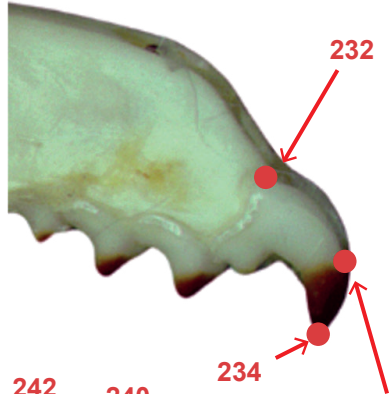
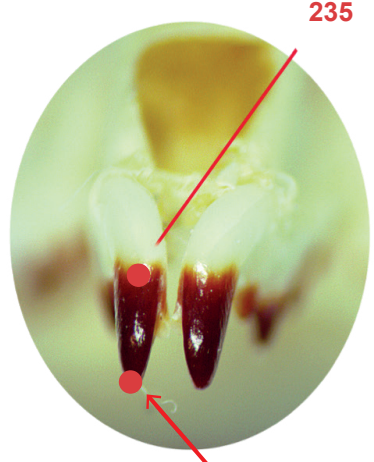
Text-fig. A2. Position of landmarks: C maxillary unicuspid 88–121, 127–130, D maxillary molariforms 122–126.



Text-fig. A3. Position of landmarks: D maxillary molariforms 133–165, E mandibular unicuspid 166–182, F mandibular molars 191–211.



Text-fig. A4. Position of landmarks:
E mandibular unicuspid 183–190,
F mandibular molars 212–231.



Text-fig. A5. Position of landmarks:
extent of teeth pigmentation 232–255.

