Boris Kryštufek

Georgy I. Shenbrot

TRUE HAMSTERS

(Cricetinae)
of the
Palaearctic
Region

True Hamsters (Cricetinae)
of the Palaearctic Region

Authors

Boris Kryštufek
Georgy Isidorovich Shenbrot

Table of Contents

Preface

The present volume on true hamsters (subfamily Cricetinae) completes the taxonomic review of the family Cricetidae in the Palaearctic biogeographic region. The review was initiated by a volume on voles and lemmings (subfamily Arvicolinae). Although Cricetinae and Arvicolinae are closely related, they differ profoundly in their morphology, physiology, ecological role and relations to humans. Contrary to the Holarctic voles and lemmings, the true hamsters are endemic to the Palaearctic realm. While Arvicolinae are the most speciose rodent group in temperate and boreal Eurasia (128 species listed in Kryštufek & Shenbrot 2022), the true hamsters contain merely 19 species. Hamsters are also less abundant in their habitats and not so well represented in mammal collections.

The entire group has been thoroughly reviewed in the 7th volume of the Handbook of the Mammals of the World (Pardiñas et al. 2017), which focused on natural history. Our review provides a complete and independent list with descriptions, identification keys, detailed distributional maps and basic taxonomic details allowing the user "to interpret intelligently and cautiously the results of taxonomists labour" (Corbet 1978: 1). In particular, we are attempting to provide for continuity between the earlier morphology-based taxonomies, karyology-based species delimitations and the current DNA-aided phylogenetic reconstructions. We hope that the present work provides novel views and will be of interest to experts engaged in medical zoology, epidemiology, biostratigraphy, zooarchaeology, population ecology, biodiversity conservation, museum collection management and several other biological subdisciplines. Many of them, though working with various true hamsters on daily basis, are baffled by the taxonomic changes and discordant classifications used in different sources.

This review is based on our first-hand experiences with various species of true hamsters throughout Europe and Asia, gained during the last half-century of our professional work. In 27 museums and collections across Europe, Asia and the USA, we examined well over 3,000 voucher specimens. Maps were derived from a basis containing 12,530 locality points. We studied literature on the topic, including original publications for nearly every taxonomic name published since 1758; the reference list contains over 700 titles. And last, but not least, we discussed various issues of taxonomy, zoogeography and biology with experts who actively study particular groups. We have received invaluable assistance from many experts, and their comments and suggestions were most helpful, though, as usual, the opinions and mistakes remain our own responsibility.

Acknowledgements

In summary, we used resource of the following 27 zoological collections (abc by acronyms):

– Natural History Museum (formerly British Museum Natural History), London, UK (BMNH);
– Cambridge University Museum of Zoology, Cambridge, UK (CUMZ);
– Field Museum of Natural History, Chicago, USA (FMNH);
– Grigore Antipa National Museum Natural History, Bucharest, Romania (GANHM);
– Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ);
– Hungarian Natural History Museum, Budapest, Hungary (MNM);
– Museum of Zoology, Dresden, Germany (MZD);
– National Museum of Natural History, Ukrainian Academy of Sciences, Kyiv, Ukraine (NHMAS);
– Naturhistoriches Museum Basel, Switzerland (NHMBa);
– Natural History Museum Berlin, Germany (NHMBe);
– National Museum of Natural History, Sofia, Bulgaria (NHMS);
– Smithsonian National Museum of Natural History, Washington D.C., USA (NMNH);
– National Museum, Prague, Czech Republic (NMP);
– Natural History Museum, Vienna, Austria (NMW);
– Natural History Museum, Belgrade, Serbia (PMB);

Taxonomy and nomenclature

The overall frame for our taxonomic underlying is explained in our earlier work on the Palaearctic voles and lemmings Arvicolinae (Kryštufek & Shenbrot 2022) and is thus not repeated here.

Taxonomic history

Common hamster *Cricetus cricetus* was validly named in the 12th edition of Systema Naturae (Linnaeus 1758), unsurprisingly as a member of the genus *Mus*. Shortly afterwards, Pallas (1773, 1779) named further 8 species, still classifying them as members of *Mus*; these names represent 3 currently valid species (*Cricetulus barabensis, Nothocrocetulus migratorius, Cricetiscus sungorus*). Erxleben (1777) transferred taxa named by Linnaeus and Pallas into genus *Glis*, but obviously did not see them as a coherent entity against other members of this genus; *e. g.* he used a vernacular name 'hamster' (in German; 'khomyak' in Russian) only for *Cricetus*. At about the same time, Leske (1779) introduced *Cricetus* as a generic name for the common hamster and two squirrels, European souslik *Spermophilus citellus* and Alpine marmot *Marmota marmota*; he was not aware of hamsters named by Pallas.

The first to merge all hamsters, and only hamsters, under the same generic name (*Cricetus*) was Johann Friedrich Gmelin (1792); he defined them as "having pouches in the cheeks, and short hairy tails" (p. 506). Gmelin (1792) classified *Cricetus* into subdivision Cunicularii of a division Mures. In 1805, however, he coined a new name 'Buccati' ("les rats à pochettes dans la bouche"; Gmelin 1805: 327) which was occasionally in use (as Mures buccati) for the rest of the century (Brants 1827, Tullberg 1899). Alternatively, hamsters were diagnosed by their complete clavicle ("rongeurs claviculés"; Milne Edwards 1834: 353; Desmarest 1820, Cuvier 1817) or by a curved mandibular corpus and the angular process raised above the line of symphysis (Waterhouse 1839b). A reader should keep in mind that

Linnaean hierarchy provided no taxonomic level between the genus and order. The concept of family is attributed to Fischer (1817) who established a family group name Cricetinorum for true hamsters. Fischer's name was ranked either as a family (Cricetidae; Gray 1825) or a subfamily (Cricetinae; Murray 1866, Winge 1887). Alternatively, *Cricetus* was classified as member of Muridae (Illiger 1811, Gray 1821, Gervais 1854, 1859, Blasius 1857, Fitzinger 1867, Alston 1876) or rarely Aspalacidae (Gray, 1825). As the content of hamsters was loosely defined, these animals were frequently classified along with various Nearctic (Lesson 1827, 1842) and Neotropical rodents (Winge 1887, Thomas 1888, Flower & Lyddeker 1891), including chinchillas *Chinchilla* (Geoffroy 1803, Lesson 1827), jirds and gerbils (Gerbillinae) (Kaup 1835), and Malagasy Nesomyinae (Major 1897, Winge 1887, Trouessart 1897, Miller & Gidley 1918). The hamster family continued to contain a number of genera, tribes and subfamilies which are now classified into distinct families, *i. e.* Calomyscidae, Muridae, Spalacidae, and Nesomyidae (*cf.* Simpson 1945). Around Simpson's time, Cricetinae thus contained between 57 (Ellerman 1941) and 66 genera (Vorontzov 1959a). The prevailing opinion was that "…the present group [Cricetidae] is the most difficult group of all living Rodents to arrange in any natural order" (Ellerman 1941: 327–328), while Rinker (1954: 9) pointed on "… the confusion and disagreement which exist in regard to the interrelationships of the cricetine genera".

Central questions which puzzled taxonomists into the late 20th century were interrelationships between true hamsters and the Nearctic hamster-like rodents on the one hand, and the mouse-like hamsters *Calomyscus* on the other hand. *Calomyscus* was included into Cricetinae as a closest relative to true hamsters (Argyropulo 1933b, c, Ellerman 1941, Simpson 1945, Ellerman & Morrison-Scott 1951, Corbet 1978, Gromov & Baranova 1981, Pavlinov & Rossolimo 1987), but is

now in a family Calomyscidae as its sole extant genus. Particularly problematic for a sound taxonomic setting were convergences of true hamsters towards the American taxa, both externally (*e. g.* between *Cricetus* and *Chinchillula*; Herskovitz 1962) and dentally (Thomas 1888). Towards the end of the 19th century, the Old-World hamsters (*Cricetus sensu lato*) and the New-World "*Hesperomys* with number of subgenera" (Thomas 1888: 133) were merged into a single genus *Cricetus* (Flower & Lyddeker 1891, Thomas 1888). Contrary to this, Ellerman (1941) stressed that no cricetid genera were common to both hemispheres; see also Vorontzov (1959a, b).

Karyological data which started emerging in the early 1950s retrieved profound differences between true hamsters and American cricetids (Makino 1951, Matthey 1952, 1960, 1961); this line of evidence was supplemented by detailed morphological study (Vorontzov 1959a). Further supportive evidence was provided by nucleotide sequences (Conroy & Cook 1999, Steppan & Schenk 2017). True hamsters (Cricetinae) are currently classified as one of 5 subfamilies of the family Cricetidae. The remaining subfamilies are the Holarctic Arvicolinae and the New World Neotominae, Tylomyinae, and Sigmodontinae (Pardiñas et al. 2017). Cricetidae form, along with Muridae (a sister family to Cricetidae), Nesomyidae and Calomyscidae, the clade Eumuroida within the superfamily Muroidea; Eumuroida have no formal taxonomic standing.

The interrelationships of hamster genera posed a similarly complex issue. Although *Cricetulus* was named already in 1860s (Milne-Edwards 1867), subsequent authors continued to classify all true hamsters as *Cricetus* (Alston 1876, Winge 1887, Tikhomirov & Korchagin 1889, Anderson 1891, Trouessart 1904). A need for taxonomic revision of hamsters was, however, apparent in the mid-19th century (Giebel 1855), with Brandt (1859) splitting *Cricetus* into 2 sections on the basis of colouration; 1 of these sections was further split into 2 "divisions":

1. Sectio A – *Criceti genuini seu melanosterni* [true hamsters with black chests], diagnosed by black ventral fur and cranial traits (skull depressed, interparietal bone triangular and small); content: *C. cricetus*;

2. Sectio B – *Criceti myoidei seu leucosterni* [mouse-like hamsters with white chests]; diagnosed by usually white (rarely rusty) chest, convex braincase and large interparietal bone (wider than long);
2.1. Divisio I – dorsum without longitudinal stripe; content: *Nothocricetulus migratorius* (*accedula, arenarius* and *phaeus* were ranked as distinct species) and *Allocricetulus eversmanni*;
2.2. Divisio II – dorsum with a distinct longitudinal stripe; content: *Cricetulus barabensis* (as *furunculus*) and *Cricetiscus sungorus*.

Trouessart (1904) split *Cricetus* with 14 extant species, into 4 subgenera:
Cricetus with the current *Cricetus cricetus* (as 3 species: *cricetus, nigricans* and *fuscatus*), *Nothocricetulus migratorius* (as *accedula*), *Allocricetulus eversmanni*, and *Cricetulus barabensis* (as *furunculus*);

Mesocricetus with the current *M. raddei* (*nigriculus* as a full species), *M. brandti* (*koenigi* as a species in its own right), *M. auratus*, and *M. newtoni*;

Cricetulus with the current *Nothocricetulus migratorius* (as 4 distinct species: *phaeus, atticus, kozlovi,* and *arenarius*), *Phodopus roborovskii, Cricetiscus sungorus, Cricetulus longicaudatus* (as *dichrootis*), and *Cricetulus barabensis* (as 2 distinct species: *obscurus* and *griseus*);

Urocricetus with the current *Urocricetus kamensis, Cricetulus longicaudatus,* and *Tscherskia triton.*

By the 1930s, all major representatives of true hamsters were already known and in 1933 a capital revision by A. I. Argyropulo followed; it was published first in Russian (Argyropulo 1933b) and in the same year also in German (Argyropulo 1933c). Argyropulo recognized 3 genera: (1) *Cricetus* (with *Mesocricetus* as a subgenus), (2) *Phodopus*, and (3) *Cricetulus* (with *Allocricetulus* and *Tscherskia* as subgenera). Ellerman (1941) and Ellerman & Morrison-Scott (1951) followed this classification, however, they elevated *Mesocricetus* to a genus in its own right. Vorontsov (1957) did the same with *Allocricetulus* and *Tscherskia*, although he was not consistent in this. These steps brought the number of recognized genera to 6.
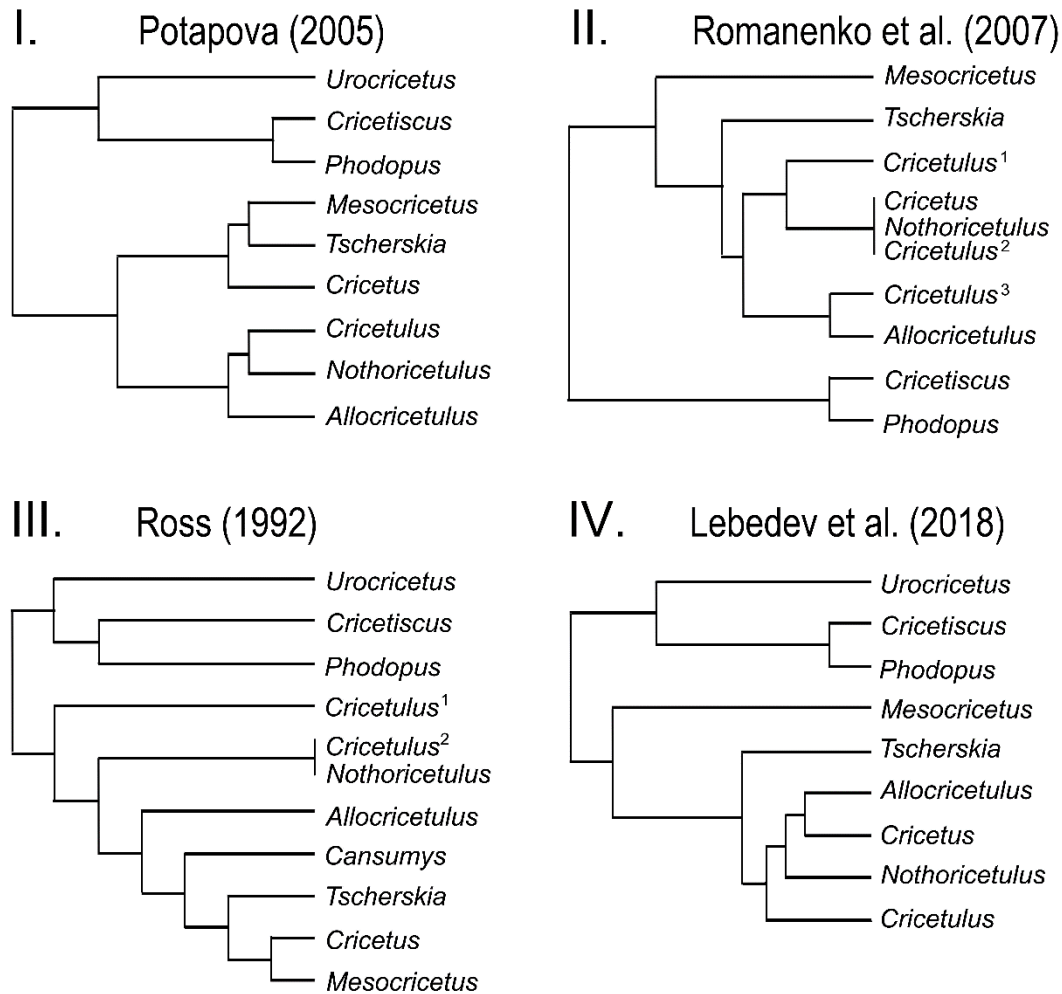
Figure 1: Phylogenetic reconstructions showing relationships among genera of Cricetinae based on different markers. I – The most parsimonious tree from cladistic analysis of 55 character-states of bulla tympany. *Calomyscus* clustered as a basal branch in the *Urocricetus + Cricetiscus + Phodopus* lineage (not shown). Modified after Potapova (2005). II – The most parsimonious tree from cladistics analysis of chromosomal characters. [1] – *Cricetulus barabensis*; [2] – *C. longicaudatus*, [3] – *C. sokolovi*. Modified after Romanenko et al. (2007). III – Cladogram based on data for 62 phenetic characters and 145 character-states. [1] – *Cricetulus longicaudatus*; [2] – *C. barabensis*, *C. sokolovi*. Modified after Ross (1992: 59a). IV – Molecular phylogeny as inferred from a concatenated alignment of 5 nuclear and 1 mitochondrial genes. Modified after Lebedev et al. (2018a).

In the late 1950s, Vorontsov initiated a series of studies devoted to various aspects of hamster morphology (Vorontsov & Gurtovoi 1959, Vorontsov 1957, 1958, 1960, 1962, 1969, Vorontzov 1959a). This resulted in a comprehensive revision of "primitive hamsters" of the Old- and New World (Vorontsov 1982) and furthermore enabled the 1st cladistic analysis, which was conducted by Ross (1992). Ross examined all living true hamsters and restored *Cansumys* and *Urocricetus* as valid genera. Her analysis revealed for the first time close phylogenetic relationships between *Urocricetus* and *Phodopus*. On the other hand, Ross (1992) failed to recognize the isolated position of *Mesocricetus*. This was accomplished in molecular phylogenies (Neumann et al. 2006, Lebedev et al. 2018a) that steadily brought the number of species and genera to the current one. The most noteworthy achievement of the last decade was a transfer of the migratory hamster into a genus in its own right (*Nothocricetulus*) (Lebedev et al. 2018a).

Family-group names

True hamsters are currently classified as a subfamily Cricetinae. In earlier times, when Cricetinae still encompassed various myomorphous rodents that are now in different subfamilies of Cricetidae (Neotominae, Tylomyinae, and Sigmodontinae), in Spalacidae (Myospalacinae), Calomyscidae, and Nesomyidae, true hamsters were ranked as a tribe Cricetini. So far, there was no attempt, however, to

arrange hamster genera into more than 1 family-group ranked either as tribe or subfamily.

At least 4 comprehensive assessments of phylogenetic relationships among hamsters have been published over the last 3 decades. These assessments were based on different markers (Figure 1): morphological (Potapova 2005), chromosomal (Romanenko et al. 2007), morphological and chromosomal (Ross 1992), and molecular (Neumann et al. 2006, Lebedev et al. 2018a). Romanenko et al. (2007) and Lebedev et al. (2018a) came to the same conclusion regarding the major hamster lineages. Since divergences between these lineages (> 7.5 Mya) largely predate heterogeneity at generic level (< 8.3 Mya; Figure 2), we classify them as tribes and subtribes.

1. Tribe Cricetini
   1.1. Subtribe Cansumyina new subtribe (*Cansumys*; 1 species)
   1.2. Subtribe Cricetina (*Tscherskia, Cricetulus, Nothocricetulus, Allocricetulus, Cricetus*; 9 species)
2. Tribe Mesocricetini new tribe (*Mesocricetus*; 4 species)
3. Tribe Urocricetini new tribe
   3.1. Subtribe Urocricetina (*Urocricetus*; 2 species)
   3.2. Subtribe Phodopina new subtribe (*Phodopus, Cricetiscus*; 3 species)
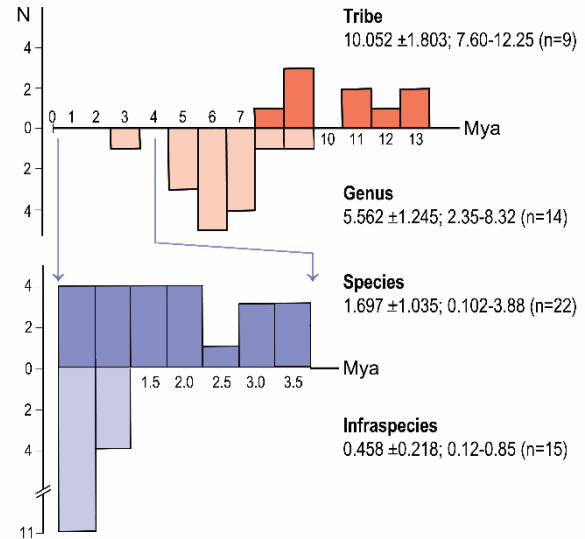
Figure 2: Histograms of pairwise divergences (in million years; Mya) at 4 taxonomic levels of true hamsters: tribal, generic, specific and infraspecific levels. Values given for each level are: mean ±standard deviation; minimum–maximum; (number of pairwise comparisons). Based on data in Neumann et al. (2006), Meshchersky & Feoktisova (2009), Lebedev et al. (2018a, b), and Gureeva (2022).
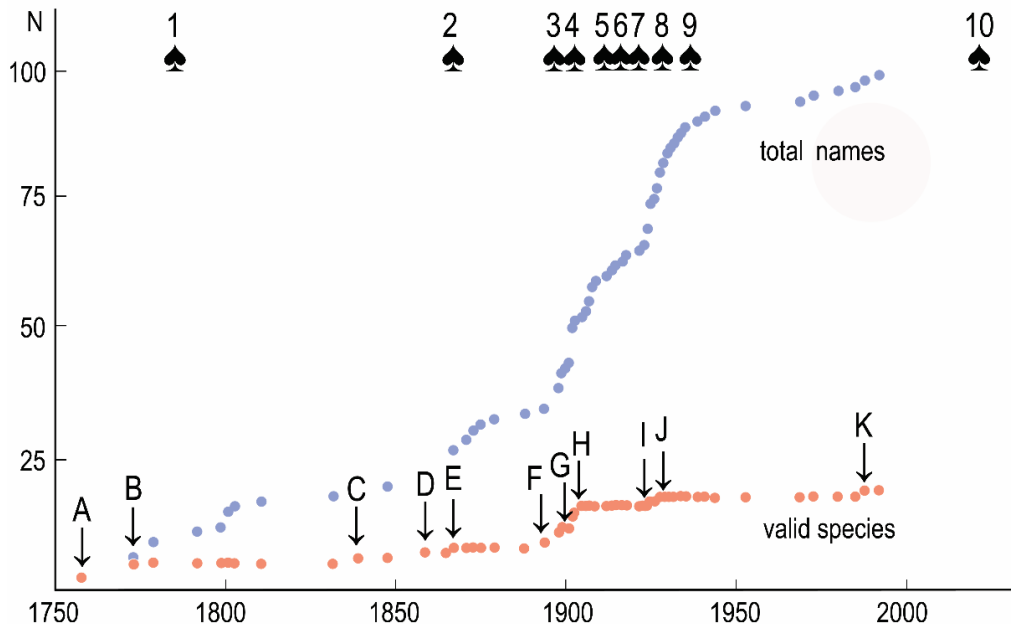
Figure 3: Cumulative curve for species of true hamsters (Cricetinae) as function of time. Blue circles show new species-group names, red circles show valid species as currently recognized; arrows point to the additions of valid species: A – Linnaeus (1758); B – Pallas (1773); C – Waterhouse (1839a); D – Brandt (1859); E – A. Milne-Edwards (1867); F – Nehring (1894); G – Nehring (1898a, b, 1899a); H – Satunin (1902, 1903), Thomas (1905); I – G. M. Allen (1925); J – G. M. Allen (1928); K – Orlov & Malygin (1988). Spade suits at the top indicate recognitions of new genera: 1 – *Cricetus* Leske, 1779; 2 – *Cricetulus* A. Milne-Edwards, 1867; 3 – *Mesocricetus* Nehring, 1898c; 4 – *Urocricetus* Satunin, 1902; 5 – *Phodopus* Miller, 1910: 6 – *Cricetiscus* Thomas, 1905; 7 – *Tscherskia* Ognev, 1914; 8 – *Cansumys* G. M. Allen 1928; 9 – *Allocricetulus* Argyropulo, 1933b; 10 – *Nothocricetulus* Lebedev et al. 2018a.

Genera and species

The majority of currently recognized genera (7 genera out of total 10) were named between 1898 and 1933, *i. e.* in a period of 35 years (Figure 3). Genera are small, containing between 1 species (*Cansumys, Nothocricetulus, Phodopus*) and 4 species (*Mesocricetus*); mean = 1.9 species / genus. Genera diverged between 2.35 Mya (*Allocricetulus–Cricetus*) and 8.32 Mya (*Tscherskia* and the remaining Cricetina; Jiang et al. 2024).

The bulk of currently valid species (8 species out of total 19) were named between 1894 and 1905, *i. e.* in a period of 11 years (Figure 3). At about same time, the concept of polytypic species and subspecies replaced the earlier idea of immutable species and varieties. The shift, however, was possible thanks to methodological innovations, above all collecting small mammals by small, cheap and easily portable traps, and preparing the animals as standard "museum specimens" (Hutterer & Kryštufek 2020). This accelerated further naming, and 49 new species group names for true hamsters were proposed in the 1900–1940 period, *i. e.* ½ of all names published since Linnaeus (1758).

From the current perspective, the species diversity of true hamsters was fully comprehended by the 1990s, when settled at 18 species (Musser & Carleton 1993, Pavlinov et al. 1995) (Table 1); a single species is a very recent addition (Jiang et al. 2024). Species of true hamsters diverged 1.02–3.88 Mya (mean = 1.697 Mya; Figure 2). The bulk of speciation events happened during the Early Pleistocene.

Subspecies taxonomy suffers from all the weaknesses that burden this issue in the Palaearctic mammalogy. The majority of infraspecific divergences date back *c.* 1 My, therefore suggesting that subspeciation was an event of the Middle and Late Pleistocene. Infraspecific diversity at the level of traditional trinomial taxonomy is, however, poorly documented and only 3 taxonomic reviews addressed subspecies of all true hamsters. These reviews were published between 1933–1951 and are more compilations of subspecific names rather than genuine taxonomic revisions. In any case, *c.* 10 species were classified as polytypic, with up to *c.* 15 subspecies per species. Median number of subspecies per polytypic species was 3–4.5, depending on the source . There was

a general agreement that the number of subspecies was the highest in *Nothocricetulus migratorius*, *i. e.* 13–16 subspecies, depending on the author. On the other hand, opinions differed radically in *C. cricetus*, with 9 and 11 subspecies in Argyropulo (1933c) and Ellerman (1941), respectively, but with only 3 subspecies in Ellerman & Morrison-Scott (1951).

Table 1: Taxonomic revisions of true hamsters (Cricetinae), published since 1900 with the number of species recognized by an author (authors) and the number of currently valid species.

Year	Authors	# recognized species	# valid species
1904	Trouessart	24	15
1933b,c	Argyropulo	15	14
1941	Ellerman	15	14
1951	Ellerman & Morrison-Scott	11	10
1978	Corbet	14	14
1980	Corbet & Hill	14	14
1982	Honacki et al.	19	16
1986	Corbet & Hill	18	15
1992	Ross	20	18
1993	Musser & Carleton	18	18
1995	Pavlinov et al.	18	18
1998	Panteleyev	19	17
2003	Pavlinov	18	18
2005	Musser & Carleton	18	18
2006	Pavlinov	18	18
2017	Pardiñas et al.	18	18
2020	Burgin et al.	18	18

In this review, we addressed subspecific taxonomy. Eight species are recognized as polytypic with 2–5 subspecies (median = 2 subspecies per polytypic species). Three species are classified as monotypic and further 3 species are admittedly polytypic. Any application of trinomials would, however, be premature at this stage.

We provide full references for all species-group names, together with type localities. If quoted from the original source, the type locality is in quotation marks and any additional information is in square brackets. Type localities for all available names are shown on the species maps. Main compilations for the genus- and species-group names are Trouessart (1897, 1904, 1910), Palmer (1904), Miller (1912), Allen (1940), Ellerman (1941), Ellerman & Morrison-Scott (1951), Corbet (1978), Pavlinov & Rossolimo (1987), Kretzoi & Kretzoi (2000), and Musser & Carleton (2005).
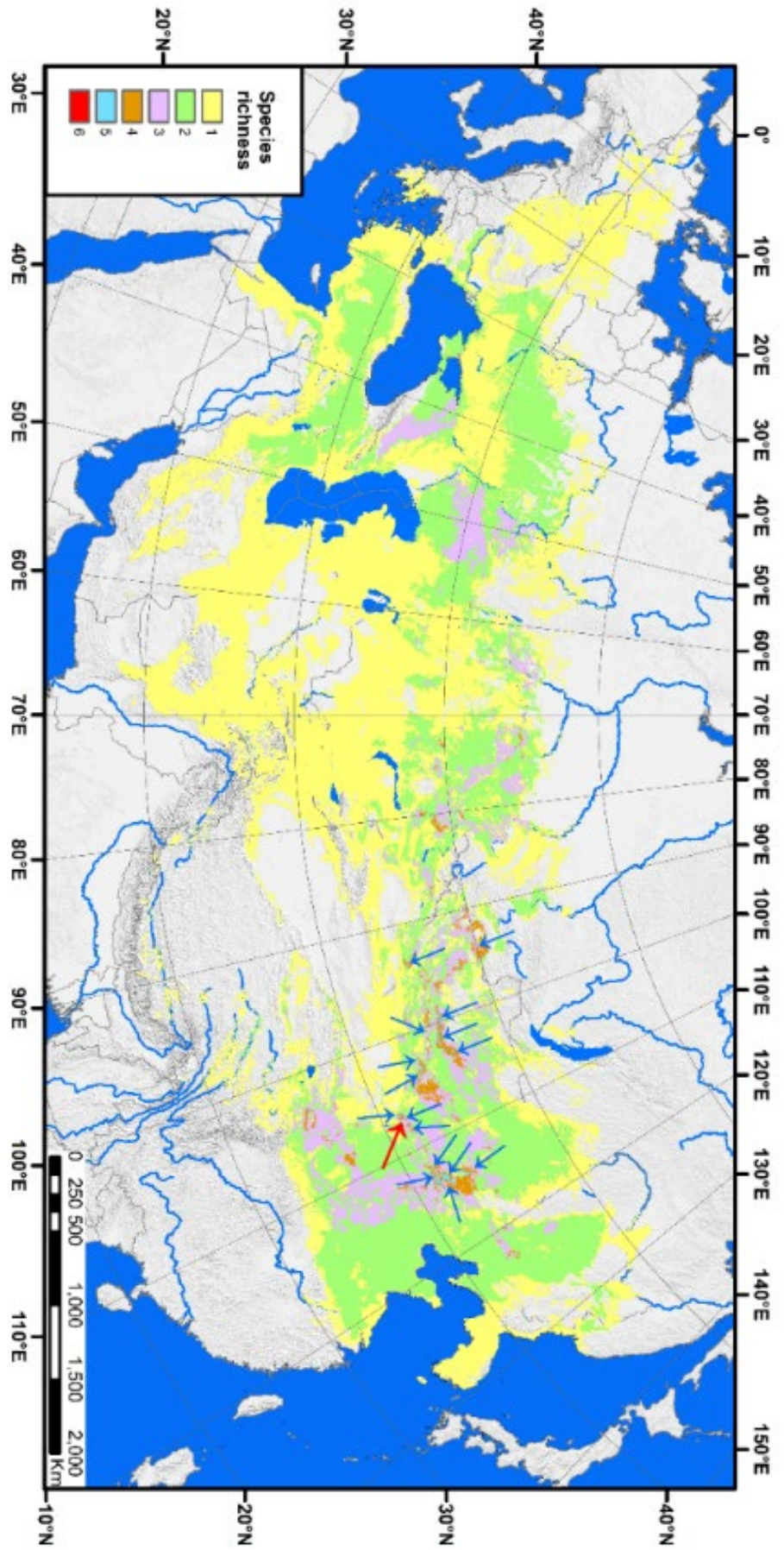
Figure 4: Species density of true hamsters. Blue arrows point to regions with 5 species; red arrow points to a region with 6 species.

Geographical settings

True hamsters are exclusively Palaearctic group and are found at present only in temperate parts of Europe and Asia. Hamsters however occupied also the Palaearctic Africa in various periods of Neogene and Quaternary (McKenna & Bell 1997). Their ranges stretch from the Rhine Valley in the west reaching Sea of Japan and Yellow Sea in the east. The northern border is largely defined by the southern extension of boreal forests (Laptev 1958) and overlaps pretty closely with large rivers, the Volga–Kama system in the west and the Amur River in the Far East; in-between, the northern range encompasses the upper reaches of Irtysh, Ob, Yenissei, and Lena. In the south, hamsters rarely cross the 30th parallel; minor transgressions are in southern Iran, southern Pakistan, and Nepal (Figure 4). The overall range closely matches the zone of Palaearctic steppes and semideserts. Although the range overlaps also large sections of the deciduous forest zone, hamsters are absent from close-canopy forests; the only exception is *Cansumy canus*.

Distributional ranges of 19 species of true hamsters cover surface areas between 24,000–7.1 million km², *i. e.* a difference of approximately 300-fold. Frequency distribution is skewed towards small areas (mean = 1,075,896 km², median = 494,197 km²), with half of all ranges measuring 92,870–1,401,000 km².

Along the elevational gradient, hamsters range from below sea level (–26 m in the Caspian Depression) to 5,114 m, hence elevational ranges are between 354–4,729 m (Figure 5). The mean (= 2,487 m) and median (= 2,423 m) are remarkably similar, and ½ of species have ranges between 1,703–3,243 m. Only 3 species (*Cricetus cricetus, Mesocricetus auratus, M. newtoni*) occupy low elevations (< 1,000 m a. s. l.), and 2 species, both from the genus *Urocricetus*, are tied to high elevations (> 2,000 m) (Figure 5).
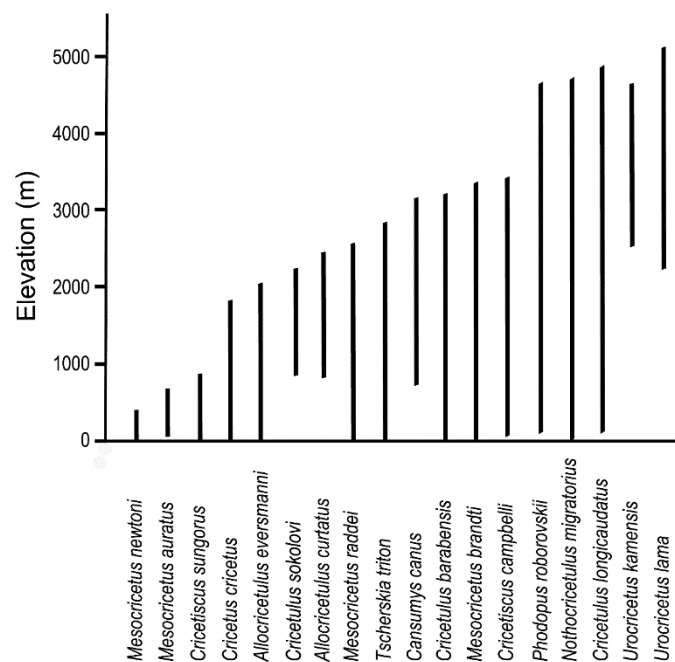
Figure 5: Elevational ranges for each of true hamsters.

Up to 6 species of hamsters are locally sympatric (Figure 4), however, a great majority of their range is occupied by 1–2 species. Areas with 3 species are scattered, though still reasonably compact in the (1) steppes to the north of the Caucasus (Ciscaucasia); (2) east-central basin of the River Volga; (3) the watershed of Tobol, Irtysh and upper Ob in northern Kazakhstan and adjacent Russia; (4) western and central Mongolia; (5) east-central Nei Mongol, Hebei, Shanxi, and northern Henan; (6) Ningxia, Gansu and Shaanxi (China). Patches having 4–6 species of hamsters are highly fragmented and scattered to the east of line Tobol–Balkhash Lake. Thus, assemblages with 5 species are present in (1) the Great Lake Depression, (2) the Khangai Mts., in (3) western Gobi in Mongolia, (4) central and southern Khingan Range (eastern Nei Mongol) and in (6) the Lang Shan Mts. at the north-west corner of the Ordos Loop. The Lang Shan is the top hot-spot in species richness with 6 hamster species (Figure 4).

Characteristics of true hamsters

True hamsters are myomorphous rodents, characterized by (1) well developed internal pouches, (2) a mid-ventral sebaceous gland in the umbilical region, (3) rooted, tubercular and brachyodont molars with cusps arranged in two longitudinal rows, (4) a pair of anteroconids / anteroconulids in 1st molars, (5) a high and falcate coronoid process, (6) a reduced fibula fused with the tibia on its distal end, (7) a two chambered stomach consisting of a corneous forestomach and glandular stomach, and (8) a primitive pattern of cephalic arterial supply system with stapedial artery preserved in its entirety (Argyropulo 1933b, c, Ellerman 1941, Vorontsov 1960, 1982, Bugge 1970, 1985, Wahlert 1984, Ross 1992, Chernova et al. 2022a. b).

External appearance

True hamsters are of generalized external form without extreme specializations. They range in appearance from slender (Figure 6a) to stout and roundish (Figure 6b) and vary in size from small (*Phodopus* has body mass of 10.5–19 g) to moderately large (body mass in *Cricetus* is up to 860 g). At least some hamsters are sexually dimorphic in size with either males (*Tscherskia triton, Cricetiscus, C. cricetus*) or females (*Mesocricetus auratus*) being the larger sex. The tail is shorter than ½ length of head and body in great majority of species. It is vestigial and hardly protruding off the hairs in *Mesocricetus, Phodopus, Cricetiscus*, and *Allocricetulus*; in adult short-tailed males, the tail is further obscured by distended scrotal sacks. The tail is longest (> ½ of length of head and body) in *Urocricetus kamensis, Tscherskia* and *Cansumys*. Eyes are on average larger and ears are longer than in voles. Limbs are short and powerful; feet are essentially as in arvicolines, but shorter and broader with not much size difference between the fore and hind paws. They have 5 digits each but the front thumb is always distinctly smaller and usually reduced to a mere vestige (Figures 33, 80, 101 & 109). Palms and soles are densely hairy in Phodopina and seasonally also in some other hamsters (*e. g. Cricetulus sokolovi*).

Skin derivatives

The rhinarium (Figure 7), a specialised skin surrounding the external openings of the nostrils (external nares), is of general murine type and does not differ appreciably from that seen in Arvicolinae. It is situated on the tip of the snout at a distance from the upper incisors which is approximately equal to the height of rhinarium. Rhinarium is hairless in all hamsters except Phodopini, in which the dorsum, the infranarial portion and the *alae nasi* are hairy.

Figure 6: Extreme hamster forms, the slender form (a – *Nothocricetulus migratorius*) and the stout roundish type (b – *Mesocricetus*). Art Jan Hošek. Used with permission of the Science and Research Centre Koper.
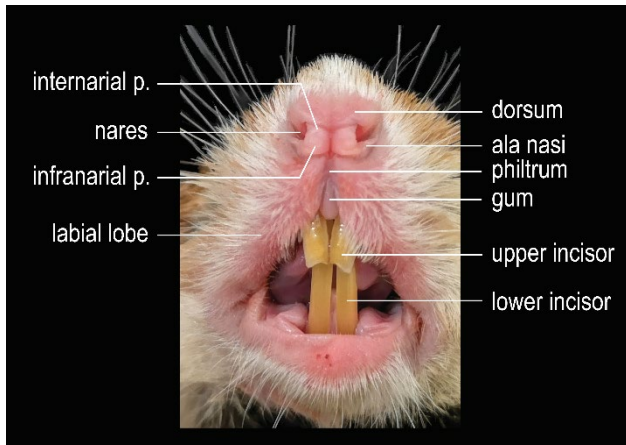
Figure 7: Rhinarium of common hamster *Cricetus cricetus* from Baranja, north-eastern Croatia. Abbreviation p. is for portion. Photo: B. Kryštufek

The auricle is moderately large to large, rounded or elongated and usually protruding above the fur. Structurally it is like in Arvicolinae (Kryštufek & Shenbrot 2022: 12), though it tends to be hairier in hamsters (Figure 8). The antitragus is frequently of weak prominence.
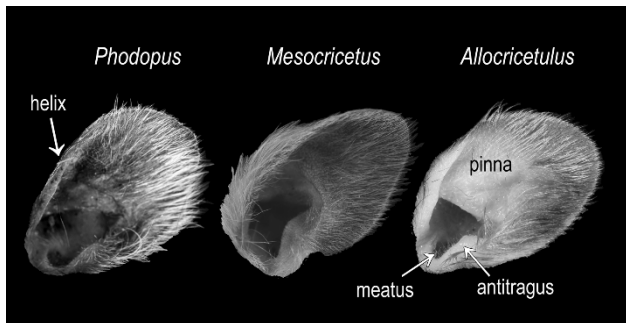
Figure 8: Left auricle in *Cricetiscus sungorus* (left), *Mesocricetus auratus* (middle), and *Allocricetulus eversmanni* (right). Photo: B. Kryštufek

Digits are equipped with curved and laterally compressed claws which closely resemble those in arvicolines. The front claws are frequently longer and more curved; the thumb has a small claw or a flat nail. There are typically 5 palmar and 6 plantar pads (Figures 33, 80 & 101). In Phodopina, where this number is reduced to 3 pads (*Cricetiscus*), or a single one (*Phodopus*), the vestiges of pads are concealed under dense hairs (Figure 109).

The integument is thin, with weakly developed epidermis and dermis layers. Unique for the subfamily is a well pronounced subcutaneous tissue with hair follicles. The adipose subcutaneous tissue penetrates

deeply into the dermal layer and also contains large hair follicles, thus obscuring the boundary between the 2 layers, which is a distinctive feature of Cricetinae (Chernova et al. 2022a).

All hamsters are densely furred. Hairs cluster into distinct bundles; there are *c.* 80–100 such bundles per cm² in *C. cricetus* (Chernova et al. 2022b). The fur is usually soft, rarely silky (*Urocricetus, Phodopus*) or slightly rough (*Tsherskia*). Pelage is denser on the back than below; in *C. cricetus*, there are 2,100–2,140 hairs per cm² on the back, ~ 1,750 hairs per cm² on the flanks and ~1,255 hairs per cm² on the belly. The pelage, however, is more homogeneous than in other muroids (Chernova et al. 2022a); members of Phodopina even lack guard hairs (Feoktisova 2008). Differentiation into tires and different categories of hair is loose, though the overhairs tend to be thicker. In *C. cricetus* their diameter ≈ 85–93 µm compared to ≈ 40–63 µm in guard hairs; downy hairs are the thinnest (≈ 10–55 µm). Besides, the same hair type tends to be thicker on the back than below. The cross-section of hair shaft is either oval or cylindrical and the thick medulla presumably increases the insulation capacity of the pelage (Chernova et al. 2022a, b). At withers, hairs of *C. cricetus* measure from 8–15 mm (guard hairs) to 21–26 mm (overhairs) in length and are longer dorsally than ventrally (Chernova et al. 2022b). In hamsters of small or medium size (*Cricetulus, Allocricetulus, Nothocricetulus*), dorsal hairs usually measure 8–13 mm. Hairs are of similar structure in Cricetinae as in Muridae and Arvicolinae. The scale-like pattern of the cuticle follows the wave-type (Trapp 1979), which is characteristic also of Arvicolinae.

The juvenile and seasonal moults in Cricetina (*Cricetulus, Allocricetulus, Nothocricetulus* and *Tscherskia*) follow the sublateral type, which is characteristic also of Arvicolinae. In this type, the new hair starts growing from the underside of the flanks and proceeds both towards the dorsum and the belly. *Cricetiscus* has a unique moulting pattern in which the hair is firstly replaced in several patches along the spine and moult progresses across the rest of the back, towards the head, the flanks and the belly (Kryltzov 1964).

Hamsters have on average a richer colouration than other species of Cricetidae and Muridae. *Cricetus*, and to a lesser degree also *Mesocricetus* and *Cricetiscus*, have

blotches of bright and dull fur. Such bright colouration associates with aggressive defending behaviour and is presumably aposematic (Vorontsov 1982); analogy with the Norwegian lemming (*Lemmus l. lemmus*; Kryštufek & Shenbrot 2022) is obvious. Some hamsters, however, have a prominent black spinal (mid-dorsal) stripe along the back (*Cricetulus barabensis* and *Cricetiscus*). Furthermore, there are blackish blocks on crown and head, shoulders, and flanks in *Cricetiscus* and *Mesocricetus*. Contrasting light (white) patches are common on the side of the head (*Cricetiscus, Cansumys*) or behind the auricle (*Mesocricetus*). Golden hamsters (*Mesocricetus*) and *Allocricetulus eversmanni* have a dark sternal stripe across the throat and chests; black underside is a norm for *Cricetus* and is frequently present also in *Mesocricetus raddei*. The area of extended cheek pouches shows a contrasting pattern in *Mesocricetus* (Figure 14a) and *Allocricetulus* (Figure 59) with a prominent oblique post-auricular stripe. Leaving aside extreme colour variants (*e. g.* melanistic or albino hamsters), the pelage is frequently monochromatic, either brown or grey dorsally; the belly is lighter, usually white. Demarcation line along the flanks is frequently distinct, either straight or sinuous; if the latter, the line is bowed upward over the shoulders, hips, and sides. Hamsters occupying rocky habitats (*Nothocricetulus, Urocricetus*) are of similar colour to rock-dwelling mountain voles *Alticola*; the similarity is close enough to cause occasional misclassifications of museum vouchers (Argyropulo 1936: 118 footnote; Lim & Ross 1992). *Cricetiscus sungorus* shows seasonal polyphenism with white winter pelage (Figures 111a2 & 119a). As is common in the majority of other muroids, including Arvicolinae, the basal $2/3$–$4/5$ of a hair is slate. White ventral hairs usually have the basal ½ slate; occasionally, ventral hairs are white to base.

In the opinion of Vorontsov (1982), black colour variant is present at various frequencies in what he called "tricolour hamsters", *i. e. Cricetus* and *Mesocricetus* (*brandti* and *raddei*). Some populations of common hamster *C. cricetus* contain high proportion (up to >80%) of black individuals, which are usually classified as melanistic. Black variant is currently still present in populations of *C. cricetus*, where it was reported in the mid-18th century. Other aberrant colour variants are rare in wild populations. Approximately 10 variants which were reported in free-living common hamsters

were present at frequencies <0.01%; unsurprisingly, they were detected thanks to huge number of skins (10^4–10^6 skins) gathered in pelt trade (Gershenson 1945, Kayser & Stubbe 2000, Kryštufek et al. 2016). Melanistic variant is not known in *Allocricetulus*, *Cricetulus s. lat*, and Urocricetina (Vorontsov 1982). Thirteen colour variants are known in captive-bred Syrian golden hamsters *Mesocricetus auratus* (Robinson 1968).
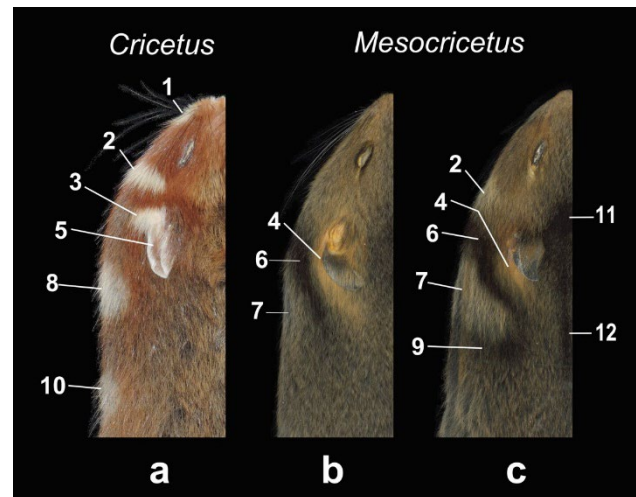
Figure 9: Dorsal colour pattern of anterior body in (a) *C. cricetus,* (b) *Mesocricetus brandti*, and (c) *M. newtoni*. Colour features: 1 – rostral light patch; 2 – cheek light patch; 3 – sub-auricular light patch; 4 – postauricular light patch; 5 – light-edged ears; 6 –subauricular (shoulder) stripe; 7 – collar stripe; 8 – neck (collar) patch; 9 – postero-lateral extension of a sternal patch; 10 – axillary light patch; 11 – crown patch; 11 – occipital stripe. Photo: B. Kryštufek

On the head are long, slender, coarse, tapered, and keratinised tactile hairs, the whiskers (*vibrissae*) which are classified according to their position, arrangement and function. Syrian golden hamster has on each side of the head 35 straight and stiff mystacial whiskers (*vibrissae mystaciales*), 2 supraorbital whiskers (*v. supraorbitales*) and 1 gental whisker (*vibrissa gentale*); the mystacial vibrissae appear in 7 longitudinal rows. At least some hamsters (*e. g. C. cricetus, Nothocricetulus migratorius*) also have antebrachial whiskers (*v. antebrachialis*). Labial vibrissae, located posterior to the proper whiskers, are smaller, disorganised and not independently mobile (Wineski 2009). *Cricetus* has 30 mystacial vibrissae in 4–5 distinct rows (Reznik et al. 1979). The length of mystacial whiskers grades from the shortest to the longest vibrissae in the antero-posterior direction. Whiskers are up to 34–38 mm long in *Mesocricetus auratus, M. brandti* and *M. newtoni*, 32–39 mm in *Cricetus cricetus*, 32 mm in

Allocricetulus eversmanni, 35 mm in *Nothocricetulus migratorius*, and 22 mm in *Cricetulus barabensis*. They are 166–191 µm thick in *Cricetus* (Chernova et al. 2022b). In *Mesocricetus*, the maximum lateral extent of the mystacial vibrissal field may reach 45.5% of the hamster's body length (Wineski 2009).

Hamsters have a pair of large sebaceous glands, organised as pads and situated on the flanks approximately in the middle between the shoulder and the hip (postero-lateral glands or flank organs; Figure 63). Each gland assumes shape of oblong-oval structure which protrudes from the surrounding skin due to its intense black colouring and hairs which differ from those of the surrounding skin. The position of flank organ is indicated by a small non-pigmented area before sexual maturity and appears at the age of 1–2 weeks in *M. auratus* (Magalhaes 1968). Glands are present in both sexes but are larger in males; their length in *Allocricetulus curtatus* is 3.8 mm in males and 2.25 mm in females (Chernova et al. 2022a). In *Mesocricetus auratus* males, the gland is 8.5 mm long and 6 mm wide; corresponding dimensions in male *Cricetus* are 20–40 and 10 mm, respectively. Flank glands are covered by thin epidermis and produce secretion for territorial marking (Lipkow 1954). Hamsters vigorously scratch the flank gland with hind foot, which is immediately followed with a perineal drag; besides, the exudate is spread on the substrate by feet as the animal moves about (Skirrow & Ryšan 1976). The postero-lateral glands in Cricetinae and Arvicolinae are homologous (cf. Kryštufek & Shenbrot 2022: 13).

True hamsters have unpaired mid-ventral gland (*glandula abdominalis*) (Figure 10) which was found in all Cricetinae studied so far: *Urocricetus, Phodopus, Cricetiscus, Mesocricetus, Tscherskia, Allocricetulus, Cricetus, Cricetulus,* and *Nothocricetulus* (Vrtiš 1932, Lipkow 1954, Vorontsov & Gurtovoi 1959, Reznik et al. 1974, Vorontsov 1982). The gland is larger in males but is frequently reduced or entirely absent in females. Mean length (in mm) of the gland in males / females is 12.2 / 6.7 in *Allocricetulus curtatus*, 10.7 / 6.5 in *A. eversmanni*, 7.8 / 4.0 in *Cricetulus sokolovi*, and 6.33 / 2.75 in *C. barabensis griseus* (Chernova et al. 2022a). The gland consists of a group of enlarged compound sebaceous glands covered with a very thick epidermis. It occurs in the umbilical region (hence the umbilical glandular organ) as a cutaneous invagination devoid of hair, frequently in combination with a greasy

discoloration of the fur along the mid-ventral line. Length × width (in mm) of the gland is 9–15 × 1–2 in *Nothocricetulus migratorius*, and 4.1 × 3.5 in *Cricetiscus campbelli* (Ross 1995), In *C. cricetus*, the mid-ventral glandular area is seen as $5 × 5$ mm^2 area of bare skin with a central excretory opening and specialized hairs. *Cricetulus* similarly shows a glandular area with hairs. The mid-ventral gland can resume a shape of glandular sac, either with specialized hairs (osmotrichia; *e. g.* in Phodopina) or without them (*Allocricetulus*) (Chernova et al. 2022a). Vrtiš (1932) believed for umbilical organ to be synapomorphic to Cricetinae, however, it occurs also in *Peromyscus* and related genera (Richmond & Roslund 1952). Postero-lateral and mid-ventral glands are of different histological structure. True hamsters also have cheek gland situated on the cheeks.
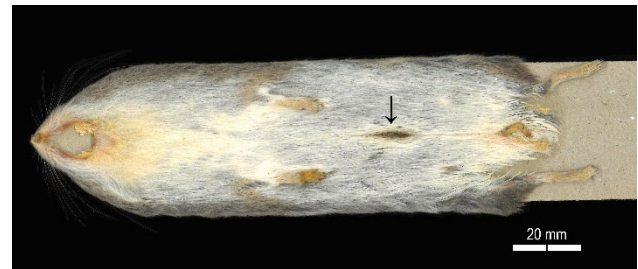
Figure 10: Ventral side of a carded skin of a male grey hamster *Nothocricetulus migratorius*. Arrow points to a mid-ventral gland, usually referred to as the umbilical glandular organ (*glandula abdominalis*). Photo: B. Kryštufek
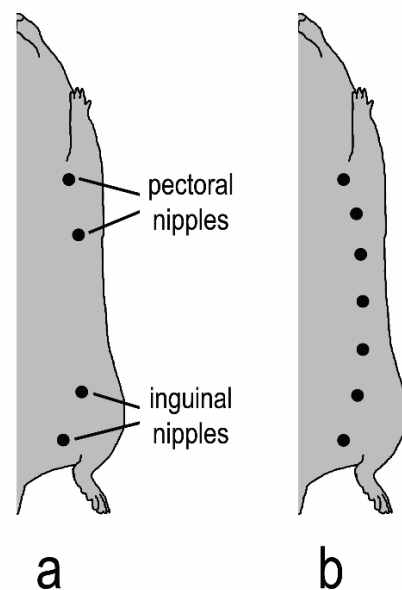
Figure 11: Complete set of mammary glands (nipples) in hamsters. a – Cricetini and Urocricetini; b – Mesocricetini. The number of teats in Mesocricetini varies from 14 to 22 (7–11 pairs); the lowest count of 7 pairs is shown in this figure.

The majority of hamsters have 4 pairs of nipples (*papillae mammae*; 8 nipples in total), which are organized in 2 pairs, the pectoral and the inguinal pair, respectively (Figure 11a). Golden hamsters (*Mesocricetus*) have 14–22 nipples (Magalhaes 1968, Vorontsov 1982), which are evenly spread between the pectoral and the inguinal region (Figure 11b). Nipples are inconspicuous in non-lactating females, however, their position can be recognized by hair swirls. Each of the teats has a single galactophore, which is typical of the remaining Myomorpha (Ching-Mei & Anderson 1975).

Soft-body anatomy

The internal anatomy is covered in considerable detail for *Cricetus* (Tullberg 1899, Reznik et al. 1979), and *Mesocricetus* (Magalhaes 1968, Kittel 1984). Vorontsov (1982) provides extensive comparisons for the entire subfamily (except *Cansumys*) and its relatives from the family Cricetidae (except Arvicolinae). Subsequently we briefly address digestive system due to its relevancy for generic classification.
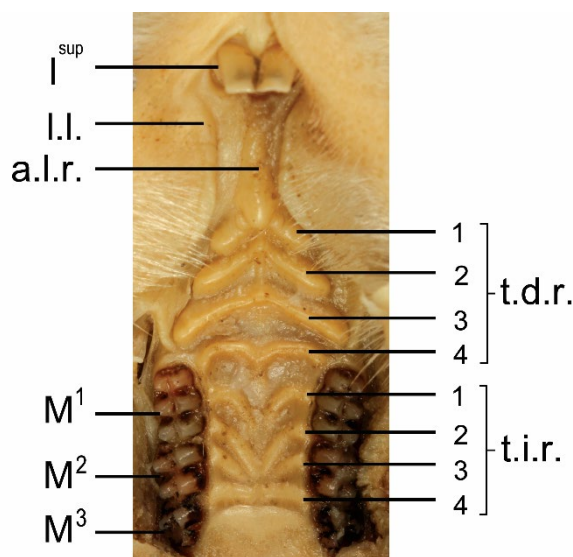
Figure 12: The diastemal palate and molar region in *Cricetus cricetus* as viewed from below to show features of surface anatomy. Abbreviations: a.l.r. – anterior longitudal (palatal) ridge; I^{sup} – upper incisor; l.l. – labial lobe (of the upper lip); M^1, M^2, M^3 – 1st, 2nd and 3rd upper molar, respectively; t.d.r. – transverse diastemal ridges; t.i.r. – transverse intermolar ridges. Photo: B. Kryštufek

The free margins of the lips form a three-cornered flap which seals the mouth opening when closed. The incisors are seen from the outside, however, the entrance to the cavity is closed by comparatively poorly developed labial lobes that do not come close together (Figures 7 &12). The hard palate is covered by a mucous membrane which forms transverse ridges (*rugae palatinae*). Usually, there are 6–8 ridges; the posterior 3–4 ridges are intermolar ridges (Tullberg 1899, Buchtová et al. 2005), and the remainder are the diastemal (antemolar) ridges (Figure 12).

Main part of the floor of the oral cavity is formed by long, narrow and thick tongue (*lingua*) which was used in phylogenetic studies of Cricetinae (Vorontsov 1958, Ross 1992) and is therefore covered in greater detail.
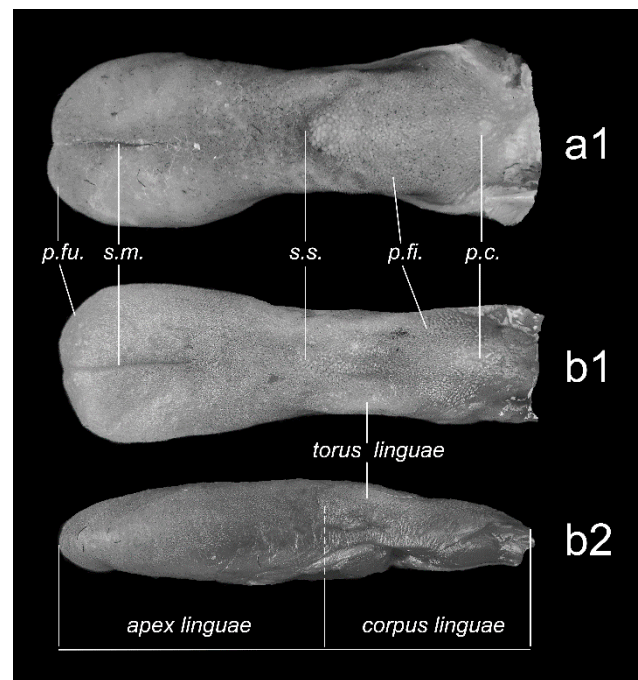
Figure 13: Tongue of *Mesocricetus auratus* (a1) and *Cricetus cricetus* (b1, b2) in dorsal (a1, b1) and lateral view (b2) to show features of surface anatomy. Abbreviations: *p.c. – papilla circumvulatus; p.fi. – papillae filiformes; p.fu. – papillae fungiformes; s.m. – sulcus medianus; s.s. – sulcus semilunaris*. Photo: David Kunc (a1) and B. Kryštufek (b)

The size of a tongue (length × width; in mm) is 30–55 × 10–12 in *Cricetus cricetus*, 24 × 7–8 in *Tscherskia*, 12 × 3.6 in *Cricetulus barabensis*, 16.5 × 4–4.5 in *Nothocricetulus migratorius*, 15.6 × 6.8 in *Allocricetulus eversmanni*, 12.8 × 3.7–4.2 in *Cricetiscus sungorus*, 23–28 × 9.1 in *Mesocricetus raddei*, and 15–18 × 6.2 in *M. brandti* (Vorontsov 1958, Reznik et al. 1979). The tongue consists of the longer anterior part (oral part; *apex linguae*) and the shorter base (intermolar eminence; *corpus linguae*) which are divided by a semilunar groove (*sulcus semilunaris*) (Figure 13). Dorsal surface of the tongue is covered by *papillae filiformes* which are numerous, minute and packed close

together; usually, they are larger on the base of the tongue, *i. e.* posterior to the semilunar groove. These papillae give the tongue its characteristic rough texture, but contain no phylogenetic information. Ross (1992) used further 2 types of papillae in her phylogenetic analysis of the subfamily. *Papillae foliatae* are arranged either in 2 rows (Mesocricetini) or in 1 row (the remaining Cricetinae) at the edge of *corpus linguae*. *Papillae fungiformes* are found only in the apex. These papillae extend to the tip of tongue (in *Cricetulus* and *Nothocricetulus*) or end before the tip (in *Cricetus*); frequently, they extend around the apex to the ventral surface of the tongue (*Allocricetulus, Tscherskia*, Mesocricetini, Urocricetini). All hamsters have a single *papilla circumvulatus*. A crescent-shaped fissure on the dorsal surface of the tongue on the boundary of the oral and basal parts (*sulcus semilunaris*) is present in *Allocricetulus, Tscherskia, Cricetus* and *Mesocricetus*, but absent in the remaining hamsters. *Torus linguae* is located on the postero-dorsal side of the tongue, behind *sulcus semilunaris*. Its function is pushing off the soil that entered the mouth during digging by incisors; the torus is well developed in *Allocricetulus, Tscherskia, Cricetus* and *Mesocricetus*. Median sulcus (*sulcus medianus linguae*) is a longitudinal groove on the distal dorsal tongue; in *Allocricetulus*, the sulcus terminates well before the apex, but in the remaining hamsters extends to the very tip (Sonntag 1924, Vorontsov 1958, Reznik et al. 1979, Ross 1992).

All hamsters have paired internal cheek pouches (*bursae buccales*) which are muscular and highly distensible (Figure 14). In *C. cricetus*, each pouch is 60–70 mm long and 12–15 mm wide when empty (Reznik et al. 1979); in mature *Mesocricetus auratus*, distended pouches measure 2.5–5.5 cm in length and ~1 cm in width (Handler & Shepro 1968; Figure 14a). The pouches are lateral evaginations of the buccal mucosa of the oral cavity and possess no glands. They consequently have no digestive function but are employed in carrying food. The pouches extend dorso-caudad over the region of the shoulder. The skin is firmly attached to underlying muscle only in the ventral thoracic region, but is capable of rather extensive movement or stretching elsewhere (Magalhaes 1968). The posterior pulling (retraction) of the pouch is accomplished by retractor muscle (*musculus trapezius auricularis*) which originates from the lumbar vertebrae. Its anterior portion is 2-headed in hamsters. The antero-dorsal head reaches the post-auricular region (*Tscherskia*) or is reduced (remaining Cricetina), while the ventral head reaches further anterior and inserts on the lateral or / and the medial wall of the pouch (Aristov 1988). The extended portions of buccinatorius muscle which originates on the rostrum and the mandible and inserts short of the caudal end of the pouch aids its emptying by contraction. The crescentic pouch aperture, which is located approximately opposite the posterior $^2/_3$ of the upper diastema (Figure 14b), is controlled by a sphincter (*musculus orbicularis oris*) which is also part of the buccinatorius muscle. The inner pouch wall has thick bands of elastin in the dermis and also consists of folds which become part of the wall when the pouch is full. In addition to this, an anteriorly projecting peninsula of highly folded tissue is integrated into the posteromedial pouch wall, thus allowing for additional
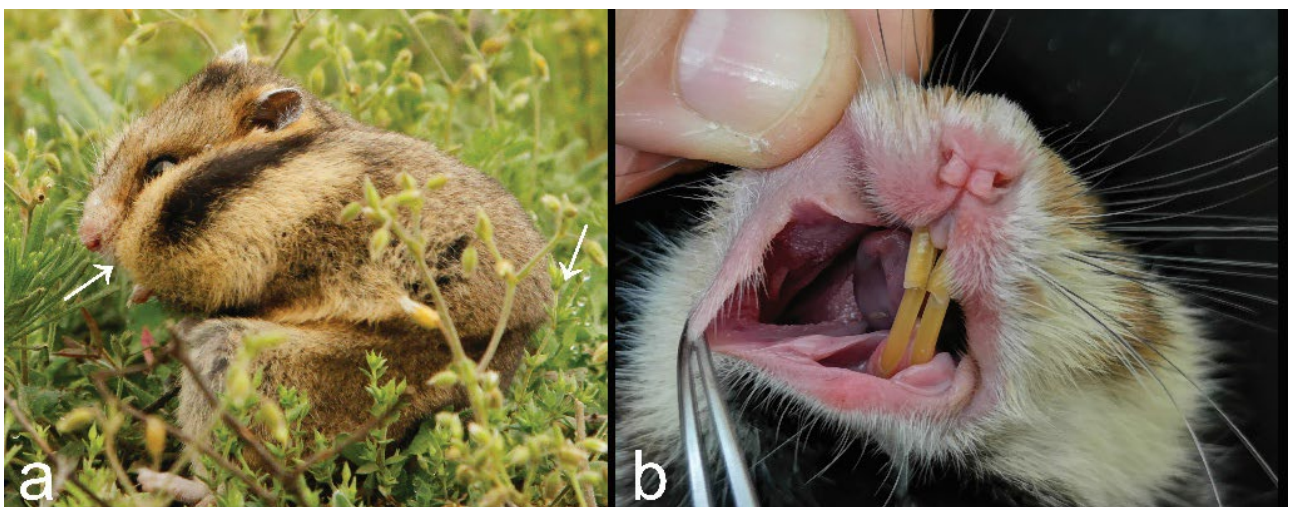
Figure 14: Romanian golden hamster (*Mesocricetus newtoni*) with fully distended cheek pouches (a). Arrows point to extreme ends of the left pouch. Entrance to the right cheek pouch (b) in common hamster *Cricetus cricetus*. Photo by Gabriel Chişamera (a) and Boris Kryštufek (b)

increase of the volume when food is stored in the pouch. The pouches empty into *vestibulum oris retrobuccalis* of the oral cavity. When empty, the pouch is in shape of coarse longitudinal folds which allow for distension (Keyes & Dale 1944, Priddy & Broddie 1948, Ryan 1986, Aristov 1988). During feeding, food items are shoved into pouches, transported and hoarded inside the burrow (Kryštufek et al. 2020). In *C. cricetus*, pouches filled with air reportedly ensure buoyancy for swimming (Sidorov et al. 2009) and females of *M. auratus* are said to carry their young inside the pouches (Witte 1971).

The stomach consists of two chambers which are sharply separated from each other by the incisurae of the greater and lesser curvatures (Figure 15). These chambers are a blind forestomach or esophageal diverticulum (cardiac part, *proventriculus*) and a true or glandular stomach (*ventriculus glandularis*). The two chambers are of approximately the same size. The esophagus enters into the forestomach, and the pyloric region of the glandular stomach empties into the duodenum of the small intestine. Length of the forestomach / true stomach is ~ 18 / 20 mm in *Mesocricetus auratus* (Magalhaes 1968) and 45–50 / 30–40 mm in *Cricetus cricetus* (Reznik et al. 1979). The forestomach lacks glands and is lined with simple keratinized (corneous) epithelium; it is putatively the esophageal diverticulum and separated from the mucosal glandular lining of the true stomach by a distinct border (*margo plicatus*). The equal division of keratinized and glandular tissue is characteristic of *Cricetulus, Tscherskia* and *Mesocricetus*. In its more derived stage, the corneous epithelium extends into glandular section of stomach, but does not cross the isthmus (*Cricetus, Allocricetulus*). In Urocricetini new tribe, the keratinized (*i.e.* non-glandular) section extends beyond the isthmus and in *Phodopus* occupies the greater part of glandular stomach (Figure 15b). The *margo plicatus* is simple, with no added folds in all hamsters with convoluted margo except *Allocricetulus*. The majority of hamsters have glands in the pyloric portion (pyloric glands) which, however, are absent in *Phodopus*.

The caecum of true hamsters is a large structure and its retaining capacity exceeds that of the stomach. Its length is up to 150 mm in *C. cricetus* and 54–82 mm in *Mesocricetus auratus*. The proximal part usually has at least 1 dilated, ampullary swelling (*ampulla coli*). *Mesocricetus*,

Allocricetulus and *Cricetus* have 3 ampullae and *Tscherskia* has 5 of them. They are formed by a colic spiral adjacent to the caecum, while additional ampullae associate with the ascending colon posterior to the colic spiral (Vorontsov 1962). Intestine is 3.4–3.7-times the length of head and body in great majority of hamsters. The intestine is relatively longer in *Urocricetus* and *Nothocricetulus* (the quotient = 4.0–4.1), *Mesocricetus* (= 5.8–6.9) and *Cricetus* (= 6.4) (Vorontsov 1962).
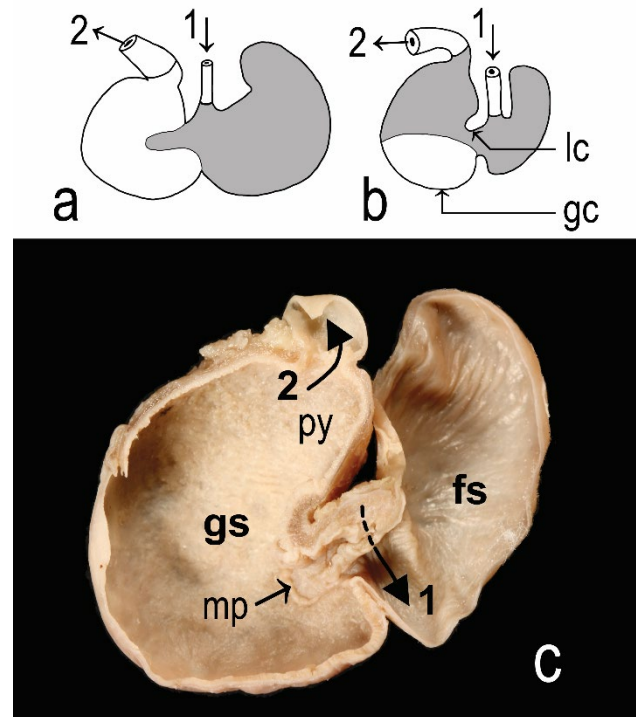
Figure 15: Stomach cut longitudinally. Schematic drawings in *Cricetus cricetus* (a) and *Phodopus roborovskii* (b); c – *Mesocricetus auratus*. The keratinized section (forestomach) is shaded grey in (a) and (b). 1 – from the oesophagus; 2 – to the intestine; fs – forestomach; gs – glandular stomach; py – *pylorus*; mp – *margo plicatus*; gc – greater curvature; lc – lesser curvature. (a) and (b) modified from Tullberg (1899) and Vorontsov (1962), respectively; (c) photo by B. Kryštufek

All true hamsters, with the exception of *Mesocricetus*, lack gall bladder (Ross 1992).

Penis and os genitale

Callery (1951) introduced the term *os genitale* to designate either the baculum of the male or *os clitoridis* of the female, and we now follow his nomenclature. Glans penis and baculum were used in traditional classification (Argyropulo 1933c) and phylogenetic reconstructions of Cricetinae (Vorontsov 1982, Ross 1992).
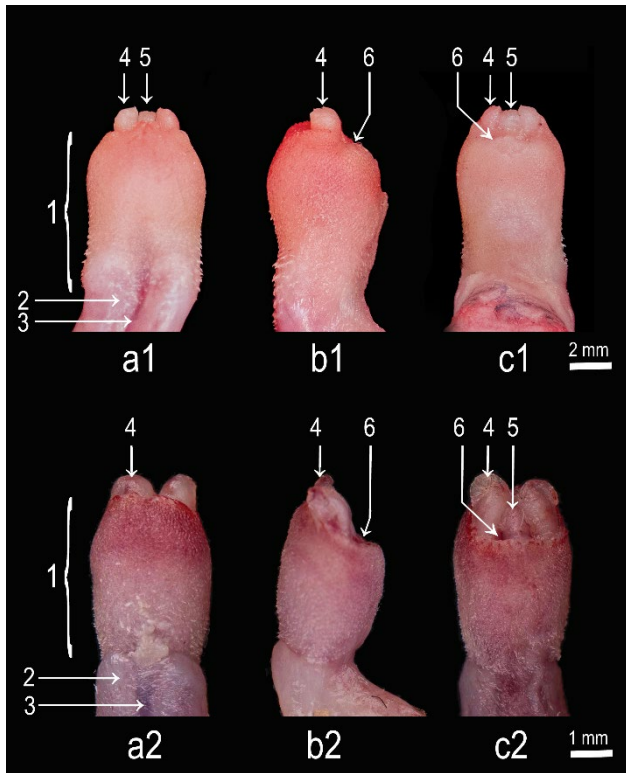
Figure 16: Glans penis in common hamster *Cricetus cricetus* (a1–c1), and Syrian golden hamster *Mesocricetus auratus* (a2–c2) in (a) dorsal view (*dorsum penis*), (b) lateral view, and (c) ventral view. 1 – glans (*glans penis*); 2 – body (*corpus penis*); 3 – dorsal vein; 4 – lateral papilla (*papilla lateralis*); 5 – central papilla (*papilla centralis*); 6 – *ostium urethrae externum*. Photo: David Kunc

Penis and baculum are of same basic type as in Arvicolinae. Therefore, when not erected, the penis directs cranidad and flexes sharply caudad; erected penis turns cranidad. The glans is cylindrically shaped with a rounded or truncate distal edge (Figure 16). Many microscopically visible spines are found on its surface. At the top are digit-like processes (papillae, bacular mounds). The three papillae surrounding the urethra, the central and 2 lateral, are frequently of sub-equal size and accommodate the tips of the 3 distal denticles of the baculum (trident). These papillae are present in all hamsters. Some hamsters also have a dorsally situated lingual papilla and / or ventrally situated 1–3 ventral papillae.

Positioned in the glans penis is a heterotopic bone called the baculum (*os penis* or *os priapi*). The baculum is situated near the centre of the glans and extends for most of its length from the erectile tissue (*corpora cavernosa penis*) to the terminal papillae. It is of a complex quadripartite type (Figure 17), composed of a bony shaft (proximal baculum) and three finger-like processes (digits or denticles) attached to the tip and forming a distal baculum (trident). Such baculum is

widespread in Cricetidae. Central denticle is usually the longest and rod-shaped. The proximal part of the bony shaft is markedly expanded laterally and grooved ventrally. Distal baculum remains cartilaginous in Phodopina and is only partially osseous in *Mesocricetus*; in the remaining hamsters, the distal baculum is more or less completely osseous (Figure 17). In Syrian golden hamster *Mesocricetus auratus*, the baculum does not reach maximum development until late in the animal's reproductive life (Callery 1951).
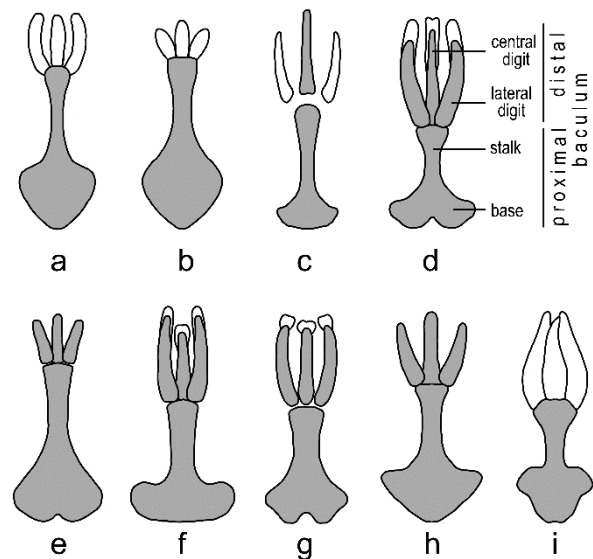
Figure 17: Outline of baculum in true hamsters: a – *Cricetiscus sungorus*; b – *Phodopus roborovskii*; c – *Tscherskia triton*; d – *Cricetulus barabensis*; e – *Nothocricetulus migratorius*; f – *Allocricetulus eversmanni*; g – *A. curtatus*; h – *Cricetus cricetus*; i – *Mesocricetus brandti*. Osseous parts are shaded grey; regions which remain cartilaginous or ossify late are white. Proximal is at the base. Modified from Bittera (1918), Argyropulo (1933c), Tokuda (1941), Callery (1951), Didier (1953), Vorontsov (1982), Ross (1992), and Yiğit et al. (2000).

Baubellum (*os clitoridis*) is considerably smaller than the baculum and of simpler shape. In Syrian golden hamster, it is spatulate and attains its maximum length (~ 1.5 mm) by the age of 50 days (Callery 1951). Baubellum was not used in taxonomy of true hamsters so far.

Skull

The appearance of skull (Figure 18) is murine in Urocricetini, *Tscherskia, Cansumys, Cricetulus, Allocricetulus*, and *Nothocricetulus* (Figures 26, 34, 48, 52, 103 & 114). Dorsal profile is more or less bowed, the rostrum is usually broad, braincase is longer than wide
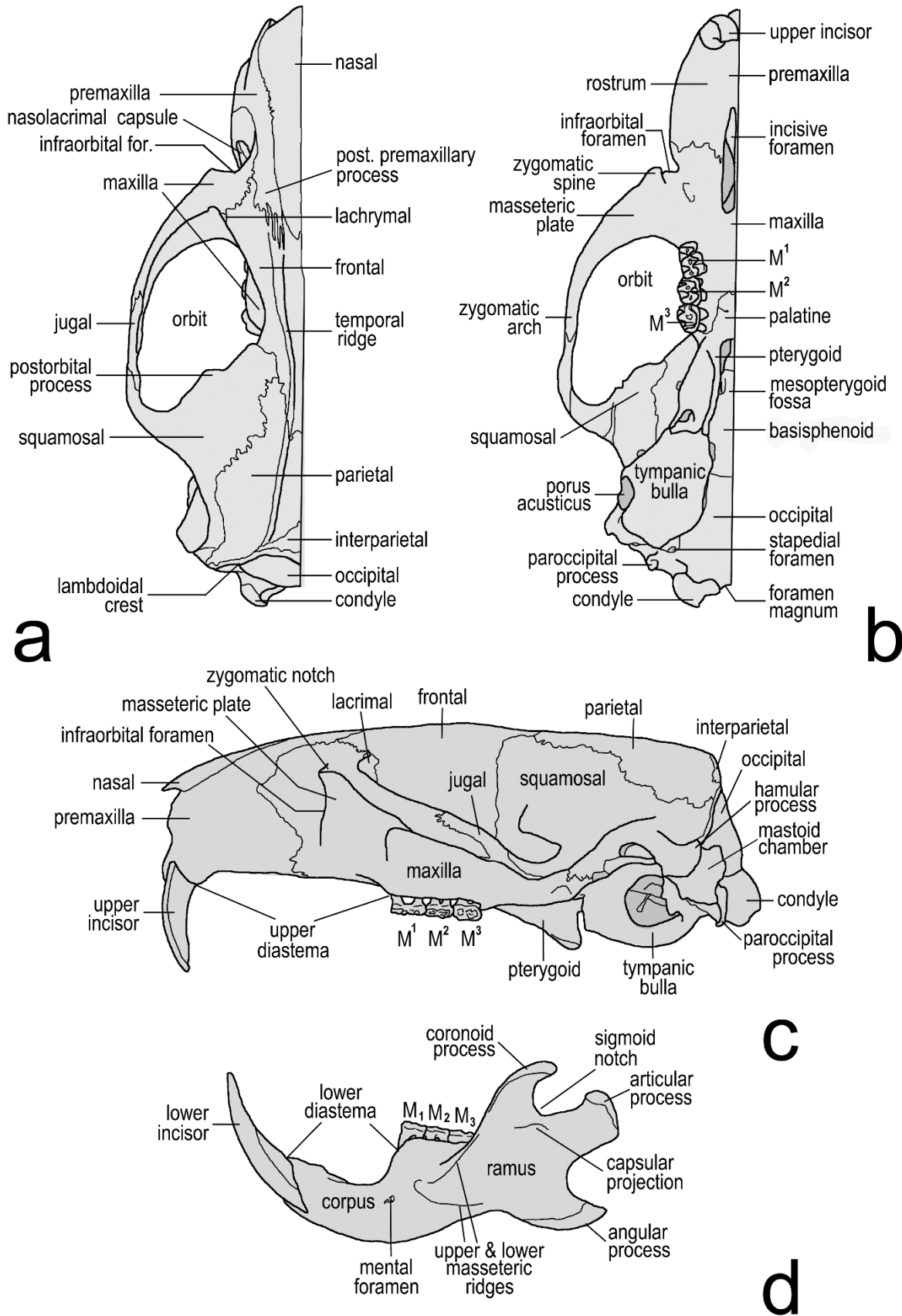
Figure 18: *Cricetus* skull in dorsal (a) and ventral (b) views (only half of the skull shown); lateral views of skull (c) and mandible (d). Abbreviations: M^1, M^2, M^3 / M$_1$, M$_2$, M$_3$ – 1st, 2nd and 3rd upper / lower molars, respectively.

(equidimensional, *i. e.* circular in *Phodopus roborovskii*), and the occipital region is occasionally shifted posteriorly, hence the condyles are seen from above. Zygomata are rather weak, either expanding evenly or displaying straight arches at their middle. Nasals are fairly long; they taper posteriorly and usually reach the level of lacrimal bones. Interorbital region shows no peculiarities except being ridged in *Tscherskia* and *Cansumys*; usually it is of about same width as rostrum. Parietals are of moderate size, therefore leaving squamosals to cover a considerable portion of dorsal neurocraniaum (*e. g. Tscherskia*); on the other extreme, the parietals expand over the entire roof of the braincase (*e. g. Phodopus roborovskii*). Interparietal is of variable shape, from octagonal to ligulate. Incisive foramina are moderately long to long and frequently reach anterior margin of M^1. Hard palate terminates at posterior edge of M^3 or behind; the length of mesopterygoid fossa is at least twice its width.

The skull is robust and heavy in *Cricetus* (Figure 18) and *Mesocricetus* (Figures 85 & 94). Dorsal profile is nearly flat, though sloping gradually in front of lacrimal region. Rostrum is clearly wider than the interorbital region,
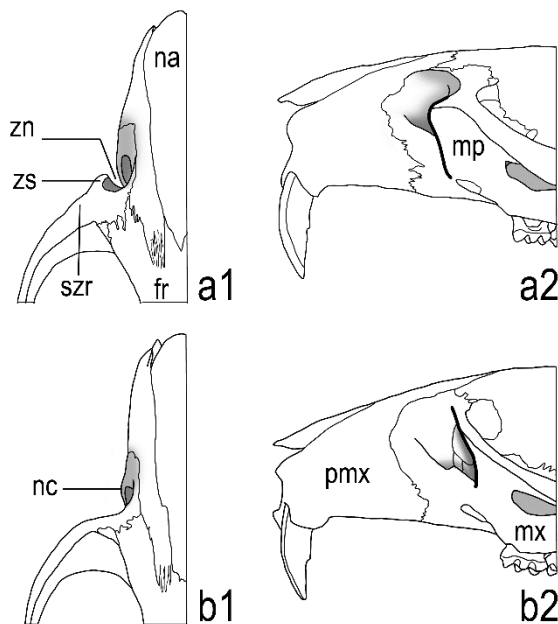
Figure 19: Dorsal (a1, b1) and lateral (a2, b2) view of the rostral and zygomatic regions, illustrating the variation in the zygomasseteric structure in *Cricetus cricetus* (a) and *Mesocricetus auratus* (b). The bold line shows the anterior margin of the masseteric plate (a2) and the inferior maxillary root of zygoma (b2). Not to scale. For acronyms see Figure 20.

and the nasals posteriorly transgress the level of lacrimal bones. Zygomatic arches are either elliptic (*Cricetus*) or run parallel (*Mesocricetus*). Brain-case is approximately as long as wide with the occipital bone strongly projecting backward; condyles are clearly seen from above. Adult skull is heavily ridged. Supratemporal ridges usually run from the naso-frontal suture backward, reaching a strong lambdoid crest situated along the posterior border of a small interparietal which is of triangular, crescentic or rectangular shape. The two ridges closely converge on the posterior frontals and diverge gradually towards the lambdoid crest. They never merge into a true sagittal crest, though the narrowed area between the converging ridges is crest-like in very old individuals. Incisive foramina are short to moderately long.

Hamsters are unique among Muroidea in their variability of zygomasseteric specialization (Figures 19 & 20). The latter denotes the development of anterior portion of lateral masseteric muscle and its insertion on the masseteric plate and / or rostrum. Typical of Muroidea, including the majority of hamsters (*Urocricetus, Cricetiscus, Tscherskia, Cricetulus,* and *Cricetus*), is myomorhmous zygomasseteric structure (Figure 19a) with well-marked external plate of infraorbital canal (masseteric or zygomatic plate), marked zygomatic spine (keel) and deep zygomatic notch; the notch and the keel are seen in dorsal view. The anterior portion of lateral masseter (*masseter lateralis anterior*) inserts on the masseteric plate, while the medial masseter (*masseter medialis anterior*) reaches rostrum through the infraorbital foramen; this is markedly wider above than below. In pseudo-sciuromorphous type (Figure 19b), the zygomatic plate is narrowed to an extent which does not prevent the lateral masseter from reaching the rostrum; the medial masseter likewise inserts on the rostrum through the infraorbital canal which typically has nearly oval outer side (Figure 20).

Zygomatic keel and notch are both absent and the anterior edge of zygoma transgresses into the rostrum as a smooth curve (Figure 19b). This type is characteristic of *Mesocricetus, Phodopus, Cansumys*, and *Allocricetulus*. Transitional morphotypes between these extremes were reported in Phodopina and *Cricetulus*. *Nothocricetulus* displays either type of zygomasseteric structure with all transitions in-between (Lebedev & Potapova 2008).
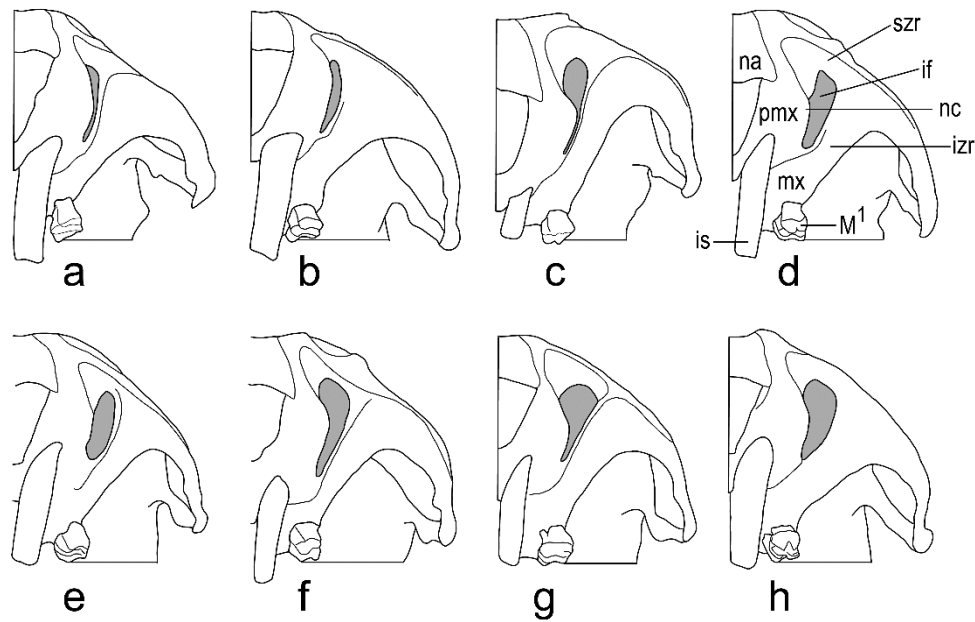
Figure 20: Frontal side of the left zygomasseteric region in true hamsters to show differences in size and shape of infraorbital foramen. The foramen is most constricted at top left and most expanded at bottom right: a – *Cricetus cricetus*; b – *Mesocricetus brandti*; c – *Cricetiscus sungorus*; d – *Nothocricetulus migratorius*; e – *Allocricetulus curtatus*; f – *Phodopus roborovskii*; g – *Cricetulus barabensis*; h – *Mesocricetus auratus*. Not to scale. Acronyms: fr – frontal bone; if – infraorbital foramen; is – upper incisor; izr – inferior maxillary root of zygoma; M[1] – 1st upper molar; mp – masseteric plate; mx – maxillary; na – nasal bone; nc – nasolacrimal capsule; pmx – premaxillary; szr – superior maxillary root of zygoma; zn – zygomatic notch; zs – zygomatic spine;

Mandible in Cricetinae is, like in Muroidea, with no specializations. The mandibular symphysis does not ossify. Corpus is slender and strongly curved. All processes are well developed; coronoid process is sickle-shaped and approximates in size and form the angular process. The root of lower incisor usually forms a slight bulge (capsular projection) on the outer wall of ramus (Figure 18d).

Dentition

Similarly to arvicolines, cricetines have 1 incisor and 3 molars in each jaw, hence the total number of teeth is 16. The dentition is monophyodont. Incisors erupt within 24 hours after birth and attain occlusion within 1 day (*Cricetulus, Mesocricetus*); in *Cricetus*, the eruption occurs at days 4–5 postpartum. Growth of lower incisors in Brandt's golden hamster *(Mesocricetus brandti)* is on average 1 cm per month (Lyman & O'Brien 1977). In Syrian golden hamster (*Mesocricetus auratus*), molars start extragingival eruption at the age 7–8 days (1st molars), 12–14 days (2nd molars) and 30–35 days (3rd molars), and molar rows come into full occlusion at the age of 40–45 days (Keyes & Dale 1944). Molars erupt between days 10 and 35 postpartum in *Cricetulus barabensis* (Kobayashi 1984), and days 10 and 33 in

Cricetus cricetus (Reznik et al. 1979). Mandibular molars emerge at same age as maxillary (*Cricetus*) or slightly earlier (*Cricetulus*).

Incisors grow from persistent pulps and have the front surface coated with enamel, thus leaving the dentine naked behind. The enamel layer is 60–65 μm thick on the upper incisors and 65–75 μm on the lower incisors (Kalthoff 2006). There is not much variation in this respect among genera and the thickness obviously does not correlate with body size (Figure 21). Unequal wear between the anterior and posterior surfaces results in a chisel point on the anterior crown. The procumbence of the upper incisors is opisthodont in *Cansumys* and *Phodopus*, and orthodont in the remaining genera. Incisors are moderately broad, with smooth front surface, which is normally pigmented from pale-yellow to yellow-orange. The upper incisors are more deeply coloured than the lower ones and the intensity increases with age. Just like in arvicolines, the upper incisors are more strongly curved and their alveolar sheet terminates in front of M[1]. The lower incisors are longer and less curved; only their distal ⅓ is erupted, while the proximal ⅔ is seated in the alveolus. The lower incisor terminates as a weak capsular projection (*processus alveolaris*) posterior to M₃ on the labial side of

mandibular ramus. The extragingival upper incisor may replace itself with a 1-week period, while the lower incisor requires 2.5–3 weeks.

On a cross-section, the upper incisors are more robust than the lower ones in all hamster genera studied by Kalthoff (2006). Length (thickness) × width ranges from 1.3 × 0.8 mm (*Phodopus*) to 1.7 × 1.5 mm (*Cricetus*); corresponding measurements on the lower incisors are from 1.1 × 0.75 mm (*Nothocricetulus, Phodopus*) to 1.4 × 1.3 mm (*Mesocricetus*). The upper incisor is comparatively the narrowest in *Phodopus* (length-to-width ratio = 1.6) and the broadest in *Mesocricetus* and *Cricetus* (= 1.1–1.2). The upper incisor is proportionally the narrowest in *Nothocricetulus* and *Phodopus* (= 1.8) and the broadest in *Mesocricetus* (= 1.25).
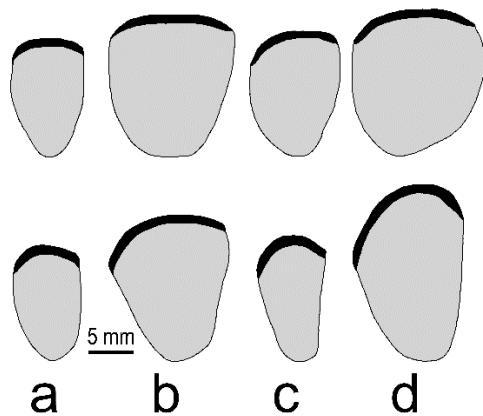
Figure 21: Incisor cross sections of (a) *Cricetiscus sungorus*, (b) *Mesocricetus auratus*, (c) *Nothocricetulus migratorius*, and (d) *Cricetus cricetus*. Dentine is shaded grey and enamel is shown in black. Upper incisors are on the top row, lower incisors are on the bottom line. Anterior is to the top and mesial is to the right. Modified from Kalthoff (2006)

Molars remain rooted throughout life (rhizodont), though the closure of pulps is retarded in *Cansumys*; they are cuspidate (polybunodont) and low-crowned (brachyodont) in the great majority of genera. *Cansumys* is the only extant hamster having high-crowned molars (mesodont or hypsodont, depending on the author). Usually, the number of roots is as follows: 4–5 on M^1, 3–4 on M^2, and 2–3 on M^3; each mandibular molar has 2 roots in an antero-posterior alignment. The 1st molar is the longest tooth in both rows. In the maxillary row, M^1 accounts for 40–45% of the tooth row, while M^3, which is usually the shortest, accounts for 25–27% of tooth row; M^3 is frequently nearly equidimensional

(length ≈ width). In the mandibular row, M_1 accounts for 35–40% of length of the entire row and the posterior molars $M_{2–3}$ are of about the same length (Wahlert 1984).

The occlusion pattern consists of cusps connected by ridges with folds and valleys (infolds) between them (Figure 22). Tubercles are arranged in two primary longitudinal rows, the inner (lingual) and the outer (buccal). In all Cricetinae, 4 main cusps are easily recognizable in both the upper and the lower molars. These cusps are readily homologized with cusps of a modified tribosphenic molar and are usually denominated as proto-, para-, hypo-, and metacone in the maxillary row; the extension -conid denotes cusps in the mandibular row (Hooper 1952, Herskovitz 1962, Topachevskiy & Skorik 1992, Ross 1992).

Both 1st molars have anteriorly a pair of conules (M^1) or conulids (M_1). Rudiments of anterobuccal conules / conulids persist as enamel ridges in the remaining posteriorly located molars. M^1 has 4 cones of the major tribosphenic pattern posterior to 2 anterocones. The basic pattern of M^1 is modified in $M^{2–3}$ by marked reduction of the buccal anterocone to a mere ridge and a complete loss of lingual anterocone. The M^2 has an additional postero-buccal ridge (posteroloph); its metacone tends toward reduction. Hypocone and metacone are evidently smaller than protocone and paracone on M^3 and frequently loose characteristic cusp-like appearance.

Alternation between the lingual and buccal cusps is more obvious on the mandibular molars and the buccal series is clearly shifted posteriorly. M_1 has 6 cusps and postero-lingual ridge (posterolophid). The anteroconids are smaller than on M^1 and frequently reduced to a crescent enamel ridge; in such cases, the conids are loosely separated by a minute anterior groove. $M_{2–3}$ retain the buccal anteroconid, which is also reduced to enamel ridge; caudally is postero-lingual ridge (cingulum sensu Niethammer 1982). Entoconid tends towards reduction on M_3. On maxillary molars, the buccal cusps are higher than the lingual ones, and the opposite is true for the mandibular row.

The cusps are separated by broad sulci and deep occlusal fossae, which are emphasized by wear. Fossae

become apparent as oval enamel islands (internal infolds) in all upper molars, but remain lingually open in mandibular molars. Internal infolds (*if*) are designated in the antero-posterior direction as *if1* and *if2*. Grooves form re-entrant loops, which are present on the inner and outer sides of all molars. Primary folds (*pf*) are on the outer side of maxillary molars and on the inner side of the lower molars. There are 2 primary folds on each molar, *i. e.* the anterior (*pf1*) and the posterior fold (*pf2*). The occlusal surface on all upper molars is marked by X-ridge connections between protocone-paracone and hypocone-metacone.
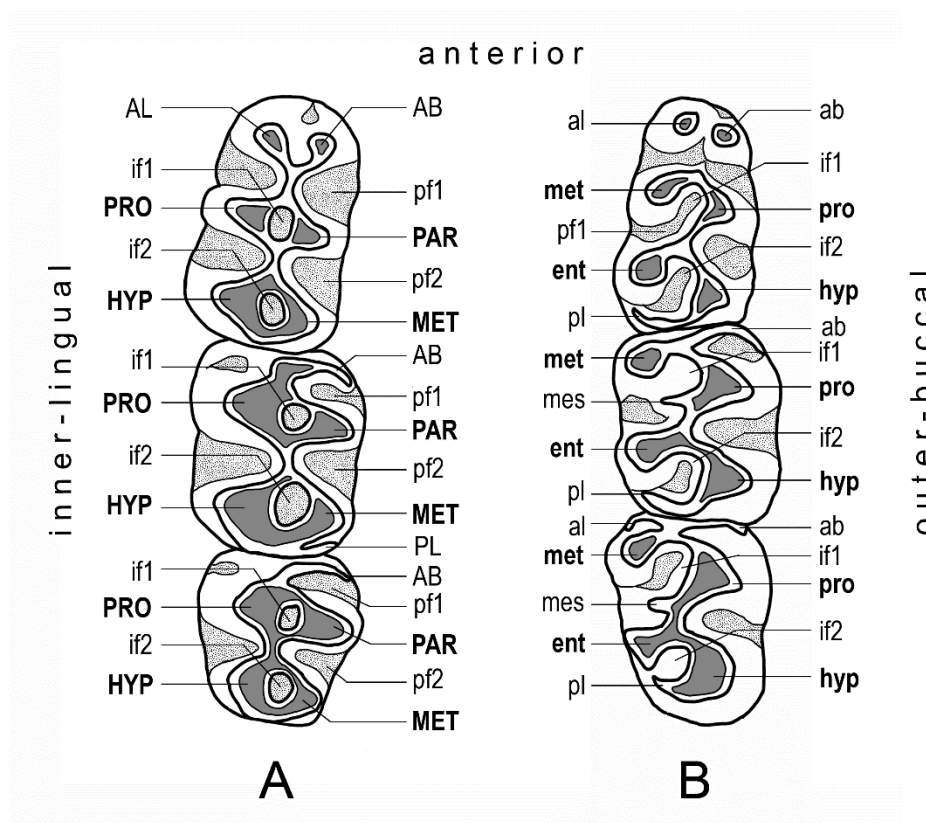
Figure 22: Upper left (A) and lower right (B) molars of a generalized hamster (Cricetinae) showing occlusal structure. Lingual is to the left and anterior is at the top. Dentine is shaded dark grey. Terminology follows Herskovitz (1962) and Ross (1992); acronyms for cones are capitalized and for conulids are given in lower-case letters. The main cones/conulids of tribosphenic pattern are highlighted in bold. AB – anterobuccal conule (buccal anterocone); ab – anterobuccal conulid (buccal anteroconulid); AL – anterolingual conule (lingual anterocone); al – anterolingual conulid (lingual anteroconulid); ent – entolophid; HYP –hypocone; hyp – hypoconid; if1 – first internal fold; if2 – second internal fold; mes – mesolophid; MET – metacone; met – metaconid; PAR – paracone; pf1 – first primary fold; pf2 –second primary fold; PL – posteroloph; pl – posterolophid; PRO –protocone; pro – protoconid.

Abbreviations

Molars are abbreviated by the upper-case letter "M" with numbers 1–3 indicating their position in the row; superscript / subscript denotes upper (maxillary) / lower (mandibular) molars. *E.g.* M^2 is the 2nd upper molar. For further abbreviations of molar morphology see Figure 18.

2n	diploid number of chromosomes
NF	fundamental number of chromosomal arms
NF_a	fundamental number of autosomal arms
mt	mitochondrial (genome, DNA)
Cyt*b*	cytochrome *b* (gene, sequence)
K2P	genetic distance calculated using the Kimura 2-parameter model
TMRCA	the most recent common ancestor
sp. / spp	species (singular / plural)
ssp. / sspp.	subspecies (singular / plural)
ky / My	thousand / million years
kya / Mya	thousand / million years ago
a. s. l.	[elevation] above sea level
cf	(*confer* or *conferatur* = compare) used to refer the reader to other material for comparison with the topic being discussed
e. g.	(*exempli gratia*) for example
i. e.	(*id est*) that is
in litt	(in litteris) information communicated in writing
l. c.	*loco citato* (in the place cited)
s. str.	*sensu stricto* (in a narrow sense)
s. lat.	*sensu lato* (in a broad sense)
v.	*versus* (against)
sic	Latin adverb (thus, so, in this manner); inserted after a quotation indicates that the quoted matter has been transcribed or translated as found in the source text, including erroneous spelling
SD	standard deviation
CI	confidence interval
~	approximately
≈	almost equal to
< / >	less than / more than
≤ / ≥	less than or equal / more than or equal

SUBFAMILY: CRICETINAE FISCHER, 1817 – TRUE HAMSTERS

Mures buccati Gmelin, 1792: 242 (with reference to "Systema Naturae").

Criceti Gmelin, 1792: 242.

Buccati Gmelin, 1805: 327.

Cricetini Fischer, 1817: 372. Not Fischer von Waldheim (e.g. Gromov & Baranova 1981, McKenna & Bell 1997); in 1817, Fisher still did not hold his noble title with the extension 'von Waldheim'.

Cricetinorum Fischer, 1817: 410. Explicitly proposed as a family.

Cricetina Gray, 1825: 342.

Criceti Pallas 1831: 160. Proposed as a division of Glires.

Cricetinae Murray 1866: 356. The first ranking as a subfamily in modern sense.

Cricetidae Rochebrune, 1883: 66. The first ranking as a family in modern sense.

Cricotini: Schegolev 1925: 19. Ranked as a subfamily; probably incorrect subsequent spelling of Cricetini.

Type genus by tautonomy is "*Cricetus* Cuv[ier]" in Fischer (1817: 410) (= *Hamster* Lacépède).

The context of true hamsters within the classis Mammalia is as follows:

Class Mammalia Linnaeus, 1758
  Subclass Theria Parker & Haswell, 1897
    Infraclass Eutheria Gill, 1872
      Magnorder Boreoeutheria Springer & de Jong, 2001
        Superorder Euarchantoglires Murphy, Eizirik, O'Brien et al., 2001
          Order Rodentia Bowdich, 1821
            Suborder Myomorpha Brandt, 1855
              Superfamily Muroidea Illiger, 1811
                Family Cricetidae Fischer, 1817
                  Subfamily Cricetinae Fischer, 1817

Cricetinae are in a sister position against voles and lemmings Arvicolianae; the two subfamilies diverged approximately 17.23 Mya (95% CI = 14.84–19.67 Mya) (Lebedev et al. 2018a), *i. e.* in Early Miocene or lower Middle Miocene. Fossils have been known since the Middle Miocene (McKenna & Bell 1997) or Late Miocene (Topachevsky & Skorik 1992). Cricetinae contain 9 extant and 15 fossil genera (McKenna & Bell 1997; this volume).

Key to tribes and genera

Fore keys to hamster genera see also Ellerman (1941: 338) and Pavlinov et al. (1995: 80–81); for a key to species see Corbet (1978: 89–93).

1a) Plantar surface is either partly hairy between the pads (Figure 101) or is furry throughout its surface (Figure 109); bullae are flattened, bony eustachian tube is elongated (Figure 99a) ……………………………..2 (tribe Urocricetini)

1b) Plantar surface is nude or furry posterior to pads (Figures 33 & 80); bullae are of normal size, bony eustachian tube is short (Figure 99b)……………………………………………....4

2a) Tail length accounts for > 30% of length of head and body; plantar surface is only partly hairy between pads; 6 plantar pads (Figure 101); sphenofrontal foramen is present.……………*Urocricetus*

2b) Tail length accounts for < 20% of length of head and body; plantar surface is fully hairy and conceals 1–3 plantar pads (Figure 109); sphenofrontal foramen is absent ………………………..
…………………………..3 (subtribe Phodopina)

3a) Spinal stripe is absent (Figure 111c); white ventral pelage extends to dorsal side of the tail base (Figure 113a); 1 plantar pad (Figure 109a); the anterior edge of the superior maxillary root of zygoma forms right angle at its junction with the rostrum; nasals do not reach the level of lacrimals; incisive foramens of approximately same length as maxillary tooth-row; upper incisors are opisthodont (Figure 114); major molar cusps oppose each other and form transverse lophs; upper molars without internal fields (Figure 115); $2n = 34$ ………………………..….. *Phodopus*

3b) Spinal stripe is present (Figure 111a, b); white ventral pelage does not extend to dorsal side of the tail base (Figure 113b); 3 plantar pads (Figure 109c); the anterior edge of the superior maxillary root of zygoma forms a smooth curve at its junction with the rostrum; nasals reach the level of lacrimals; incisive foramens longer than maxillary tooth-row; upper incisors are orthodont (Figure

114); major molar cusps alternate; internal fields present on upper molars (Figure 117); $2n = 28$ ……………………………..……………....... *Cricetiscus*

4a) Subauricular dark stripe is present (Figure 9b, c); soles are largely nude between the metatarsal pads and on heels (Figure 80); > 10 mammae; subsquamosal foramen is absent and hamular process is not separated from squamosal (Figures 85 & 94); M_3 is larger than M_2; width-to-length ratio for 2nd and 3rd molars < 0.75 (Figures 86 & 95); entepicondylar foramen is absent in the distal end of humerus (Figure 78a); trident of baculum is largely cartilaginous even in adults (Figure 17i); $2n = 38–44$ ………..……………..…… *Mesocricetus*

4b) Subauricular dark stripe is absent; soles are hairy posterior to pads (Figure 33); 8 mammae; subsquamosal foramen is present and hamular process is separated from squamosal (Figure 34); M_3 is smaller than M_2; width-to-length ratio for 2nd and 3rd molars = 0.80–1.00 (Figure 35); entepicondylar foramen is present in the distal end of humerus (Figure 78b); trident of the baculum (at least the central digit) is osseous (Figure 17d–h); $2n = 20–34$ ………………….. 5 (tribe Cricetini)

5a) Tail accounts for ~ 70% of head and body length and is thickly clad with shaggy hairs which cover annulation; rostrum is parallel-sided; interparietal is broad and strap shaped; pterygoids are shorter than the maxillary tooth-row; coronoid process is short and blunt, not extending beyond the level of sigmoid notch; upper incisors are opisthodont; maxillary tooth-row slightly shorter than diastema, surrounded by a bony ridge (Figure 75); molars are robust and high-crowned (Figure 76b) …………………………………..…… *Cansumys*

5b) Tail accounts for < 65% of head and body length and is sparsely haired, annulation is exposed; rostrum is narrow anteriorly and widest at nasolacrimal capsule; interparietal is triangular or diamond-shaped; pterygoids are longer than the maxillary tooth-row; upper incisors are orthodont; maxillary tooth-row shorter than diastema,

without surrounding ridge (Figures 26, 34, 52 & 67); molars are weaker and low crowned (Figure 76a) ……………………..... 6 (subtribe Cricetina)

6a) Length of maxillary tooth-row ≥ 6.6 mm; belly is black throughout; 4 contrasting light patches present along the side (Figure 63); skull is robust with heavy temporal ridges; interparietal is triangular and small (Figure 67) ……………………………………….…. *Cricetus*

6b) Length of maxillary tooth-row < 6.6 mm; no contrasting light patches along the side; skull is less heavy and temporal ridges are weak or absent; interparietal is not triangular and extends across the majority of the cranium roof (Figures 26, 34 & 52) ………………………...….…………..7

7a) Size larger: length of head and body > 135 mm, condylobasal length of skull > 34 mm, length of maxillary tooth-row > 4.9 mm; tail long, accounting for > 40% of head and body length; distal tail frequently white; bullae are larger and elliptic; interparietal bone is hexagonal (Figure 26); coronal (fronto-parietal) suture is square-edged; 2n = 28 ………………..…………………….. *Tscherskia*

7b) Size smaller: length of head and body < 150 mm, condylobasal length of skull < 34 mm, length of maxillary tooth-row < 5.1 mm; tail usually shorter, accounting for < 42% of head and body; tail is of uniform colour; bullae are smaller and circular; interparietal bone is lingulate or diamond-shaped (Figure 34, 48 & 52); coronal (fronto-parietal) suture is rounded or W-shaped; 2n = 20–26 …………..……………………………………… 8

8a) Zygomatic notch and keel not visible in dorsal view; length of incisive foramina equals ~ ½ of diastema length (Figure 52); coronal suture usually W-shaped; coronoid process is long and extends back to the anterior margin of mandibular condyle ………………………………………….. *Allocricetulus*

8b) Zygomatic notch and keel usually visible in dorsal view; incisive foramina evidently longer than ½ of diastema (Figure 34 & 48); coronal suture smooth; coronoid process shorter and does not extend back to the anterior margin of mandibular condyle …………………………..………………… 9

9a) Distal baculum is of about same length as proximal stalk (Figure 17d); fronto-temporal angle of parietals closely approaches the posterior orbital edge, *sutura squamosa cranii* is consequently short in dorsal view (Figure 34); metalophule is absent; no X-pattern of enamel ridges between the proto-paracone and hypocone-metacone of M^{1-2}; mesolophid absent on M_3 (Figure 35 & 44) …………………...………………..... *Cricetulus*

9b) Distal baculum is much shorter than proximal stalk (Figure 17e); fronto-temporal angle of parietals does not closely approach the posterior orbital edge, *sutura squamosa cranii* is consequently longer in dorsal view (Figure 48); internal fold 2 is closed by metalophule, which creates X-pattern of enamel ridges between proto-paracone and hypocone-metacone of M^{1-2}; mesolophid present on lingual side of M_3 (Figure 49) ……………………………....…..... *Nothocricetulus*

TRIBE: Cricetini Fischer, 1817

Diagnosis and Comparisons. A central tribe of true hamsters Cricetinae which contains ½ of extant species and occupies the great majority of the range of the subfamily. The tribe is well defined by nucleotide sequences (Neumann et al. 2006, Lebedev et al. 2018a) and chromosomal data (Romanenko et al. 2007). However, not a single morphological trait is synapomorphic for all Cricetini. (1) Papillae fungiformes are present only on the dorsal side of the tongue and do not extend to its ventral surface as in the remaining Cricetinae (Vorontsov 1958). (2) Plantar pads are furry posterior to pads in Cricetini (Figure 33) and in Urocricetina (Figure 101), while they are largely nude in Mesocricetini (Figure 80) and densely furry in Phodopina (Figure 109). (3) Ossification of distal baculum is synchronous with the proximal baculum, while it is heavily postponed or entirely absent in the remaining hamsters (Figure 17). (4) Diploid number of chromosomes (2n ≤ 28) and fundamental number of autosomal arms (NF ≤ 42) are both low, while these parameters have higher values in the remaining hamsters (2n ≥ 28 and NF ≥ 48). Cricetini differ from Urocricetini by having (1) large and round bullae with short eustrachian tube; bullae are flattened and the eustachian tube is long in Urocricetini (Figure 99). (2) Lateral line is serpentinous with deep dorsal expansion of light ventral fur in Urocricetini (Figures 102 & 116), while it is less serpentinous or straight in Cricetini. (3) Corneous epithelium of the stomach is mainly restricted to the forestomach in Cricetini, while it may occupy most of glandular region in Urocricetini (Figure 15).
Cricetini differ from Mesocricetini in a series of traits. (1) Subauricular dark stripe is absent in Cricetini (present in *Allocricetulus*), while it is present in Mesocricetini (Figure 9b, c). (2) Papillae foliatae are arranged in 1 row (2 rows in Mesocricetini; Vorontsov 1958). (3) Gallbladder is absent, but present in Mesocricetini (Carleton & Musser 1984). (4) M_3 is smaller than M_2 in Cricetini and larger in Mesocricetini (Gromov et al. 1963, Ross 1992). (5) Width-to-length ratio for the 2nd and 3rd molars (maxillary and mandibular) is 0.80–1.00 in Cricetini, while the ratio is < 0.75 in Mesocricetini (Lozan 1971). (6) Rostrum is the widest at nasolacrimal capsule in Cricetini (with the exception of *Cansumys*), but is rectangular with parallel lateral margins in Mesocricetini. (7) Subsquamosal foramen is present between hamular process and squamosal in Cricetini, but absent in Mesocricetini (hamular process is not separated from squamosal). (8) Entepicondylar foramen is present in Cricetini and absent in Mesocricetini (Figure 78). (9) Number of mammae is low (8 nipples) in Cricetini but high (> 10 nipples) in Mesocricetini (Figure 11).

Distribution is Palaearctic, from West Europe to Korea, and from southern Siberia and Russian Far East to the Levant Coast, Iran, Afghanistan and Pakistan, north-western India, Nepal, and the Three Rivers Source Region (Sanjiangyuan) in China.

Content. The tribe includes 2 subtribes (Cricetina and Cansumyina) with 6 extant genera (*Cansumys, Tscherskia, Allocricetulus, Cricetus, Nothocricetulus, Cricetulus*) and 10 species.

SUBTRIBE: Cricetina Fischer, 1817

Subtribe Cricetina is the central group of true hamsters, comprising all genera of the tribe Cricetini, except *Cansumys*. For comparison see under Cansumyina new subtribe.

Diagnosis and Comparisons are detailed under Cansumyina new subtribe.

Distribution is as for the tribe.

Content. The subtribe includes 5 extant genera (*Tscherskia, Allocricetulus, Cricetus, Nothocricetulus, Cricetulus*) with 9 species.

GENUS: *Tscherskia* Ognev, 1914 – Rat-like Hamsters

Tscherskia Ognev, 1914: 102. Type species by monotypy is *Tscherskia albipes* Ognev [= *Cricetus triton* Winton].

Asiocricetus Kishida, 1929: 148. Type species is *Asiocricetus bampensis* Kishida [= *Tscherskia triton nestor* Thomas].

Tsherskia: Argyropulo, 1933b: 241. Incorrect subsequent spelling of *Tscherskia* Ognev.

Tscherkia: Fulton, 1968: 3. Incorrect subsequent spelling of *Tscherskia* Ognev.

Taxonomy. Ognev (1914) named and described *Tscherskia* as a genus for rat-like hamsters from the southernmost part of the Russian Far East on the Korean border. He suggested its close links to Nearctic wood rats (*Neotoma*) and climbing rats (*Ototylomys*). Ognev, however, overlooked that by than 3 taxa of rat-like hamsters had already been named by Winton (1899) and Thomas (1907, 1908a) as members of the genus *Cricetulus*. Satunin (1902) classified *triton* into *Urocricetus*, which he established as a subgenus of *Cricetulus* and also incorporated *Urocricetus kamensis* and *Cricetulus longicaudatus*; Trouessart (1904) promptly grasped this arrangement. Tate (1947) spread different names for rat-like hamsters into 2 groups; the "little hamsters" (*Cricetulus*) with long tail but short hind-foot included *triton* and *kamensis* (now in *Urocricetus*); *nestor* and *arenosus* were in a group characterized by long hind foot.

Howell (1929) and after him Argyropulo (1933b, c) downgraded *Tscherskia* to a subgenus of *Cricetulus* and their view persisted in the mainstream taxonomic literature for the rest of the century (Corbet & Hill 1980, 1986, Honacki et al. 1982, Kowalski 2001). Tokuda (1941), however, restored the generic status of *Tscherskia* which started to be accepted in 1950s, particularly by students of hamsters' karyology (Makino 1951, Won 1961, Kartavtzeva et el. 1980, Kartavtseva & Alekseeva 1987) and gained general credit in the 1980s (Gromov & Baranova 1981, Vorontsov 1982, Kostenko 1984, Pavlinov and Rossolimo 1987). Some authors, the Chinese in particular, continued to classify *Tscherskia* as a subgenus of *Cricetulus* well into the 1990s (Corbet & Hill 1992, Li & Wang 1996, Zhang et al. 1997) and even after 2000 (Luo et al. 2000, Chen et al.

2002, Wu & Fu 2005, Xie & Zhang 2005b, Wu et al. 2015, Ding et al. 2016a).

In Miljutin's (2011) view, *Tscherskia* is characterised by generalized muroid body plan to a greater extent than other hamsters and is as such the least advanced member of the subfamily. Phylogenetic analyses based on nucleotide sequences (Lebedev et al. 2018a, Jiang et al. 2024) and chromosomal data (Romanenko et al. 2007) ranked *Tscherskia* as a sister genus to the remaining Cricetina. Application of molecular clock on the concatenation of five nuclear genes yielded divergence time against the remaining Cricetina of 6.36 Mya (95% CI = 4.83–8.01 Mya; Lebedev et al. 2018a). Neumann (2007) obtained similar divergences, which varied from 4.8±0.2 to 6.7±1.4 Mya, depending on the calibration point; the recent estimate by Jiang et al. (2024) is significantly higher (8.32 Mya). Chromosomal data returned much lower divergence (2.8 Mya) between *Tscherskia* and *Mesocricetus* (Kartavtsev et al. 1984a, b) *i. e.* the genera with the least similar karyotypes of any Cricetinae.

Fossil record of *Tscherskia* is contested; remnants from Middle Pliocene pretty closely resemble the extant species. The putative ancestor is either *Cricetinus varians* Zdansky, 1928, or *Kowalskia* from the Pliocene (Zheng 1984). *Tscherskia* occupied Europe prior to the Early Pleistocene and was present in Asia east of the Baikal Region ever since the Early Pleistocene (Gromov & Baranova 1981). The extinct *Tscherskia rusa* Storch, 1974, which is known only from the Holocene of Bastam (north-west Iranian Azerbaijan), does not fit this picture neatly. *T. rusa* differs from the extant *T. triton* by having a smaller dorso-temporal vacuity, a smooth coronal suture (square-edged in *T. triton*), a triangular interparietal (hexagonal in *T. triton*), a clearly proodont incisors, decidedly shorter nasals, proportionally small coronoid process and a large angular process.

Tscherskia was treated as a monospecific genus (or subgenus) in the majority of taxonomic works (e.g. Allen 1940, Ellerman 1941, Corbet 1978, Wang 2003). As an exception, Tate (1947) recognized 3 species (*triton*, *nestor* and *arenosus*). Vorontsov & Radjabli (1969), who misinterpreted supernumerary B chromosomes as a trait of taxonomic importance, linked different

chromosomal numbers with species names: *triton* (2n = 30) and *albipes* (2n = 28); their proposition was refuted by Kartavtseva et al. (1980). Gromov & Erbajeva (1995) still regarded *T. albipes* as a species in its own right. A 2-species taxonomy as adopted in this volume follows Jiang et al. (2024) with nomenclatural amendments.

Argyropulo (1933b, c) relegated *Cansumys canus* to a subspecies of the common rat-like hamster, which persisted in the literature until Ross (1988) showed that *Cansumys* and *Tscherskia* are distinct genera (see under *Cansumys*). Irrespective of this, some authors synonymized *ningshaanensis* with *Cansumys canus* (e.g. Zhang et al. 1997, Wang 2003, Liao et al. 2007). Song (1985) named *ningshaanensis* as a subspecies of *triton* diagnosing it by an extensive white tail tip (tail is uniformly dark in *Cansumys*). Musser and Carleton (2005: 1041) stressed that molar tooth-row in *ningshaanensis* (= 4.7–5.7 mm) is of same length as in *triton* and decidedly shorter than in *Cansumys canus* (= 6.4–6.6 mm). Jiang et al. (2024) provided molecular evidence showing that *ningshaanensis* was part of *Tscherskia* and distinct from *Cansumys*.

Characteristics. *Tscherskia* differs clearly from the remaining Cricetina morphologically (Ross 1992), chromosomally (Romanenko et al. 2007), and genetically (Lebedev et al. 2003, 2018a, Neumann 2007). Ross (1992) diagnosed the genus by the (1) presence of 5 saccular dilatations (*ampullae colli*) associated with caecum (cf. Figure 127 in Vorontsov 1967), (2) a square-edged coronal (fronto-parietal) suture, and by (3) occasional presence of supernumerary (B) chromosomes (which were never reported in other Cricetinae). In addition, *Tscherskia* shows (4) a weakly developed semilunar sulcus on the tongue (absent in *Cricetulus* and *Nothocricetulus*), (5) well-developed *torus linguae* (weak in *Cricetulus* and *Nothocricetulus*), and (6) longer median sulcus (shorter in *Allocricetulus*). Glandular and corneous epithelium of stomach are of about equal extent, while in *Cricetus* and *Allocricetulus* the corneous epithelium extends into the glandular portion. In comparison to *Cricetus* and *Allocricetulus*, *Tscherskia* has shorter intestine relative to head and body length.

Key to species

1a) Dorsal pelage blackish-brown; feet white; sagittal suture longer than the width of parietal; incisive foramina longer, their posterior margin terminates just anterior to the M^1 level (Figure 26); present in western Henan (west of 112th meridian) and southern Shaanxi (south of 34.5th parallel) (Figure 28) ………………………………………. *collina*

1b) Dorsal pelage buffy-grey or drab-grey; feet frequently with dusky ankles and proximal metatarsal area (Figure 25); length of sagittal suture approximately equals width of parietal; incisive foramina shorter, their posterior margin terminates well in front to the M^1 level (Figure 26); the only rat-like hamster throughout much of the generic range; in Henan present east of 111th meridian, in Shaanxi present north of 34.5th parallel (Figure 23) …………………..……. *triton*

Tscherskia triton (Winton, 1899) – Common Rat-like Hamster

Cricetus (Cricetulus) triton Winton, 1899: 575. Not "de Winton and Styan" (Lee et al. 2014: 167). Type locality: "N[orthern] Shantung [Shandong]", China.

[Cricetus (Urocricetus)] triton: Trouessart, 1904: 395. Name combination.

Cricetulus nestor Thomas, 1907: 466. Type locality: "Kimhoa [Gimhwa], 65 miles [105 km] N.E. [north-east] of Seoul, 300' [914 m]", South Korea.

Cricetulus triton: Thomas, 1908b: 9. Name combination.

Cricetulus triton incanus Thomas, 1908a: 45. Type locality: "Near Ko-lan-chow, Shan-si"; emended to "12 miles N.W. [north-west] of Ko-lan-chow [Kelan], Shan-si [Shanxi]. 7000' [2,134 m]" (Thomas 1908b: 974).

Tscherskia albipes Ognev, 1914: 103. Type locality: "долина р. Туманъ-ганы (Туманъ-ула), граница Российской Имперіи и Кореи"; in German summary (p. 125): "sandige, durch Graswuchs befeistige Dünen auf dem linken Ufer des Flusses Tuman-Gan (im südlichen Teil des russischen Primorsky-Gebietes, in der Nähe der Grenze mit Korea)." Pavlinov & Rossolimo (1987: 170) give the type locality as: "Приморский кр., р. Тумыньцзян", i.e. Primorskiy Krai, Tymyn'tszyan [Tumannaya] River, Russian Federation.

Cricetulus triton nestor: Howell, 1929: 50. New rank for n*estor*.

Cricetulus triton fuscipes G. Allen, 1925: 5. Type locality: "Peking [Beijing], Chili [Zhili] Province [Beijing Province], China."

Asiocricetus bampensis Kishida, 1929: 148, 150. Type locality: Bam-po (also Bampo or Man'po), Kankyo-hokudo (north Hangieng), 50 feet (15 m), South Korea (cf. Kuroda 1934: 231, Jones & Johnson 1965: 370).

Asiocricetus yamashinai Kishida, 1929: 156. Type locality is the same as for *bampensis*; the two taxa were based on vouchers belonging to different age groups: the adult individual was named as *bampensis* and the subadult one as *yamashinai* (see Kuroda 1934: 232).

Cricetulus (Tscherskia) triton: Argyropulo, 1933b: 247. Name combination.

[Cricetulus (Tscherskia)] triton nestor: Argyropulo, 1933b: 149. Name combination.

[Cricetulus (Tscherskia)] triton incanus: Argyropulo, 1933b: 149. Name combination.

[Cricetulus (Tscherskia)] triton fuscipes: Argyropulo, 1933b: 149. Name combination.

Cricetulus arenosus Mori, 1939: 21 (Japanese text) & 64 (English text). Type locality: "Tung-liao [Tongliao], North-East of Jehol", Nei-Mongol, China.

Cricetulus triton bampensis: Ellerman, 1941: 435. Name combination.

Cricetulus triton yamashinai: Ellerman, 1941: 435. Name combination.

Tscherskia triton: Tokuda 1941: 36. First use of the current name combination.

Asiocricetus hampensis: Tate, 1947: 257. Incorrect subsequent spelling of *bampensis* Kishida.

Tscherskia triton albipes: Kartavtseva & Alekseeva, 1987: 97. Name combination.

Tscherskia triton arenosus: Kartavtseva & Alekseeva, 1987: 97. Name combination.

Tscherskia triton nestor: Ross, 1992: 104. Name combination.

Tscherskia triton fuscipes: Ross, 1992: 105. Name combination.

Tscherskia triton incanus: Ross, 1992: 105. Name combination.

T[scherskia] (Cricettilus) triton: Borisov, 2012: 541. Incorrect subsequent spelling of *Cricetulus* in combination with *triton*.

T[scherskia] t[riton] incana: Shenbrot, 2017e: 285. Change of extension for gender agreement.

Cricetulus triton nester: Jo, Baccus & Koprowski, 2018: 169. Incorrect subsequent spelling of *nestor* Thomas.

Etimology. *Tscherskia* is eponym for Aleksandr Ivanovich Cherskiy (Александр Иванович Черский [Russian]; 1879—1921), a Russian naturalist who made his name in zoological explorations of the Russian Far East, and in September 1913 collected the type series of *Tscherskia albipes* (Borissenko et al. 2001: 198). Cherskiy has species group eponyms in mammology, ornithology, ichthyology and entomology (as *czerskii* and *tscherskii*). The meaning of the species epithet *triton* is less clear. In Greek mythology, Triton was a God of the Sea and is frequently portrayed with a human head and torso and a long fish tail; *triton* is thus possibly in allusion to the tail which is proportionally longer in *Tscherskia* than in any other hamster known to Winton.

Common name for *Tscherskia*, which is in prevailing use, is a greater long-tailed hamster. We reinstall here a rat-like hamster, which was frequently used in the past: "hamster rat" (Sowerby 1923), giant rat-headed hamster (Loukashkin 1944) or "rat-like hamster"; the latter is English translation of "Крисовидный хомяк" [Russian] and Rattenähnliche (or Rattenartige) Hamster [German]; Ognev 1914, Flint 1966b).

Distribution. The range covers an estimated 1,632,084 km² in eastern Asia between the 100th meridian and the shores of the Sea of Japan and the Yellow Sea (Figure 23). The great majority of the range is in China in the provinces of Heilongjiang, Jilin, Liaoning, south-eastern Nei Mongol, Beijing, Hebei, Tianjin, Shandong, Jiangsu, Anhui, Henan, Shaanxi (north of the Wei-He River), Shanxi, Ningxia, Zhejiang, and south-western Gansu (*cf.* Jiang et al. 2015, 2024). The most obvious distributional gap in China coincides with the Ordos Plateau and very few records are situated on the left bank of the Yellow (Huang He) River to the west of the Ordos Loop in the Helan-Shan Mts. The south-western range transgresses the Yangtze River in Anhui and Jiangsu, reaching the extreme northern Zhejiang. The common rat-like hamster is seemingly widespread in the Korean Peninsula, and reaches in the north the southern Primorsky Krai of the Russian Far East up to Khanka Lake and the upper part of Ussuri River valley.
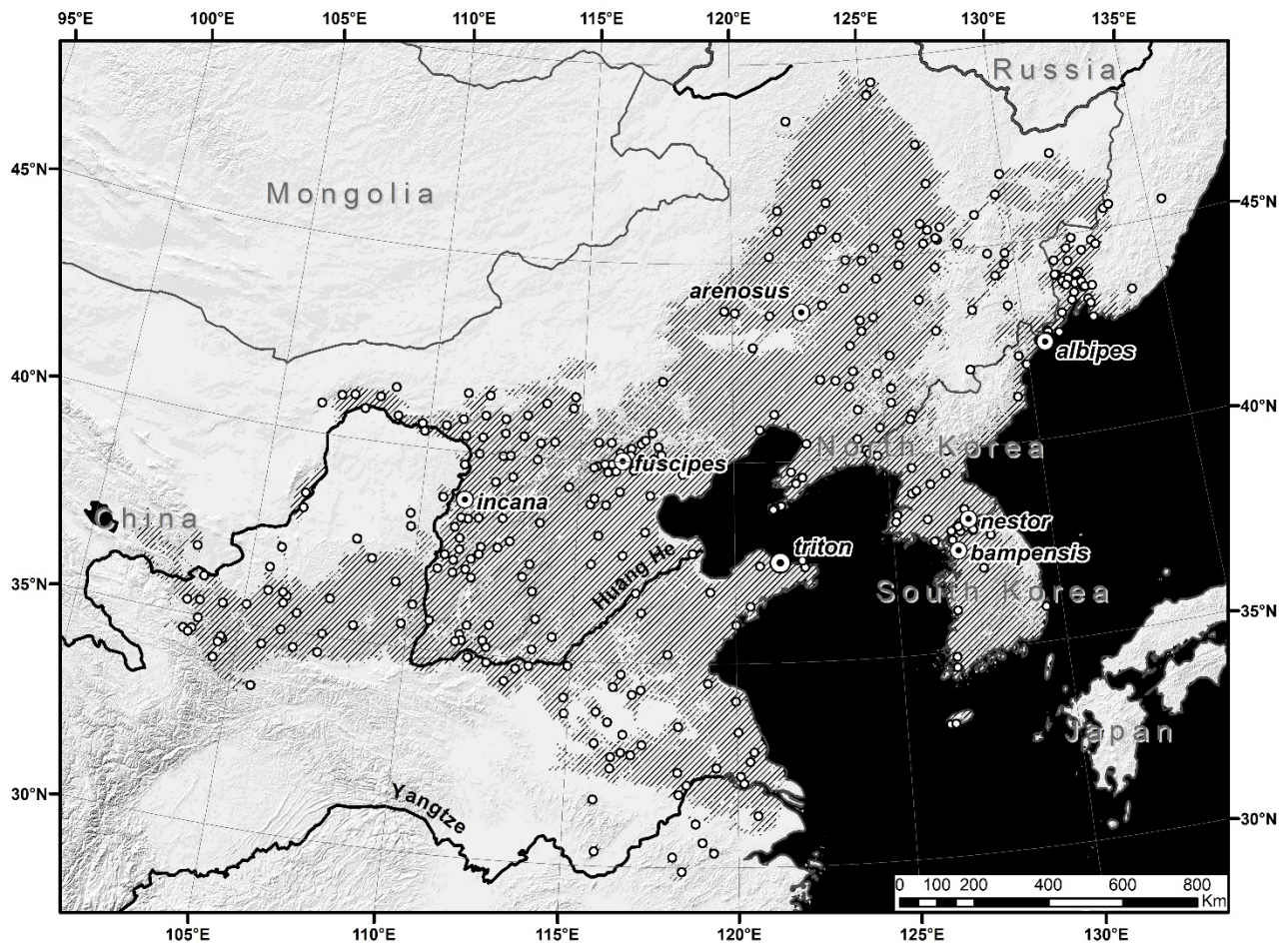
Figure 23: Distributional range of the common rat-like hamster *Tscherskia triton*.

It occupies several islands, including Putyatin Is. in the Strelok Bay, 1.5 km offshore the mainland Russian Primorye, and Jeju (Cheju) Is. (Jones & Johnson 1965) 83 km off the nearest point on the coast of South Korea. The species was also recorded on an unnamed island on the upper Razdolnaya (Suyfun) River in the Oktyabrskiy Rayon (Primorsky Krai).

Within the majority of its range, *T. triton* is one of the most widespread small mammals. It is common in many places and can be locally abundant. The species is catholic in habitat preferences, occupying cultivated areas (particularly rice fields) as well as abandoned farmland, dry hillsides covered with grass or scrub, dense bushes, grassy lowlands, coppices, coniferous plantations and woodlands (Won 1961, Jones & Johnson 1965, Luo et al. 2000). Preferred are uplands and upper edges of ravines (Kostenko 1984, Shenbrot 2017e). On the Jeju Is. and in the Ussuri Region (Primorsky Krai), common rat-like hamsters inhabit humid to damp places inside shaded forests (Zolotarev

1936, Jo et al. 2012). Elevational range is from sea level up to 2,827 m (mean elevation = 532 m).

Characteristics. A moderately large hamster of rat-like external appearance (Figure 24). In contrast to the brown rat of comparable size, the rat-like hamster has smaller feet and shorter tail, both absolute and relative to head and body. The tail is comparatively long, accounting for 40–74% (usually 45–57%) of head and body length. Ears protrude well above the fur and the eyes are of normal size. Dimensions: body mass = 80–285 g, length of head and body = 135–223 mm, length of tail = 65–110 mm, length of hind foot = 22–29 mm, length of ear = 17–23 mm, condylobasal length of skull = 34.6–46.0 mm, zygomatic width = 16.0–26.3 mm, length of maxillary tooth-row = 4.9–6.5 mm. Secondary sexual dimorphism in size is weakly expressed or absent (Li et al. 1990). As typical of hamsters, the feet are rather short. There are 5 toes on front and back feet; the small front thumb is equipped by a claw and is shifted posterior. Palms have 5 pads and soles have 6 pads each. Interdigital palmar pads are of about same

Figure 24: Common rat-like hamster *Tscherskia triton* from Primorsky Krai, south-eastern Russian Federation. Note the white-tipped tail and dusky proximal metatarsals. Photo courtesy of Irina V. Kartavtseva.

size as metatarsal pads; the plantar pads are large and closely packed together (Mori 1930). The fur is soft and silky, at least in some populations. Dorsal hairs are 11–15 mm long, interspersed with sparse all-black or dark-brown stiff hairs which stick out by 3–4 mm. Vibrissae are short. Females have 8 nipples (Ognev 1914).

General colour is buffy-grey or drab-grey and varies from pale buffy-grey to smoke-grey without the buffy shade. The colour depends on the locality and is usually uniform within the same population. Difference in overall colour of the pelage is due to the length of ochraceous-buff or beige terminal band of hairs and the number of all-dark stiff hairs (Ross 1992). Fur is darker on the dorsal line, which is mixed to a greater extent with all-black or black-tipped hairs; there is, however, no distinct streak. The posterior back is darkened in some populations. Underside ranges from white or greyish-white to dull grey, which is only slightly lighter than the back. This depends on the extent of slaty hair

bases below the white tips. A white throat patch of irregular shape is usually present, with hairs white to the bases. Upper lips and chin are pure white. Demarcation on the flanks is either blurred or sharply defined.

Figure 25: Dorsal side of hind foot in *Tscherskia triton*. Note that the proximal ½ of the metatarsal region of the foot is dusky. The voucher is from Ussuriysk, Russian Far East. Photo B. Kryštufek.

Tscherskia   collina
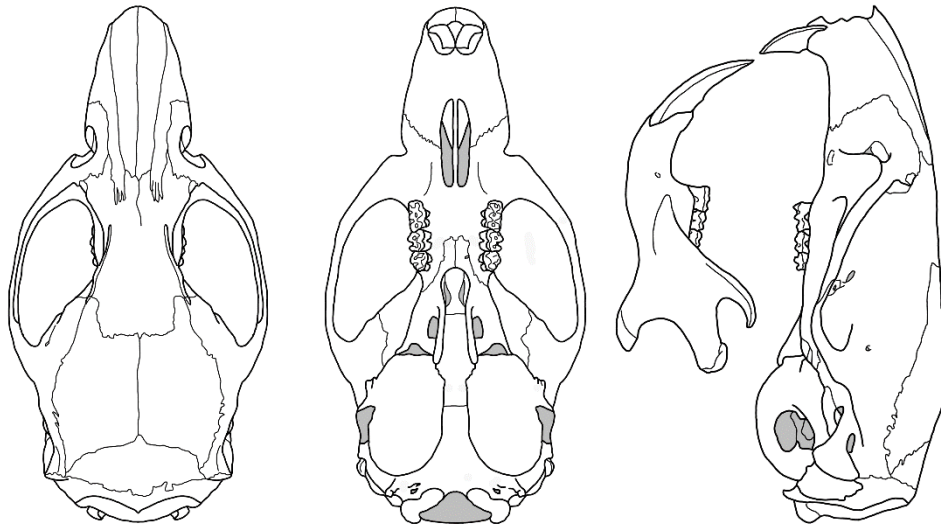
Tscherskia   triton
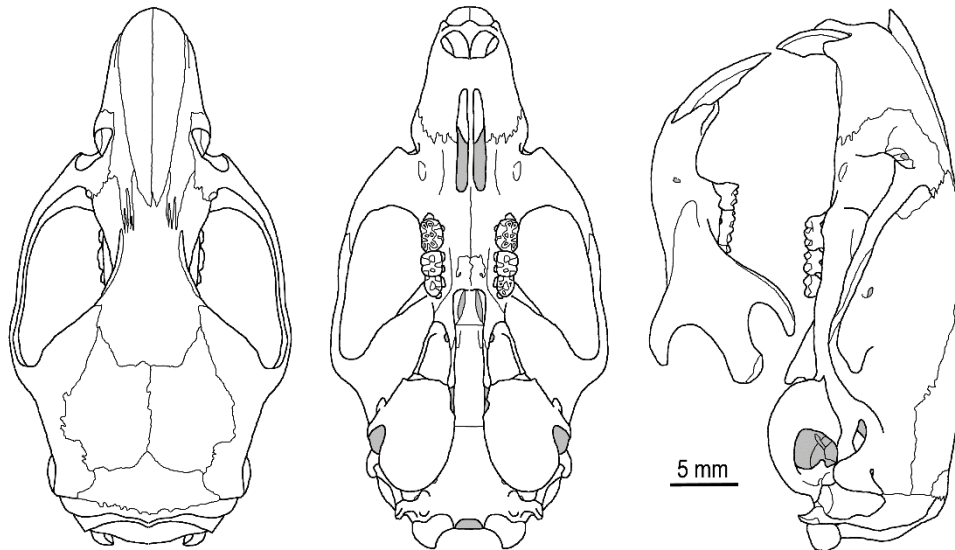
Figure 26: Skull and mandible in rat-like hamsters *Tscherskia*. Top to bottom: *T. collina* and *T. triton nestor* (Primorsky Krai, south-eastern Russian Federation).

Juveniles are uniformly slaty-grey and nearly without brownish wash above; their underside is slaty and less tipped whitish than in adults (Kuroda 1939). The paws are pure white, though the proximal metatarsal area and the ankles are dusky (fuscous) in some populations (Figure 25), particularly in the northern part of the range. Ears are thinly covered with short dull brown hairs except for the extreme rim which is white. Vibrissae are blackish brown or whitish. Tail is thinly covered with short hairs which leave the underlying annulation exposed; dorsal side is blackish brown, dark brown to dusky and the ventral side is greyish or whitish. The terminal tip is frequently beige or white, usually for < 5 mm.

The skull is of similar shape as in *Cricetulus* and *Nothocricetulus*, but is more stoutly built (Figure 26). Adult skulls are clearly ridged on the frontals and show medial (interorbital) groove; the ridges are weak on the parietals but reach the lambdoidal crest. Zygomatic arches are moderately expanded (zygomatic width accounts for 56–61% of condylobasal length) and the dorsal profile is evenly though moderately bowed. The rostrum is heavy; its breadth across the capsular projection of the upper incisors (the nasolacrimal capsule) exceeds the interorbital width. The nasals are narrow and long with a pointed apex; posterior premaxillary process extends into the maxillary region
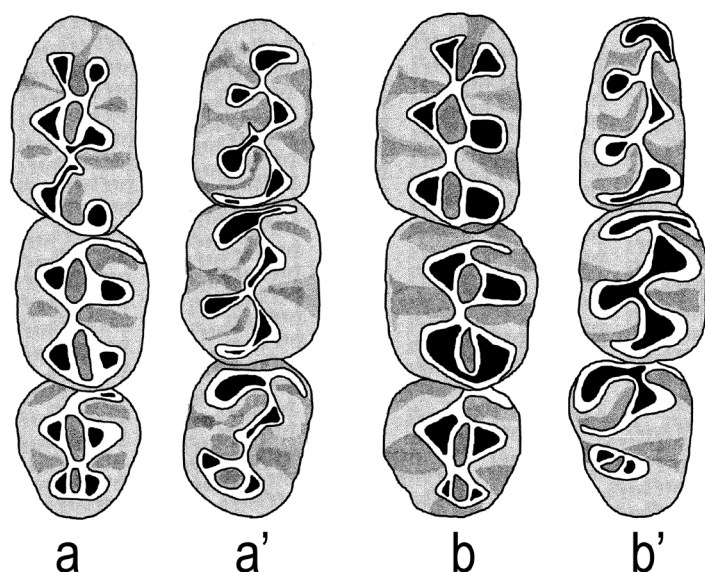
Figure 27: Grinding pattern of upper (a, b) and lower (a', b') molars in common rat-like hamster *Tscherskia triton* from Primorsky Krai, Russian Federation (a) and Jilin Province, China (b). Lingual is to the left; scale bar = 1 mm.

beyond the naso-frontal suture. The coronoid (fronto-parietal) suture is characteristically square-edged. Parietals are rather small and the interparietal is usually hexagonal and extends across the greater part of the roof of the cranium. The orbits give less rounded appearance than in *Cricetulus*; bullae are large, inflated and of oval shape; subsquamosal foramen is small and not visible in dorsal view; stapedial and sphenofrontal foramina are present; pterygoid fossae are deep. Masseteric plate is rather broad with a straight or slightly concave anterior margin. Paroccipital process is well developed and is shifted towards the occipital condyle. Incisive foramina are of normal size, only rarely reaching the level of cheek teeth; the hard palate margin is at the level of the posterior edge of M^3. In dorsal plane, the occipital condyles project beyond the occiput. Mandible is comparatively low and long; a sickle-shaped coronoid process is large and the remaining processes are of moderate size.

The incisors are orthodont and coated with pale-to-dark orange enamel. In both rows (maxillary and mandibular), the molars gradually decrease in size in anterior-to-posterior direction; M^1 is relatively the longest molar (Figure 27), M_1 is relatively the slenderest and the posterior two molars are comparatively the broadest. Relative molar length (M1-M2-M3) is 0.41–0.31–0.28 for the maxillary row and 0.38–0.32–0.30 for mandibular row; relative width of molars (width/length) is 0.65–0.92–0.90 for the maxillary row and 0.58–0.85–0.80 for mandibular row. Tubercles on M^{1-2} are of comparable size, however, the lingual pair is slightly shifted posteriorly. Hypocone and metacone of M^3 are reduced and obviously smaller than the anterior cones. The conulids of lower molars clearly alternate and the labial ones are shifted posteriorly; the anteroconulids of M_1 which are of comparable size, form a transverse crescent.

Glans penis is ~5.5 mm long, and ~2.9 mm deep; it is urn-shaped and therefore broader distally (~3.9 mm) than basally (width at the lining of prepuce ~2.8 mm). Dorsal papilla is prominent and divided into 5 lobes; lateral papillae are narrower and shorter than the central papilla; all these papillae project beyond the annular fold and are visible from the outside (Tokuda 1941). Ventral papilla bifurcates apically; it is of about the same size as *papillae laterales*, and is hidden by the expanded ventral rim of *meatus urinarius*. The epidermal spines cover the entire glans; they are smaller on the anterior surface of the glans and obviously larger on the proximal dorsal side. The baculum consists of proximal stalk and distal trident; digits are not fused; the central distal digit (length ≈ 70% of the proximal baculum) is longer than lateral digits. Shaft of the proximal baculum is slender, and the manubrium is laterally expanded, though still weak (Figure 17c); width across manubrium is less than the length of the distal trident (Tokuda 1941). Ossification of the lateral digits is postponed (Vorontsov 1982).

Karyotype: 2n=28; 11 pairs of acrocentric and 2 pairs of metacentric autosomes (NF$_a$=30). Of the sex chromosomes, the X is large subtelocentric or submetacentric and the Y is metacentric or submetacentric of average size (Tsuchiya & Won 1976, Kartavtzeva et al. 1980, Wang et al. 1999). In diakinesis, the heterosomes pair side by side (Ross 1992). In contrast to the remaining Cricetinae, *Tscherskia* shows extensive intra- and extra-chromosomal rearrangements (Romanenko et al. 2012) and is the only true hamster with supernumerary (B) chromosomes. The earliest reported karyotype showed diploid number 2n = 30 due to the presence of 2 B-chromosomes (Makino 1951). So far, 1–2 B chromosomes have been reported and the proportion of somatic cells carrying supernumerary chromosomes varied slightly between studies: 34.9–55.9% in the Russian Far East (Borisov 2012) and 67.5% in the Shandong Province, China (Wang et al. 1999). Diploid number in individuals with B-chromosomes is 2n = 28–30 (Russia) and 2n = 28–29 (China). The proportion of individuals with B chromosomes in 2 samples from the Russian Far East was 10.3% (n = 39; Kartavtzeva et al. 1980) and 11.1% (n = 45; Borisov 2012). Wang et al. (1999) detected supernumerary chromosomes in Shangdong but not in Jilin and Shaanxi. *Tscherskia triton* differs from the remaining hamsters in having large C-positive heterochromatin blocks in the centromeric region of 11 autosomal pairs and the pericentromeric region on both sex chromosomes (Borisov 2012, Kamimura et al. 2022).

Variation and subspecies. In the literature, the common rat-like hamster is invariably reported as a polytypic species and since the revision by Argyropulo (1933b, c) 5 subspecies were recognized by the great majority of authors. Ellerman (1941) listed 8 subspecies and Chinese authors, who frequently omit *nestor* from their lists of Chinese mammals, recognized 4 subspecies in the country (e.g. Luo et al. 2000, Wang 2003); Smith & Hoffmann (2008) accepted for China also *ningshaanensis* as a subspecies in its own right, which we synonymize with *T. collina* (see under that species). Corbet (1978: 92), however, was sceptical over the validity of so many infraspecific taxa stating that "the very slight differences involved [between populations] the amount of intergradation and the apparent continuity of range make it unlikely that really discrete races exist."

Ross (1992) reassessed the validity of subspecies by using multivariate analyses of linear craniodental measurements. She concluded that *nestor* was the only subspecies of common rat-like hamsters deserving recognition, in addition to the nominal subspecies *triton*. Her study, however, remained uniformly ignored and we resuscitate it here by classifying the common rat-like hamsters into the northern (*nestor*) and the southern (*triton*) subspecies groups based on cranial traits exposed by Ross (*l. c.*). The latter group is further split into 2 subspecies (*triton* and *incana*) as they were recognized by earlier authors (Allen 1940, Luo et al. 2000). Differences in colouration are due to the length of the buffy subterminal band and the number of longer all-brown hairs (Ross 1992). Colour reflects differences in climate and substrate with pale hamsters occupying arid regions and dark hamsters being present in humid climate.

Tscherskia triton fuscipes G. Allen is usually recognized as a subspecies in its own right (Allen 1940, Luo et al. 2000, Wang 2003, Smith & Hoffmann 2008, Shenbrot 2017e), but this requires clarification. Subspecies *fuscipes* is diagnosed by dusky (fuscous) tarsal joint and the proximal ⅓–½ of the metatarsals which are normally white in the majority of hamsters. Dusky ankles, however, were observed also in other races (*triton* and *nestor*; *cf.* Howell 1929), and Allen (1940: 770) himself noted that "the form [*fuscipes*] is not a strongly marked one." The range of *fuscipes* is usually given as the entire north-east China (Beijing, northern Hebei, Heilongjiang, Jilin, Liaoning, eastern Nei Mongol; Luo et al. 2000, Wang 2003, Shenbrot 2017e) though the eastern border against *T. t. nestor* remains unresolved. Rat-like hamsters from the extreme north-eastern China (Provinces of Heilongjiang and Jilin), the entire Korean Peninsula and the Russian Far East are cranially *nestor*, while those from Tianjin and the entire Shandong, as well as the topotypes of *fuscipes* from Beijing, are cranially *triton* (Ross 1992).

Phylogeographic structure is known only from a limited geographic sampling and therefore provides little information for testing subspecific taxonomy. So far, 3 phylogeographic lineages are known from the mainland

(Xie & Zhang 2005b, Sheremetyeva et al. 2017). The Northern lineage is allopatric in the Russian Far East and adjacent China. Further two lineages (the Central and the Southern, sensu Sheremetyeva et al. 2017) widely overlap in the North China Plain (Provinces of Beijing, Hebei, and Henan) and occupy both banks of the Yellow (Huang He) River. In phylogenetic trees constructed from mitochondrial and nuclear genes (Jiang et al. 2024), *arenosus, fuscipes, incana*, and topotypical *triton* from the Shandong Peninsula clustered together, though the Shandong samples hold independent position in the cytochrome *b* tree. Genetic diversity is comparatively high in all populations studied so far (cf. Xie & Zhang 2005a). Karyology also provides no evidence that would be useful in subspecies delimitation of the common rat-like hamster (Wang et al. 1999).

Subspecies group *triton*

Distribution. Southern part of the rat-like hamster range, tentatively southward of the 40th parallel.

Characteristics. Usually smaller and of lighter colour. Palate and rostrum narrower, diastema shorter, posterior margin of incisive foramina terminates just anterior to the M^1 level, shape of coronal suture rounded.

Tscherskia triton triton (Winton, 1899)

Distribution. China, tentatively between the 40th parallel and the Yangtze River and eastward of about the 110th meridian (cf. Luo et al. 2000). The subspecies was reported for the following provinces: Hebei, Beijing, Jiangsu (Xuzhou), Henan (Linxian), Shanxi (Taiyuan and Lishi), Shaanxi (central Guanzhou Plain), Anhui and northern Zheijiang (Wang 2003).

Characteristics. Mean values for 3 external and 2 craniodental traits (n = 21): body mass = 81.7 g, length of head and body = 142 mm, length of hind foot = 24.1 mm, condylobasal length = 33.3 mm, length of maxillary tooth-row = 5.37 mm (Luo et al. 2000). Tail is comparatively short and on average accounts for 49% of head and body length. Pelage is smoke-grey; the head and front back are dark grey. Ross (1992) exposed differences in fur texture and pelage colouration

between local populations occupying the Shandong Province.

Tscherskia triton incana (Thomas, 1908)

Synonyms. *Cricetulus triton fuscipes* G. Allen, 1925, *Cricetulus arenosus* Mori, 1939.

Taxonomy. In Allen's view (1940: 771), *incana* is "a barely distinguishable race" and the difference in fur colouration against the nominal subspecies is slight (Howell 1929).

Etymology. The subspecific epithet *incana* is Latin for 'light-grey' in allusion to the fur colouration.

Characteristics. Mean values for 3 external and 2 craniodental traits (n = 4–7): body mass = 68.5 g, length of head and body = 150 mm, length of hind foot = 23.7, condylobasal length = 37.5 mm, length of maxillary tooth-row = 5.41 mm. Tail is moderately long; its length accounts on average for 56% of head and body length. Fur is paler (drab-grey) than in other races of the common rat-like hamster; the head and front back are pale grey.

Distribution. Arid habitats at the edge of the Ordos Plateau and eastward and southward of the Mu Us Desert in western Shanxi (Kelan), northern Shaanxi, eastern Gansu, Ningxia, and south-central Nei Mongol; present on both banks of the Yellow (Huang He) River. This is a rare subspecies occurring at low population densities (cf. Howell 1929, Allen 1940).

Subspecies group *nestor*

This group contains a single subspecies.

Tscherskia triton nestor (Thomas, 1907)

Synonyms. *Tscherskia albipes* Ognev, 1914; *Asiocricetus bampensis* Kishida, 1929; *Asiocricetus yamashinai* Kishida, 1929.

Etymology. In Greek mythology, Nestor of Gerenia was a legendary king of Pylos (Peloponnese, Greece)

and a prominent secondary character in Homer's Iliad and Odyssey. He is described as a large, wise, grey-haired elderly warrior. Though Thomas did not explain his choice of the name, he perhaps alluded on a large size of *nestor*, which was in his time "by far the largest known [sub]species" of common rat-like hamsters (Thomas 1907: 466). The grey fur of *nestor*, which contrasted more buffy hair in the nominal subspecies, may also play a role in selecting the name.

Taxonomy. The *nestor* of Thomas is the 2nd oldest species-group name in the genus. It was ranked in the past either as a species in its own right (Allen & Andrews 1913, Sowerby 1923, Kishida & Mori 1931, Tate 1947) or a subspecies of *triton* (Howell 1929, Argyropulo 1933b, c, Kuroda 1934, and subsequent authors). This is the only subspecies listed for Korea (e.g. Allen & Andrews 1913, Jones & Johnson 1965, Won 1968, Jo et al. 2018) and for the Russian part of the species' range (Argyropulo 1933b, Gromov et al. 1963). Chinese authors, on the other hand, frequently ignore *nestor* and classify common rat-like hamsters from north-western China as *fuscipes* with *arenosus* as its synonym.

Kartavtseva & Alekseeva (1987) elevated both, *albipes* and *arenosus,* to subspecies in their own right, justifying this decision by size differences. Size, however, varies in *nestor* even within the Korean Peninsula; *e. g.* specimens in northern parts are on average smaller than those occupying central regions of the Peninsula (Jones & Johnson 1965).

Based on 2 skulls from Jeju Is., Jones & Johnson (1965) stressed the differences between this insular population and its mainland counterparts. The Jeju skulls were narrower, with not so well-developed supraorbital ridges, more evenly rounded bulla, shorter incisive foramina and paler enamel on the upper incisors. Analysis of 2 partial mitochondrial genes retrieved moderately deep genetic divergence (> 3.5%) between the Jeju and the mainland common rat-like hamsters (Koh et al. 2013). In their overall size, the Jeju hamsters do not differ appreciably from the grand mean for the subspecies (see below). Means for the Jeju sample (n = 14) are: body mass = 114.6 g, length of head and body = 175.0 mm, length of hind foot = 25.6 mm (Park & Oh 2017).

Distribution. Northern part of the common rat-like hamster range, tentatively northward of the 40th parallel. Present in Russian Far East (Primorsky Krai), throughout Korea and in north-east China (Heilongjiang, Jilin, Liaoning, eastern Nei Mongol, north Hebei).

Characteristics. On average larger and darker than the *triton* subspecies group. Mean values for 3 external and 2 craniodental traits (n = 59–75): body mass = 116.1 g, length of head and body = 162.5 mm, length of hind foot = 25.2 mm, condylobasal length = 37.2 mm, length of maxillary tooth-row = 5.5 mm. The tail is comparatively short and accounts on average for 49% of head and body length. Dorsal fur is frequently dark grey, occasionally almost blackish, without the buffy or clay-coloured shade. Underside is usually greyish white and the slaty bases of the hairs are exposed below their white tips; the pectoral spot of irregular shape is white to hair bases. Summer pelage is darker than winter pelage. Tail tip is white for ~10 mm, rarely more (up to 50 mm; Zimmermann 1964). Palate and rostrum are broader than in the *triton* subspecies group, diastema is longer, posterior margin of incisive foramina terminates well before the M^1 level, and shape of coronal suture is square edged.

Tscherskia collina (G. Allen, 1925) – Tsinling Rat-like Hamster

Cricetulus triton collinus G. Allen, 1925: 5. Type locality: "base of Tai-pei-shan, Tsing-ling [Tsinling] Mountains, Shansi Province, China." 'Shansi' (now Shanxi) is obviously incorrect spelling for "Shensi" (now Shaanxi) (*cf.* Howell 1929: 49, Allen 1940: 771). We therefore place the type locality of *collina* in Shaanxi.

[Cricetulus (Tscherskia)] triton collinus: Argyropulo, 1933b: 149. Name combination.

Cricetulus triton meihsienensis Ho, 1935: 288. Type locality: Meihsien [Mian Xian], Shensi, China (Allen 1940: 771).

Cricetulus triton ningshaanensis Song, 1985: 137. Type locality (in English summary, p. 139): "Ningshaan district [Ningshan County] (alt. 1050 m), Shaanxi", China.

Tscherskia triton collinus: Ross, 1992: 105. Name combination.

C[ansumys] c[anus] ningshaanensis: Lu & Wang, 1996: 121. Name combination.

C[ricetulus] c[anus] nighshaanensis: Zhang, Jin, Quan, Li, Ye, Wang & Zhang, 1997: 216 (Chinese) & 217 (Eng.). Incorrect subsequent spelling of *ningshaanensis* Song.

Cansumys canus ningshanensis: Wang, 2003: 166. Incorrect subsequent spelling of *ningshaanensis* Song.

T[scherskia] t[riton] collina: Shenbrot, 2017e: 285. Change of extension for gender agreement.

Tscherskia ningshaanensis: Jiang, Wang, Yang, Pan, Liu & Lu, 2024: 1231. New rank for *ningshaanensis*.

Etymology. The specific epithet "collinus" (collina*)* is Latin for 'hilly' in allusion to its habitat in "the hills of southern Shansi and Shensi" (Allen 1925: 5). Adjective in the common name alludes to Mt. Tsinling (Qinling) within the range of the species.

Taxonomy. Based on deep molecular divergence separating *triton* proper and *ningshaanensis* (K2P = 15.1%, *i. e.* 3.88 Mya), Jiang et al. (2024) classified these taxa as distinct species of rat-like hamsters *Tscherskia*.

synonymize *ningshaanensis* with *collina*. This follows Luo et al. (2000: 72); *meihsienensis* was regarded as junior synonym of *collina* already by Allen (1940: 771).

Lu & Wang (1996) classified *ningshaanensis* as a subspecies of *Cansumy canus*, which remained the prevailing view for the rest of the century (Zhang et al. 1997, Luo et al. 2000, Wang 2003); *ningshaanensis* was again synonymized with *Tscherskia triton* by Musser & Carleton (2005). Ross (1992) maintained very different view on this issue; on the one hand she overlooked *ningshaanensis* and on the other hand classified *collina* and *meihsienensis* as synonyms of the nominotypical subspecies *T. t. triton*.

Distribution. Range covers an estimated 55,563 km² in southern Shaanxi to the south of Wei-He River valley, and western Henan (Figure 28). Identical range was defined already for subspecies *collina* (Allen 1940: Figure 28 on page 766). Occupies warm and humid forests in a hilly countryside at elevations between 475 and 2,470 m (mean = 1,110 m).
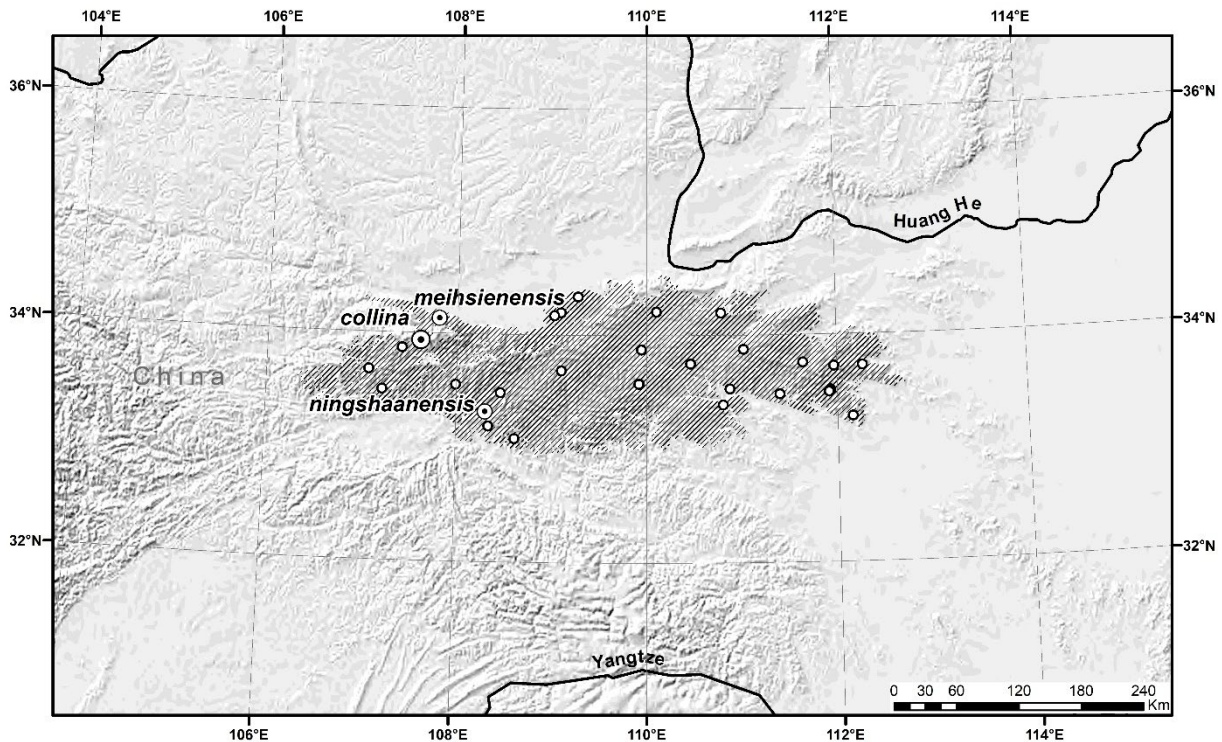
Figure 28: Distributional range of the Tsinling rat-like hamster *Tscherskia collina*.

Two names (*collina* and *meihsienensis*) from the Tsinling Mts., however, antedate *ningshaanensis*, and Jiang et al. (*l. c.*) sequenced hamsters from none of them. Given the proximity of their type localities, we tentatively

Characteristics. Similar to *T. triton* but on average smaller. Dimensions: body mass = 38–93 g, length of head and body = 112–185, length of tail = 72–114 mm, length of hind foot = 23.5–27.0 mm, length of ear =

20–24 mm, greatest length of skull = 29.3–37.5 mm, zygomatic width = 14.7–19.0 mm, length of maxillary tooth-row = 4.9–5.7 mm. The tail is comparatively long, accounting on average for 60% of head and body length. Dorsal fur is dark greyish-brown with ample blackish shade; all-black hairs are numerous and the remaining hairs have broad beige subterminal band and a minute black tip. Buff tint predominates on the side of the head and body; demarcation line is blurred. The underside is dark grey grizzled by contrastingly white hair tips; the chin and a small median spot on the throat are white to hair bases. Ears are thinly covered with short blackish brown hairs; feet and ankles are whitish. The tail is all-blackish or indistinctly bicolour due to white hairs on the ventral side. Its distal portion is pure white for the terminal 3–52 mm (Song 1985). The skull is essentially as in *T. triton* with minor differences (Figure 26): palate and rostrum are narrower, diastema is shorter, posterior margin of incisive foramina terminates just anterior to the M^1 level, supratemporal ridges are weaker, and the sagittal suture is longer. Karyotype is as in *T. triton*; B-chromosomes were so far not detected but the number of karyotyped animals was small (Wang et al. 1999).

Variation and subspecies. The extent of terminal white area on the tail varies among populations; it is usually short (length = 3–10 mm) and occasionally covering 40–60% of the tail (Liang et al. 2024). The species is presumably monotypic.

GENUS: *Cricetulus* A. Milne Edwards, 1867 – Lesser Hamsters

Cricetulus A. Milne Edwards, 1867: 376. Not 1871 (Corbet & Hill 1992: 391). Type species by monotypy is *Cricetulus griseus* A. Milne Edwards, 1867 (cf. Palmer 1904: 203)

Etymology. *Cricetulus* is diminutive of *Cricetus,* which is the name for hamsters (Palmer 1904: 203). Milne Edwards (1867: 375–376) who coined the name *Cricetulus*, stressed that small hamsters of China, although externally resembling arvicolines, actually possess cheek pouches and display molar morphology typical of hamsters, yet still cannot be classified "in the same genus" with *Cricetus* ("ils se rapprochent donc des Hamsters, sans cependant pouvoir prendre place dans

le même genre"). By using a diminutive for *Cricetus,* Milne Edwards intended to stress the mutual "analogies" ("Pour rappeler ces analogies") between the large and the small hamsters.

Nomenclature. Recent literature usually hyphenates the taxon-authorship name Milne Edwards, spelling it Milne-Edwards (e.g. Ellerman & Morrison-Scott 1951, Corbet 1978, Pavlinov et al. 1995, Wilson & Reeder 2005, Pardiñas et al. 2017). This was not always so in the past. Some authors either used a hyphen (Trouessart 1897, Palmer 1904) or not (Palmer 1897, 1899), or were inconsistent in this (Trouessart 1904). The composite name Milne Edwards was created by Henri Edwards (1800–1885) who added one of his first names (Milne) to the family name Edwards in order to be recognized among all his relatives (he had 27, or perhaps 28, brothers and sisters) (Hansson not dated). Hansson claimed that Henri (the father) usually did not use the hyphen, while Alphonse (the son; 1835–1900) "always did". Our search through contemporary literature revealed inconsistency in this respect in both members of the Edwards family. We therefore strictly adopted the spelling as it appeared in the title of the original publication. In the joint work by the father and son Milne Edwards (Milne Edwards & Milne Edwards 1868–1874), the hyphen was not used (see also Milne Edwards 1871).

Taxonomy. Milne Edwards proposed *Cricetulus* as a new genus (see also David 1871: 93), however, he himself downgraded it to a subgenus of *Cricetus* shortly afterwards (Milne Edwards 1871). In the early 1900s, several authors adopted *Cricetulus* as a genus in its own right (*e. g.* Trouessart 1904) which is still a practice. The scope of *Cricetulus,* however, varied. For the greater part of the 20th century, the name covered all current species of Cricetina except *Cricetus*, and all members of Urocricetini. Given the diversity of incorporated forms, *Cricetulus* was soon split into subgenera. Argyropulo (1933b, c) recognized 3 subgenera: *Tscherskia* (with *Cansumys*), *Allocricetulus*, and *Cricetulus s. str.* The latter included *migratorius* (now in *Nothocricetulus*) and the current *Urocricetus*. Argyropulos' classification was retained in major revisions which emerged around 1950 (Allen 1940, Ellerman 1941, Kuznetzov 1944, Bannikov 1954, and Ellerman & Morrison-Scott 1951). Flint (1966b) was perhaps the first to restrict *Cricetulus*

to its current scope, although with the inclusion of *Urocricetus* and *Nothocricetulus,* while Ross (1982) extracted *Urocricetus* from *Cricetulus.* Taxonomic solutions proposed by Flint and Ross were regrettably overlooked and *Cricetulus* continued to serve as collective name for species that are now in 5 independent genera: *Urocricetus, Tscherskia, Cansumys, Nothocricetulus,* and *Allocricetulus* (Wang & Cheng 1973, Corbet 1978, Corbet & Hill 1980, 1986, Honacki et al. 1982, Zhang et al. 1997, Luo et al. 2000). The species of *Urocricetus* and *Nothocricetulus* were retained inside *Cricetulus* until very recently (Musser & Carleton 2005, Smith & Hoffmann 2008, Lebedev 2012, Jiang et al. 2015, Pardiñas et al. 2017), until removed from its scope by Lebedev et al. (2018a). Currently, 6 species are listed inside *Cricetulus* (Pardiñas et al. 2017), and this number was similarly high (around 5 species) in the 1990s (see under *C. barabensis*).

Based on multigene phylogenetic analysis, *Cricetulus* holds basal position to a clade consisting of *Nothocricetulus + Allocricetulus + Cricetus* (Neumann et al. 2006, Lebedev et al. 2018a). Similar analyses, which used morphological and / or chromosomal markers, failed in confirming monophyly of *Cricetulus* (Ross 1992, Romanenko et al. 2007) or placed it in a sister position against *N. migratorius* (Potapova 2005) (Figure 1). The divergence time between *Cricetulus* and the clade consisting of *Nothocricetulus + Allocricetulus + Cricetus* (the *Cricetus* clade) was estimated at 5.61 Mya (CI = 4.43–6.99 Mya) (Lebedev et al. 2018a), which is a close match to 4–6 My old fossils from the Early Pliocene of China (Lindsay 1994). The entire *Cricetus*-clade is heterogenous, therefore *Cricetulus* differs from *Cricetus* and *Allocricetulus* in many aspects of external and cranial morphology. On the other hand, *Cricetulus* resembles *Nothocricetulus* in external appearance and cranial morphology. The following traits differentiate well between the two genera: (1) in *Cricetulus* the baculum has a long trident, which is of approximately same length as the proximal baculum (Figure 17d); trident is rudimentary in *Nothocricetulus* (length of trident equals ~¼ that of proximal baculum) (Figure 17e); (2) M^{1-2} lack metalophule (the antero-lingual ridge of the hypocone; cf. Figure 35), which in *Nothocricetulus* contributes to an X-pattern of enamel ridges between the medial and posterior pair of cusps; (3) the fronto-temporal angle of the parietals (in dorsal view)

approaches the orbit and restricts the squamosal suture (*sutura squamosa cranii*) (Figure 34); in *Nothocricetulus*, the squamosal suture is longer and the fronto-temporal angle does not approach closely the orbit (Figure 48).

Distribution. East Asia between the 70th meridian in the west and the Sea of Japan and the East China Sea in the east. Northern border is on the upper reaches of the Irtysh, Ob, Yenisei, Angara, and Lena Rivers, the Baykal Lake and the Amur Valley; usually the range does not surpass the 55th parallel. The southern border tentatively coincides with the line estuary of the Yangtze to the upper reaches of the Yangtze, Mekong and Salween.
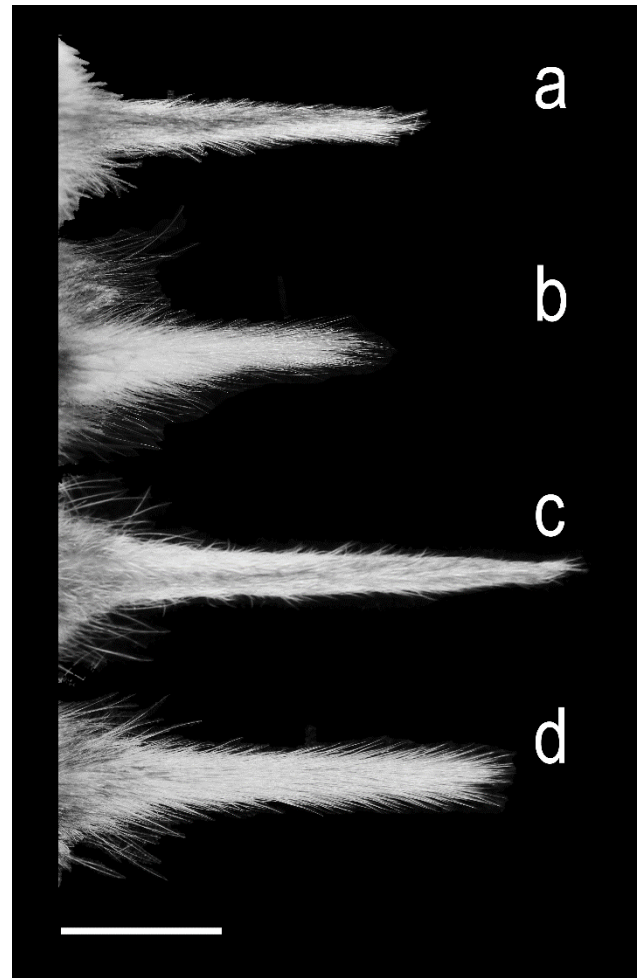
Figure 29: Tail in *Cricetulus barabensis* (a), *C. sokolovi* (b), *C. longicaudatus* (c), and *Nothocricetulus migratorius* (d). Specimens are of comparable size. Scale bar = 10 mm.

Characteristics. Small hamsters with the tail shorter than ½ of head and body length; tail is tapering gradually from the broad base towards the tip (Figure 29a–c). Snout is pointed, eyes are rather large and ears

are long, delicate and rounded. Feet are shortened and less adapted for burrowing than in *Cricetus*, toes are comparatively short; soles may be partly hairy. Fur is thick and soft; colour of the back varies from light greyish or buff, to dull grey-brown; belly is grey and in some taxa the hairs are white-tipped. Testicles of sexually active males are exceptionally large (Figure 39b); females have 4 pairs of nipples (exceptionally 5 pairs; Zimmermann 1964).

The skull is of murine type and not much specialized. It is comparatively shallow and narrow; zygomatic arches account for 50–60% of condylobasal length. Condylobasal length is shorter than the profile length and occipital condyles are not visible in dorsal view (Figure 34). Rostrum is moderately long and braincase is large; frontals, parietals and occipitals are not ridged. Interorbital constriction is wide, and the interparietal bone is of broad diamond shape, unrestrained and expanding across the whole roof of the skull. The masseteric plate is relatively small with a straight anterior margin; it is invariably of the myomorphous type. Incisive foramens are as long as hard palate, approaching posteriorly the M^1 level. The palate terminates behind the M^3. Bullae are of moderate size and shifted well anterior of occipital condyles. Mandible shows no peculiarities. The upper incisors are orthodont to opisthodont; molars are decidedly shorter than the incisive foramina. Diploid number of chromosomes is either 20, 22, or 24.

Key to species

1a) Dorsal side plain-grey with no dark spinal stripe; tail is long relative to body (usually >30% of head and body length) and to hindfoot (> 1.95-fold the hindfoot length); skull is comparatively narrow; coronoid and articular processes are slim (Figure 30); the X chromosome is the largest element in the set ……………………......... *longicaudatus*

1b) Dorsal side usually with a dark spinal stripe (Figures 32, 36, 37, 39 & 40); tail is comparatively short (< 1.95-fold of hindfoot length); rostrum is comparatively broad; coronoid and articular processes are robust (Figure 30); the X chromosome is of medium size……………….. 2

2a) Dorsal pelage usually light reddish-brown or light grey; mid-dorsal stripe obscure or absent (Figures

39 & 40); hair bases grey; soles hairy in winter, concealing the pads; number of chromosomal arms NF = 40; present in Mongolia, to the west of the 113th meridian and to the south of the 46th parallel, and in adjacent Nei Mongol (north of Ordos loop)[1] ……………......................……. *sokolovi*

2b) Dorsal fur usually intense reddish-brown or dark grey; mid-dorsal stripe usually prominent and sharp (Figures 32, 36 & 37); hair bases slate; soles nude year-round, pads exposed and evident; number of chromosomal arms NF = 38; absent from parts of Mongolia and Nei Mongol[1] ………………………………….………. *barabensis*

[1] In Mongolia, the northern-most occurrence of *C. sokolovi* is at 46.5° and the southern-most occurrence of *C. barabensis* is at 45.8°
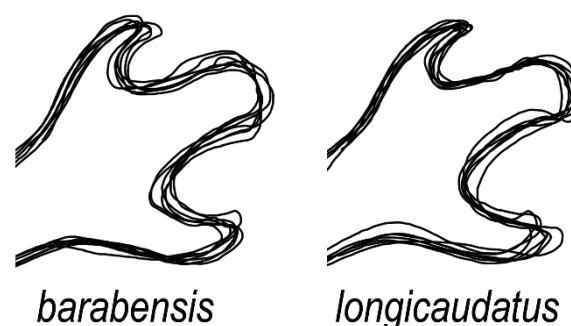
Figure 30: Superimposed outlines of mandibular ramus in *Cricetulus barabensis* (left) and *C. longicaudatus* (right). Note that *C. barabensis* is equipped with a heavier ramus and more robust coronoid process.

SUBGENUS: *Cricetulus* A. Milne Edwards, 1867

Taxonomy. The subgenus *Cricetulus* contains 2 species: *C. barabensis* and *C. sokolovi*. For further details see the account on *Ourocricetulus* new subgenus.

Characteristics. Defined by *mt*DNA sequences (Lebedev et al. 2018a, Poplavskaya et al. 2018b). The X chromosome is of medium size (Orlov et al. 1978). Mid-dorsal (spinal) stripe is nearly always present and is usually well defined (Figures 32, 36, 37, 39 & 40); tail is rather short, accounting to 24–31% of head and body length (Figure 29a, b). Rostrum tends to be broader and zygomatic arches are more expanded than in *Ourocricetulus* new subgenus; palate is broader, maxillary tooth-row is shorter, and diastema is longer (Figure 34).

The coronoid and the articular processes of the mandible are robust (Figure 30). The 2nd internal fold (*if2*) and 2nd primary fold (*pf2*) of M^1 are separated by metacone (Figure 35).

Cricetulus barabensis (Pallas, 1773) – Striped Lesser Hamster

Mus barabensis Pallas, 1773: 704. Type locality: "in arenoſis ad Ob fluuium, non longe ab argentaria fabrica quae S. Paulo nomen habet"; restricted to "Kasmalinskoi-Bor [Kasmalinskiy Bor], Pawloswk [correctly Pawlowsk = Pavlovsky District], near Barnaul, S.W. [south-western] Siberia" (Chaworth-Musters 1933: 223) in Altaysky Kray of Russian Federation. An earlier restriction of the type locality to "Irtish" (Thomas 1917: 452) is erroneous.

Glis barabensis: Erxleben 1777: 374. Name combination.

Mus furunculus Pallas, 1779: 273. New name for *barabensis* Pallas (Chaworth-Musters 1933: 221). Pallas renamed *barabensis* because Messerschmidt (quoted from Pallas 1779) used in 1742 *furunculus* (as *Furrunculus myodes*) for a striped lesser hamster from "Dalai Nor" [Dalai Nur, Nei Mongol, China] (Pallas 1779: 273, footnote). For more discussion, see *Cricetulus barabensis griseus* (below).

M[us] Cricetus Furunculus: J. F. Gmelin, 1792: 245. Name combination.

Cricetus furonculus: Lesson, 1842: 119. Name combination and incorrect subsequent spelling of *furunculus* Pallas.

Cricetus Furunculus: Brandt, 1859a: 208. Name combination.

Cricetulus griseus A. Milne Edwards, 1867: 376. Type locality was not reported in the description but in the accompanying set of plates (Milne Edwards & Milne Edwards 1868–1874); the figured *C. griseus* was from the "environs de Pékin" (Plate 12, Figure 1). In his 1871 paper, Milne Edwards stated on p. 133 that the species was very common around Beijing ("très-commune dans les champs aux environs de Pékin") and Rode (1945: 20) is explicit that the type was from "Pékin". Although Chaworth-Musters (1933: 222) accepted "the neighbourhood of Pekin" as the type locality of *griseus*, Ellerman & Morrison-Scott (1951: 624) relied on a manuscript note by Oldfield Thomas that a "Specimen marked as type in Paris Museum [was]

from Suen-hoa-fu, near Kalang" (footnote in Chaworth-Musters 1933: 222) and erroneously fixed "Suenhoafu, near Kalgan, Mongolia" as the type locality. For reasons not explained, Allen (1940: 758) claimed that the type was from "the vicinity of Peiping, Hopei, China", which is in any case close to Beijing. The correct type locality, however, is Beijing, China (*e. g.* Kuroda 1939: 23).

Cricetus (Cricetulus) obscurus A. Milne Edwards, 1871: 136. Accompanying illustrations (Plate 12: Figure 1; Plate 13: Figures 2, 2^a, 2^b, 2^c) appeared in Milne Edwards & Milne Edwards (1868–1874). Type locality is "Sartchy sur le bord du Hoangho, dans la Mongolie chinoise". Chaworth-Musters (1933: 223) defined the type locality as "Sartchy, Hoang-ho, inner Mongolia", now Linfen in Shanxi, China. For 1871 as the date of publication (instead of 1867, 1868, 1868–1874, or 1874), see the account on Taxonomy below.

Cric[etulus] obscurus: A. Milne Edwards, in David (1871: 93). Name combination.

Cricetus mongolicus Thomas, 1888: 134 (footnote). New name for *Cricetus obscurus* Milne Edwards, for which Thomas presumed to be a secondary homonym of *Hesperomys obscurus* (Waterhouse, 1837), now *Necromys obscurus* (Akodontini, Sigmodontinae).

[Cricetus (Cricetulus)] griseus: Trouessart, 1904: 395. Name combination.

Cricetulus griseus obscurus: Thomas, 1908a: 107. Name combination and new rank for *obscurus*.

Cricetulus griseus fumatus Thomas, 1909: 503. Type locality: "Chu Chia Tai [Cihu Chia Tai], near Chang Chun, Kirin [Jilin] Province", China.

Cricetulus furunculus: Formozov, 1929: 40. Name combination.

Cr[icetulus] griseus fumotus: Formozov, 1929: 40. Incorrect subsequent spelling of *fumatus* Thomas.

Cr[icetulus] furunculus obscurus: Formozov, 1929: 47. Name combination.

Cricetulus manchuricus Mori, 1930: 419. Type locality: "Harbin, North Manchuria", now Heilongjiang Province, China.

Cricetulus furunculus: Kuznetsov, 1932: 97. Name combination.

Cr[icetulus] (*Cricetulus*) *barabensis*: Argyropulo, 1933b: 246. First use of the current name combination.

[Cricetulus (Cricetulus) barabensis] obscurus: Argyropulo, 1933b: 246. Name combination and new rank.

[*Cricetulus (Cricetulus) barabensis*] *griseus*: Argyropulo, 1933b: 246. Name combination and new rank.

Cricetulus barabensis fumatus: Chaworth-Musters, 1933: 233. Name combination.

Cricetulus barabensis manchuricus: Chaworth-Musters, 1933: 233. Name combination.

C[ricetulus] f[urunculus] barabensis: Vinogradov, 1933: 45. Name combination.

C[ricetulus] griceus: Mori, 1939: 23. Incorrect subsequent spelling of *griseus* Milne Edwards.

Cricetulus barabensis ferrugineus Argyropulo, in: Vinogradov & Argyr[opulo], 1941: 170. Type locality: "южные районы Уссурийской обл.", i.e. southern Ussuri region, Russian Federation. Baranova & Gromov (2003: 46) restricted the type locality by designating the lectotype (ZIN S. 18889) from "дер. Сергиевка, Гродековский р-н, Владивостокский окр. (Партизанский р-н, Приморский кр.)" [village Sergievka, Grodekovskiy Rayon, Vladivsotokskiy Okrug (Partizanskiy Rajon, Primorskiy Krai)]. Lectotypification, however, does not contain an express statement of deliberate designation as requested by the amended Article 74.7.3 of the Code (Declaration 44; ICZN 2003) and is therefore not valid (Kryštufek & Shenbrot 2023).

[Cricetulus (Cricetulus) barabensis] furuuculus: Kuznetzov, 1944: 321. Incorrect subsequent spelling of *furunculus* Pallas.

Cricetus (sic) *pseudogriseus* Iskhakova, 1974: 231. Type locality: "southern Transbaikal region", subsequently restricted to "на юге Бурятской АССР, Кяхтинском р-не, в окресностях станции Наушки", i. e. the vicinity of Naushki station, Kyakhtinskiy rajon, southern Republic of Buryatiya, Russian Federation.

C[ricetulus] b[arabensis] tuvinicus Iskhakova, 1974: 232. Not 'Orlov & Iskhakova' (Gromov & Baranova 1981: 157). The name *tuvinicus* was proposed for hamsters occupying Tuva and northwestern Mongolia. Nomen nudum (cf. Corbet 1984: 14, Gromov & Erbajeva 1995: 319).

Cricetulus pseudogriceus: Orlov, Radzhabli, Malygin, Khotolkhu, Koval'skaya, Bulatova, & Baskevich, 1978: 157. Incorrect subsequent spelling of *pseudogriseus* Iskhakova.

C[ricetulus] b[arabensis] ferruguneus Iskhakova, 1974: 232. Incorrect subsequent spelling of *ferrugineus* Argyropulo

Cricetulus barabensis xinganensis Wang, 1980: 316. Type locality: "Moli Dawa Banner, Heilongjiang", China (Molidawa, Heilongjiang Province, China; Corbet 1984: 14).

[Cricetulus (cf.) pseudogriseus] manchuticus: Malyguin [typographical error for Malygin], Startzev & Zima, 1992: 37. Incorrect subsequent spelling of *manchuricus* Thomas.

Cricetulus barabensis tuvinicus Iskhakova, Lebedev & Lissovsky, in Lebedev & Lisovsky [sic] 2008: 371. Type locality: "в окрестнятх с. Саглы, Овюрского р-на, Тувинской АССР (в настоящее время Республика Тыва" [vicinity of village Sagly, Ovyrskiy Rayon, Tyva Autonomous Soviet Socialist Republic (currently Republic of Tyva)], Russian Federation.

Etymology. Type locality of *Cricetulus barabensis* is in Baraba steppe or Baraba Lowland (Барабинская низменность) in western Siberia (Russia). The species' epithet therefore alludes on the geographic origin of the type.

Nomenclature. The year of publication for *obscurus* and *longicaudatus*, which is nearly uniformly reported as 1867 (Trouessart 1897, Ellerman 1941, Ellerman & Morrison-Scott 1951, Pavlinov & Rossolimo 1987, Luo et al. 2000, Wang 2003, Musser & Carleton 2005, Jiang et al. 2015, etc.), with reference to "Rech. Mamm." [Recherches pour servir à l'histoire naturelle des Mammifères], is obviously erroneous because "Recherches" by Henry and Alphonse Milne Edwards were released between 1868 and 1874 (Anonymous 1875, Allen 1940: 761) and therefore postdate 1867. Chaworth-Musters (1933: 223) quoted for *obscurus* the year 1868, while some authors (Allen 1940: 761, Ross 1982: 248, Orlov & Malygin 1988: 304) gave the entire range of dates (1868–1874). As stipulated by the Code (Art. 21.6; ICZN 1999), in such cases the work should be dated from the final day of the range (*i. e.* 1874), as was done by Rode (1945: 30). However, since the work was published on different days (cf. Günther 1871: 2), the date of the Chapter "Études pour servir a l'histoire de la faune mammologique de la Chine" with *Cricetulus obscurus* and *longicaudatus* is to be determined.

Zoological Record registered these names in 1871 (Günther 1871: 2) and the "Études [...]" (Milne Edwards 1871: 284) date the 7th volume of the "Nouvelles Archives du Muséum" as released in 1871. David, in his 1871 report addressed to the Muséum d'histoire naturelle in Paris, lists *longicaudatus* and *obscurus* (David 1871: 93), hence the two names were available no later than 1871. The exposed evidence shows beyond doubt that *longicaudatus* and *obscurus* were published in 1871 (*cf.* Corbet & Hill 1992: 392).

Taxonomy. The name *Mus barabensis* Pallas was overlooked throughout the 19th century until being simultaneously restored by Chaworth-Musters (1933) and Argyropulo (1933b, c). Prior to this, the striped lesser hamster was referred to as *griseus* (Thomas 1888, 1908a, 1909, Trouessart 1904, Kashchenko 1910, Allen 1925, Howell 1929, Kuroda 1939) or *furunculus* (Gmelin 1792, Lesson 1827, 1842, Kashchenko 1910, Formozov 1929, Kuznetsov 1932, Beljaev 1933, Vinogradov 1933). Taxonomic scope was fairly stable with a single obvious deviation, specifically the inclusion into *barabensis* of *C. dichrootis* Satunin, 1902 (now a synonym of *C. longicaudatus*) and *C. kozlovi* Satunin, 1902 (now in *Nothocricetulus migratorius*) (Allen 1940).

In 1960, Matthey (1960) reported differences in the diploid number between *barabensis* (2n=20) and *obscurus* (2n=22), which he considered to be an intraspecific phenomenon. Regardless of this, Vorontsov (1960) elevated the two cytotypes to species rank, hence *barabensis* and *obscurus* started to be treated as species in their own right (Zimmermann 1964, Flint 1966b). In 1970s, Iskhakova (1974) described an additional cytotype (2n = 24) of the striped lesser hamster and named it as a new species *pseudogriseus* (nomen nudum; properly named in Orlov & Iskhakova 1975). The majority of authors writing on striped lesser hamsters during 1980s (Sokolov & Orlov 1980, Gromov & Baranova 1981, Vinogradov & Gromov 1984, Pavlinov & Rossolimo 1987) and beyond (Malygin et al. 1992, Ross 1992, Gromov & Erbajeva 1995, Panteleyev 1998, Wang 2003) accepted a tripartite taxonomy. Honacki et al. (1982) and Corbet & Hill (1986) even recognized 4 species of striped lesser hamsters (*barabensis, griseus, pseudogriseus,* and *obscurus*)

Major evidence for tripartite taxonomy was therefore provided by karyology (Corbet 1978, Ross 1992). Various authors, however, stressed the absence of cytological differences between the 3 cytotypes besides the count of chromosomes. These cytotypes share identical number of chromosomal arms (NF = 38) and differential staining allowed for a full homologation of these arms. The differences in the diploid counts can be explained by 1–2 Robertsonian fusions. Furthermore, nucleolus organizer regions (NOR) were found in 6 identical chromosomal pairs in all 3 cytotypes. These homologies questioned the utility of chromosomal evidence in species delimitation (Král et al. 1984). Furthermore, a recent phylogenetic reconstruction based on *mt*DNA cyt*b* gene questioned the monophyly of *barabensis* as defined by Orlov & Iskhakova (1975). Viable F1 hybrid offsprings were produced in breeding trials between all 3 cytotypes (Poplavskaya et al. 2012) despite some sporadic disorders in meiotic prophase I in hybrid hamsters (Matveevsky et al. 2014). In nature, the intermediate karyotype (2n = 21) was found only in Central Mongolia in the contact zone between the 20 and 24 cytotypes (Poplavskaya et al. 2012). There is also little phenetic alteration among the cytotypes of striped lesser hamsters (Ross 1992, Lebedev & Lisovsky 2008), though Orlov & Iskhakova (1975) report on differences in shape of baculum and sperm head. Application of molecular clock on *mt*DNA sequences estimated TMRCA at 0.16 Mya (CI = 0.01–0.34 Mya), which is much less than is the TMRCA for *C. longicaudatus* (0.33 Mya, CI = 0.02–0.68 Mya) (Lebedev et al. 2018a). Fossils attributed to *C. barabensis* are from the latest Early Pleistocene (Erbajeva et al. 2021) and thus predate TMRCA.

Relying on the above evidence, particularly on Král et al. (1984), many authors continued classifying the striped lesser hamster as a single polytypic species *C. barabensis* (Corbet 1978, Corbet & Hill 1980, Vinogradov & Gromov 1984, Musser & Carleton 1993, 2005, Pavlinov et al. 1995, Zhang et al. 1997, Luo et al. 2000, Pavlinov 2003, 2006, Smith & Hoffmann 2008, Lebedev 2012, Korablyov et al. 2013, Matveevsky et al. 2014, Jiang et al. 2015, 2017, Pardiñas et al. 2017, Lissovsky et al. 2019). The authors who opposed this view exposed restricted gene flow between the 20 and 24 cytotypes (e.g. Vakurin et al. 2014, Poplavskaya et al. 2017b). In biomedical research, the striped lesser

hamster is still referred to as the Chinese (grey) hamster *Cricetulus griseus* (Chang et al. 1987, Field & Sibold 1999, Bihun & Bauck 2005, Feeney 2012, Becvar et al. 2024).

Cricetulus barabensis is a sister species to *C. sokolovi*; divergence time is estimated at 0.33 Mya (CI = 0.05–0.69 Mya; Lebedev et al. 2018a).

Distribution. The range covers 2,736,000 km² in eastern Asia, specifically in Russia (south-eastern parts of West Siberian Plain, southern Siberia, and Primorye), northern and central Mongolia, north-eastern China and marginally north-eastern Kazakhstan (provinces of East Kazakhstan and Pavlodar) and North Korea (provinces of North Hamgyong and North Pyong-An) (Figure 31). The western border is approximately 150 km to the west of the middle reaches of the Irtysh, and the eastern border is set by the Ussuri and Yalu Rivers, and the shores of the eastern Korean Bay, Bohai Sea, and the Yellow Sea as far south as the estuary of the Yangtze River. The northern border is tentatively set by the middle reaches of the Irtysh, the upper reaches of

other large Siberian Rivers (Ob, Yenisei, Angara, and Lena), Lake Baikal, and the upper and middle flow of the Amur River. The southern border is defined by the upper reaches of the Irtysh, the Altai, Mongol Altai, Gobi Altai, and Gobi Desert. In eastern Mongolia, the range border turns sharply south and west towards the eastern Qilian Mts. From there, the range border turns south-east, encompassing the Ordos Loop and the plains between the lower Huang He and the Yangtze Rivers.

The striped lesser hamster occupies steppe and forest-steppe zones and penetrates marginally into semideserts. It is inhabitant of structurally simple grassland habitats (usually with *Caragana* shrubs), farmland, scrubs and hedgerows, and was occasionally captured in light woodland. Prefers sandy substrate; in semideserts frequents fixed sands with shrubs and also settles on saline substrate. Synanthrope in many parts of its range. Elevational range is from sea level up to 3,200 m a. s. l.; the majority of records are from low elevations (mean = 780 m).
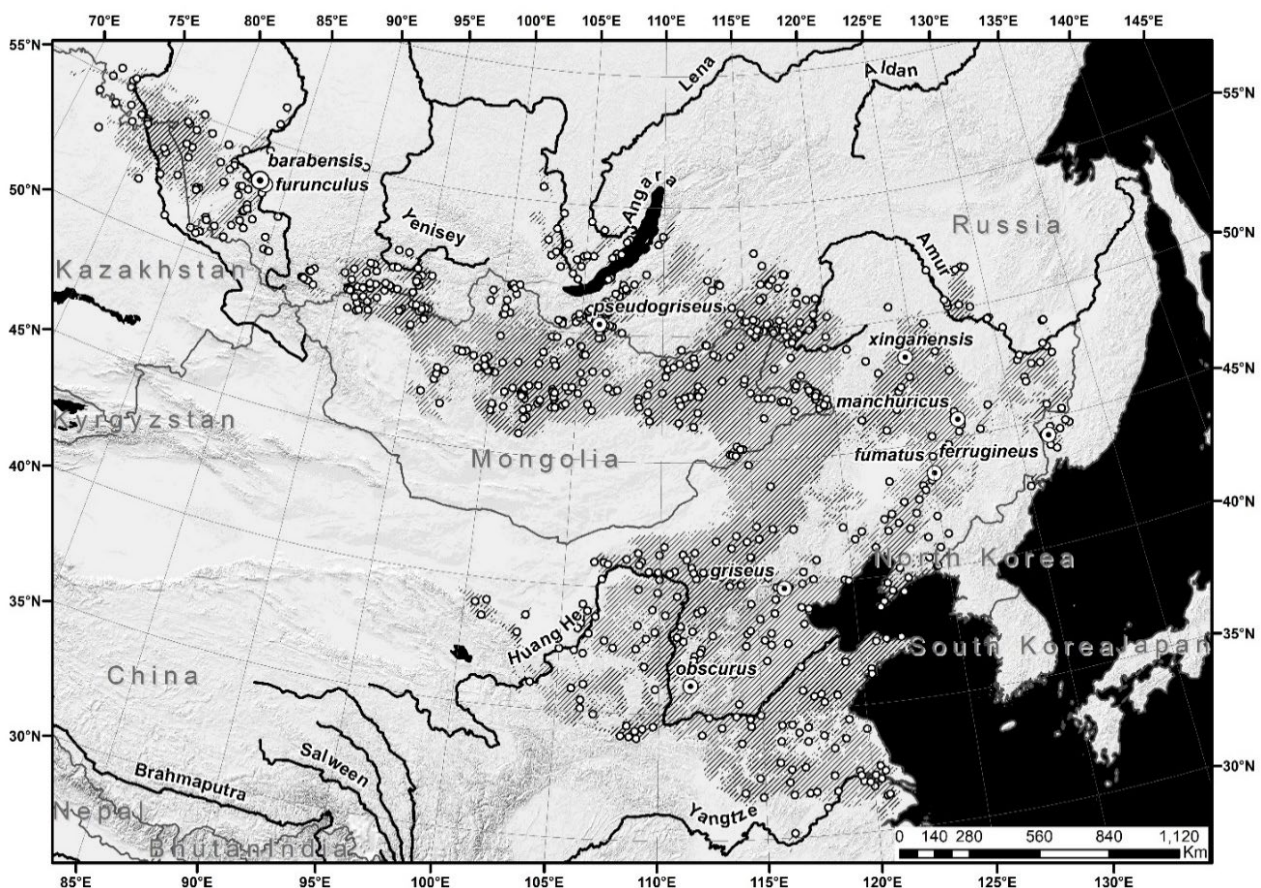
Figure 31: Distributional range of the striped lesser hamster *Cricetulus barabensis*.

Figure 32: Striped lesser hamsters *Cricetulus barabensis* from Mongolia. a – *C. b. barabensis*; b – *C. b. pseudogriseus*. Note a bold stripe on the forehead of individual in inset (a). Photo courtesy of Annegret Stubbe

Characteristics. Small and short-tailed hamsters (tail accounts for 24–31% of head and body length) with moderately large eyes, pointed snout, and long circular ears (Figure 32). Dimensions: body mass = 21–41 g, length of head and body = 90–117 mm, length of tail = 20–30 mm, length of hind foot = 14–17.5 mm, ear length = 13–17 mm, condylobasal length = 21.2–27.5 mm, zygomatic width = 12.2 –16.2 mm, length of maxillary tooth-row = 3.5–4.4 mm. Males are on average heavier (mean body mas $\pm$ SD = 37.7 $\pm$ 1.38 g) than females (33.4 $\pm$ 1.30 g; data from captive *C. b. griseus*; Chernova et al. 2022a). Vibrissae are up to 22–27 mm long, either white or blackish-brown. The inner side of pinnae is pigmented grey and is sparsely covered with whitish hairs; hairs on the outer side are black; the top of the ear is bordered white. There is a white post-auricular tuft. Short hairs covering paws, wrists and ankles are white to base. The soles are densely furred posterior to pads with spares hair between them (Figure 33a). Tail is thick at the base and gradually tapers towards its tip; it is densely covered by spinous hairs, which form a feeble pencil; additional longer whitish hairs protrude from the tail's base (Figure 29a).

Fur is soft and dense, 7.5–11 mm long on the mid-back with sparse longer hairs protruding for additional 1–1.5 mm. Hairs on the dorsal side are typically tricoloured, with slate base, buffy subterminal band and black tip.
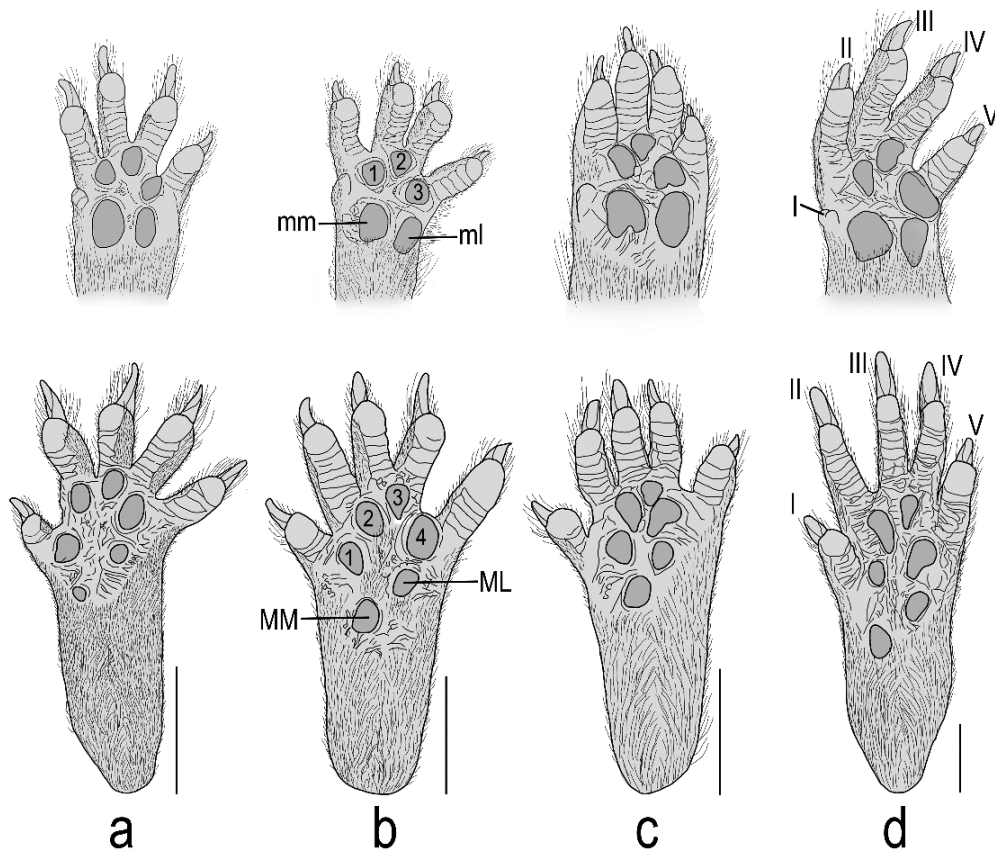
Figure 33: Left palm (top row) and sole (bottom row) in hamsters from the subtribe Cricetina: a – *Cricetulus barabensis* (China); b – *Nothocricetulus migratorius* (bottom – Afghanistan; top – Izmir, Turkey); c – *Allocricetulus eversmanni* (Tatarstan, Russia); d – *Cricetus cricetus* (Hungary). Digits are shown in Roman numerals (thumb = I) and interdigital pads are shown in Arabic numbers; pads: mm / MM – medial metacarpal / metatarsal pad; ml / ML – lateral metacarpal / metatarsal pad. Scale bars = 5 mm.

Colouration of the dorsal surface, from the muzzle to the root of the tail, the cheeks, upper arms and thighs, is highly variable, ranging from ochraceous buff to reddish-brown and to dull grey (see under subspecies). The mid-dorsal stripe is usually present but varies individually and among subspecies, being either black and bold, thin and interrupted, dissolved or even obscured entirely (Figures 36 & 37). It extends from the crown of the head to tail base, but this also varies; the stripe is 1.5–4 mm wide. Underside is grey; hair bases are slate and tips are either grey or white. Dark slate of hair bases clouds the underside dark grey. Demarcation line on the flanks is distinct and almost straight. Tail is usually sharply bicolour, black or dull brown above, white below. Juveniles are usually duller and greyer than adults; they already have a mid-dorsal line.

Glans penis is of cylindrical shape with truncate distal end; it is 5.1 mm long, 2.9 mm wide and 2.6 mm deep. Distally, the glans is densely covered with spines which on the ventral side expand posteriorly covering ~½ of the surface. At the base is a prominent protuberance covered by spines which are 2–3-times the size of spines on the distal glans. The central papilla bifurcates and is wider than lateral papillae (Tokuda 1941); there are also 2 ventral papillae, while the dorsal papilla is absent (Vorontsov 1982). Baculum is slender and usually with expanded base (17d). Trident is of approximately same length as the proximal shaft; lateral denticles are gently bent and are of same size as the straight central denticle (Argyropulo 1933c, Ross 1992). The skull has comparatively short rostrum; nasals reach further posteriorly than in *C. longicaudatus,* and the posterior edge of palate is closer to M^3 than in *C. sokolovi*. Zygomatic arches tend to be more expanded than in *C. longicaudatus;* zygomatic width accounts for 50.0–59.5% of condylobasal length (mean = 54.9%) (Figure 34). Dentition shows no peculiarities (Figure 35).

Cricetulus barabensis
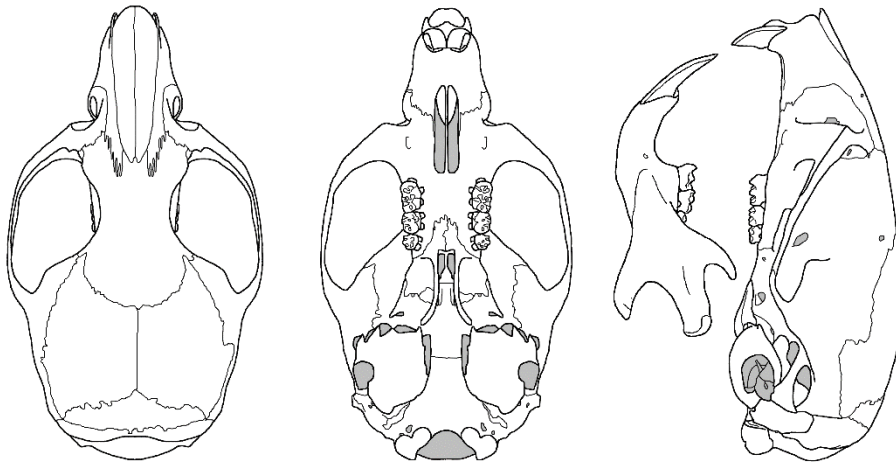
Cricetulus sokolovi

Cricetulus longicaudatus

5 mm
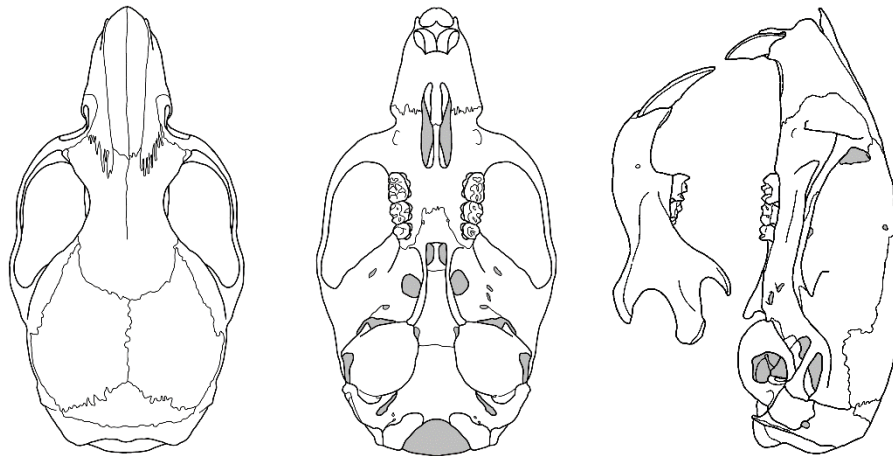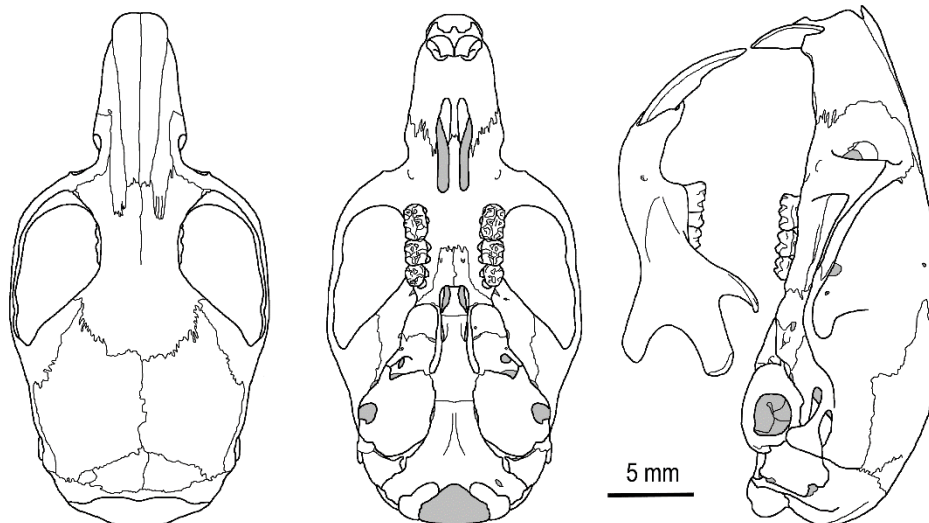
Figure 34: Skull and mandible in lesser hamsters *Cricetulus*. Top to bottom: *C. barabensis* (Xing'an, Shaanxi, China), *C. sokolovi* (Orog Nuur, Mongolia), and *C. longicaudatus* (Mongolia).

Cricetulus barabensis   *C. sokolovi*
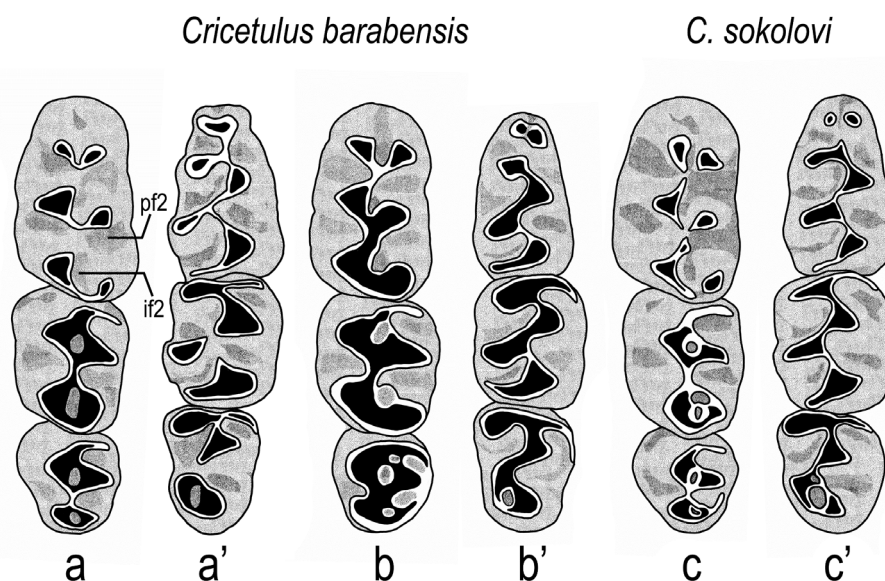
Figure 35: Grinding pattern of upper (a, b, c) and lower (a', b', c') molars in lesser hamsters of different age: *Cricetulus barabensis* (a, b) and *C. sokolovi* (c). Acronyms: *if*2 – the 2nd internal fold; *pf*2 – the 2nd primary fold. Origin of vouchers: a – Buir nuur, Mongolia; b – Ononsky Rayon, Russian Federation; c – Orog Nuur, Mongolia.

Karyotype is polytypic with 3 allopatric cytotypes differing in diploid numbers. These cytotypes are frequently labelled by taxonomic names, which we parenthesize: 2n = 20 (*barabensis* cytotype), 2n = 22 (*griseus* cytotype), and 2n = 24 (*pseudogriseus* cytotype). Fundamental number is the same across all cytotypes (NF = 38) and heterochromosomes are invariably bi-armed (submetacentric or metacentric), either medium-sized (the X chromosome) or rather small (the Y chromosome); *pseudogriseus* was originally reported to have acrocentric Y chromosome (Orlov & Iskhakova 1975). The autosomal complement consists of 8 pairs of metacentric and 1 pair of acrocentric chromosomes in the *barabensis* cytotype, 7 pairs of metacentric and 3 pairs of acrocentric chromosomes in the *griseus* cytotype, and 6 pairs of metacentric and 5 pairs of acrocentric chromosomes in the *pseudogriseus* cytotype (Orlov et al. 1978, Král et al. 1984).

Variation and subspecies. Individual and geographical variation is most obvious in colouration, and Vorontsov (1982) considered this trait dimorphic. He classified hamsters either as reddish or greyish. Though the reality is more complex, this simplification exposes the latitudinal trend along the northern edge of species' distribution. All hamsters are grey in the western part of their range in Siberia, contrary to 95.5% of reddish individuals at the eastern edge in the Ussuri Region. Morphometric studies stressed great similarity among populations (Ross 1992). Craniometric study by Lebedev & Lisovsky (2008) demonstrated a north-to-south trend in size, with smaller hamsters in the north (Russia and western Mongolia), and larger hamsters in the south (eastern Mongolia and China). The species is neatly structured into 3 allopatric chromosomal races (see below and Characteristics above). Phylogeographic structuring similarly shows a clear pattern which is largely consistent with the distribution of cytotypes. A phylogenetic tree based on *mt*DNA cyt*b* gene yielded 2 clusters, one containing the 2n = 20 cytotype, and another with 2 monophyletic lineages, comprising the 2n = 22 and 2n = 24 cytotypes, respectively (Poplavskaya et al. 2018a).

Variation as outlined above can be reasonably well accommodated with traditional trinomial taxonomy. So far, the majority of authors have recognized 4 subspecies (Argyropulo 1933b, c, Ellerman 1941, Iskhakova 1974) or 5 subspecies (Chaworth-Musters 1933, Ellerman & Morrison-Scott 1951, Corbet 1978). Four subspecies have been recognized in the former Soviet Union (Vinogradov & Argyropulo 1941, Kuznetzov 1944, Gromov et al. 1963, Kuznetsov 1965, Gromov & Erbajeva 1995) however Chinese authors admitted higher number of subspecies for China: 5 subspecies (Zhang et al. 1997, Luo et al. 2000) or 6 subspecies (Wang 1980); Wang (2003) listed 8 subspecies which he grouped into 3 species.
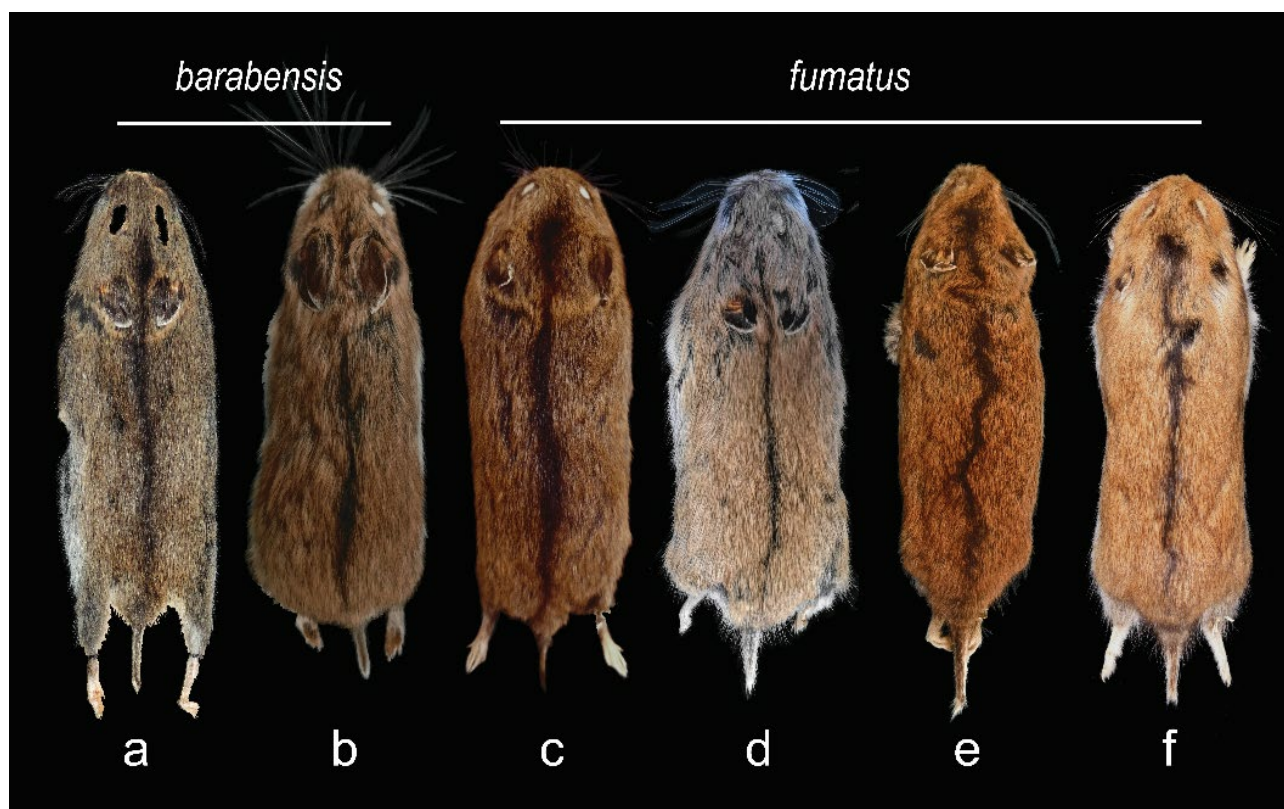
Figure 36: Skins of striped lesser hamster *Cricetulus barabensis* from the subspecies group *barabensis*: a – Kyakhtinskiy Rayon, Buryatia, Russia; b – Khovsgol nuur, Mongolia; c – Sretenskiy District, Zabaykalsky Krai, Russian Federation; d – Borzinskiy Rayon, Russian Federation; e – 200 km west of Heihe, Nei Mongol-Heilongjiang border, China; f – Xing'an, Shaanxi, China. Subspecies identities: *C. b. barabensis* (a, b), *C. b. fumatus* (c–f).

Subsequently, we recognize 5 subspecies in 2 groups. Sampling for karyological and molecular phylogenetic analyses was dense in Russia and Mongolia, but sparse in China. The provinces of Heilongjiang, Jilin, and the eastern parts of Nei Mongol with type localities for 3 nominal taxa (*fumatus, manchuricus, xingangensis*) remain particularly under-sampled, which poses some uncertainty in the proposed subspecific taxonomy.

Subspecies group barabensis

The group contains 3 subspecies sharing the diploid number 2n = 20. Spinal stripe is black, heavy and distinct, frequently bold, carried forward on the crown of the head where typically expanded into a patch (Figures 32a, 36a, c, e & f). In comparison with the *griseus* group, the proximal baculum is wider across its base, but has a narrower stalk and the transition between the two is rather abrupt; the medial denticle of distal baculum is narrower. Sperm head (without acrosome) is shorter and wider; length-to-width ratio = 3.1 (Orlov & Iskhakova 1975).

Cricetulus barabensis barabensis (Pallas, 1773)

Synonyms: *Mus furunculus* Pallas, 1779 (unnecessary renaming of *barabensis* Pallas); *Cricetulus barabensis tuvinicus* Iskhakova, 1974 (nomen nudum); *Cricetulus barabensis tuvinicus* Lebedev & Lissovsky, 2008.

Taxonomy. Phylogenetic reconstruction by Poplavskaya et al. (2018a) clustered *tuvinicus* with the nominotypical *barabensis* and we classify these names as synonymous. When described (Lebedev & Lisovsky 2008), *tuvinicus* was defined by colouration, but was not compared with the nominotypical *barabensis*.

Distribution. The western and north-central part of species' range in Russia, Kazakhstan, and Mongolia, as far east as the line: Hujirt and Kharkor (Ovorkhangai Province, Mongolia) – confluence of the Uur Gol and Uilgan Gol Rivers (Hovsgol Province, Mongolia) – Zarubino and the Chikoi River (Republic Buryatia, Russia) – Sokhondo Nature Reserve (Zabaikalsky Krai,

Russia) – central Lake Baikal and the upper Lena River (Russia; Poplavskaya et al. 2018a).

Characteristics. Characterized by the nucleotide sequence of cyt*b* (Poplavskaya et al. 2018a). A small subspecies with dark dorsal pelage and distinct black stripe (Figures 32a & 36a, b); individuals with reddish shades are exceptional. The eastern populations are paler and greyer than the western ones.

Cricetulus barabensis fumatus Thomas, 1909

Synonyms: *Cricetulus manchuricus* Mori, 1930; *Cricetulus barabensis xinganensis* Wang, 1980.

Etymology. Latin 'fumus' (fumare) translates as 'smoke' (smoked); the subspecific epithet *fumatus* therefore means 'smoked' in allusion to greyish tint of dorsal pelage.

Taxonomy. Luo et al. (2000) and Wang (2003) classified *fumatus, manchuricus*, and *xinganensis* as subspecies in their own right with ranges in south-eastern Heilongjiang, Jilin, and Nei Mongol (*fumatus*), eastern Heilongjiang (*manchuricus*), northern Heilongjiang and Nei Mongol (*xinganensis*). Any of these subspecies has been karyotyped or screened for molecular makeup, hence their taxonomic assessment relies entirely on morphology. The results of different authors are unsurprisingly contradictory. For example, Orlov & Iskhakova (1975) classified striped lesser hamsters from Heilongjiang and Jilin as members of the *barabensis* group, while Lebedev & Lisovsky (2008) pooled them into the *griseus* group. Similar discrepancies are to be found elsewhere as well; *e. g.* H. K. Won (1968) quote for North Korea a subspecies *fumatus* (the *barabensis* group), while Jo et al. (2018) state it is *griseus* (the *griseus* group).

Distribution is in several fragments. The north-western fragment in Zabaikalsky Krai (Russia) is tentatively delimited by the line Shaksha – Lake Balzinskoe – Maly Bator – Nerchinsk – Mankovo – Kuznetsovo – Gazimursky Zavod – Zhidka (Poplavskaya et al. 2018a). The north-eastern fragment stretches along the mid-flow of the Amur River in the Amur Region and Jewish Autonomous Region in

Russia (Poplavskaya et al. 2018a) and most probably encompasses also north-eastern Heilongjiang (China). Borders in Heilongjiang and Jilin are not resolved. A distributional range, very similar to the one defined here, was in the past proposed for *fumatus* by various authors (Vinogradov & Argyropulo 1941, Kuznetsov 1944, Kuznetsov 1965, Gromov & Erbajeva 1995).

Characteristics. Characterized by the nucleotide sequence of cyt*b* (Poplavskaya et al. 2018a). Colouration is variable but rusty tints usually dominate (Figure 36c–f); in Russia, Vorontsov (1982) classified 82–83% of hamsters as being reddish; the remaining are greyish-brown. Russian authors (e.g. Gromov et al. 1963) frequently claim that *fumatus* is intermediate in colouration between *barabensis* proper and *ferrugineus*. Black dorsal line is usually heavy and distinct, carried forward on the crown of the head. Ventral side is grey, though hairs are frequently tipped white.

Cricetulus barabensis ferrugineus Argyropulo, 1941

Etymology. The Latin 'ferrugo' (ferruginis) translates as 'iron rust', hence the epithet *ferrugineus* means 'rusty-coloured' in allusion to the fur colouration.

Taxonomy. Russian authors usually restrict *ferrugineus* to the Ussuri region (Vinogradov & Argyropulo 1941, Kuznetsov 1944, Gromov et al. 1963, Kuznetsov 1965, Iskhakova 1974, Orlov & Iskhakova 1975), which accords the molecular results (Poplavskaya et al. 2018a). Lebedev & Lisovsky (2008) mapped *ferrugineus* for Heilongjiang and along the entire Amur River from its source (here classified as *fumatus*). Chinese authors (Luo et al. 2000, Wang 1980) synonymized *ferrugineus* with *C. b. manchuricus*.

Distribution. Known from the vicinity of Lake Khanka, south-western Ussuri region (Primorye Region, Russia; Poplavskaya et al. 2018a). Lebedev & Lisovsky (2008) reported *ferrugineus* for central Heilongjiang and set the western border on the Songhua River, the tributary of the Amur. Probably occurs also in Korea (Gromov & Erbajeva 1995).

Characteristics. Characterized by the nucleotide sequences of cyt*b* (Poplavskaya et al. 2018a) and
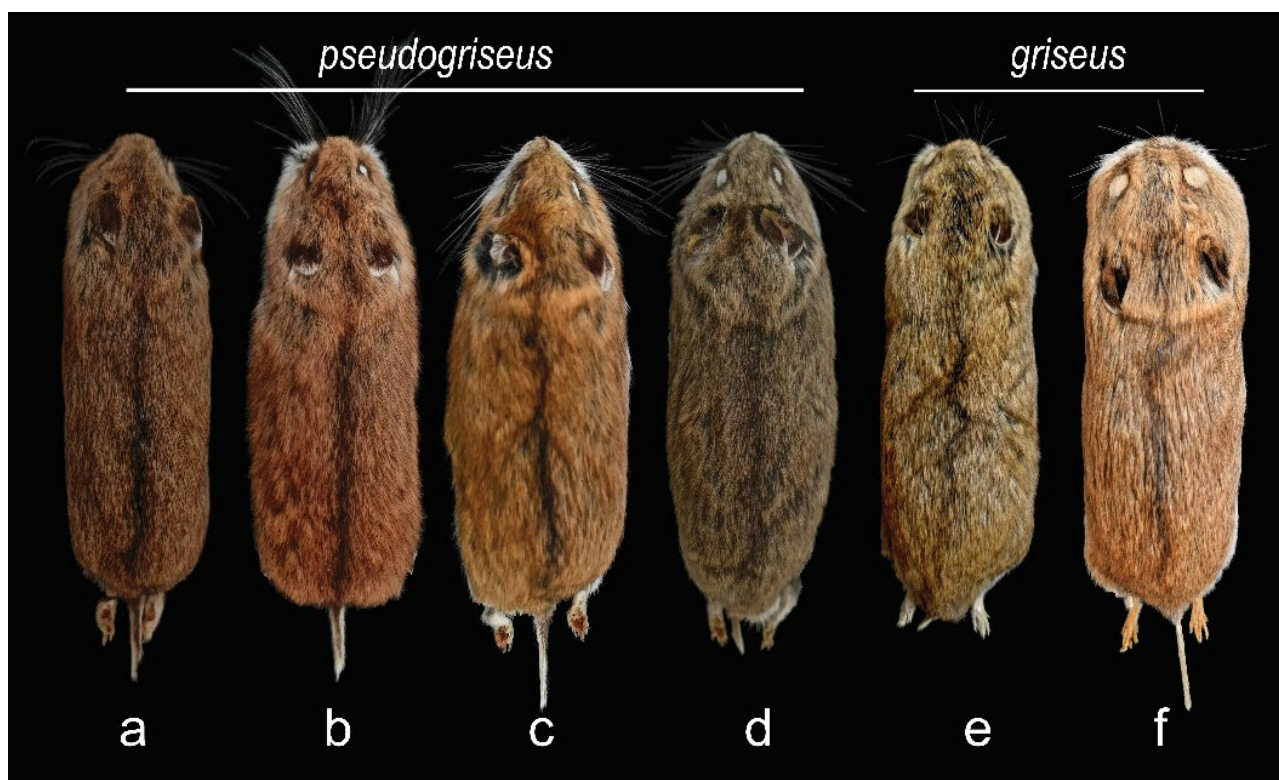
Figure 37: Skins of striped lesser hamster *Cricetulus barabensis* from the subspecies group *griseus*: a–d Buir nuur, Mongolia; e, f – 200 km north-east of Chengde, Hebei. Subspecies identities: *C. b. pseudogriseus* (a–d), *C. b. griseus* (e, f).

colouration. Argyropulo diagnosed *ferrugineus* as dull coloured, with ample reddish tint (Vorontsov & Argyropulo 1941); this subspecies is gloomier than *fumatus* (Orlov & Iskhakova 1975). According to Vorontsov (1982), 95.5% of hamsters of this subspecies are reddish. The stripe is clear.

Subspecies groups *griseus*

The group contains 2 subspecies with diploid number of chromosomes 2n > 20. Spinal stripe is narrower and less distinct than in the *barabensis* group, frequently truncated at both ends, and therefore not always reaching the crown of the head. The stripe is occasionally interrupted, obscured or even obliterated (Figure 37e, f). In comparison with the *barabensis* group, the stalk of baculum is narrower across its base, but has a chunkier stalk and the transition between the two is smooth; the medial denticle of the distal baculum is heavier. Sperm head (without acrosome) is longer and narrower; length-to-width ratio is 5.8 (Orlov & Iskhakova 1975). In the cyt*b* phylogenetic tree, the *griseus* group emerged as a monophyletic lineage (Poplavskaya et al. 2018a).

Cricetulus barabensis griseus A. Milne Edwards, 1867

Synonyms: *Cricetus obscurus* A. Milne Edwards, 1871; *Cricetus mongolicus* Thomas, 1888 (unnecessary renaming of *obscurus*).

Etymology. In Latin, 'griseus' (griseum) means 'grey', which is allusion on pelage colouration of these hamsters.

Taxonomy. Since the 19th century, *griseus* has been in use as a species epithet for all striped lesser hamsters and still is used this way in biomedical research. Traditionally, *C. griseus* was split into 2 subspecies, the nominotypical and *obscurus* (Allen 1925, and subsequent authors). In Allen's view, *obscurus* is "[a]t best […] a poorly marked subspecies". Corbet (1978) synonymized *obscurus* with *C. b. griseus*, which is followed here. Wang (2003), on the other hand, classified *obscurus* as a subspecies of *C. barabensis*, and elevated *C. griseus* to a species in its own right. Within *C. griseus*, Wang (*l. c.*) recognized 2 subspecies, the nominal with a range in Liaoning, Nei Mongol, Hebei, Beijing, Tianjin, Shandong, Henan, and Shanxi, and an undescribed

"Anhui form" from Anhui and northern Jiangsu; he reported *obscurus* for eastern Gansu, central Nei Mongol, Ningxia, norther Shaanxi, and Shanxi.

The names *griseus* and *obscurus*, as applied in the past to striped hamsters from Mongolia, represent the current *pseudogriseus* and *sokolovi*, respectively (Allen 1925, 1940, Formozov 1929, Vinogradov & Argyropulo 1941, Bannikov 1954, Zimmermann 1964, Sokolov & Orlov 1980).

Distribution. Endemic to Chinese provinces of Hebei, Beijing, Shanxi, Shandong, Jiangsu, Anhui, Henan, Hubei, central Nei Mongol, Ningxia, central Gansu, Shaanxi, and Tianjin. The northern border is tentatively on the eastern Qilian Mts., the Ordos loop, and the line Xilingol – Yellow Sea.

Characteristics. Characterized by nucleotide sequences of cyt*b* (Poplavskaya et al. 2018a), the karyotype (2n = 22), and colouration. Dorsal pelage is generally paler and lacks reddish tinge which is typical of the *barabensis* group. The mid-dorsal stripe is commonly not so well defined or fades entirely; on the crown of the head, the stripe is hardly noticeable (Figure 37e, f). Back is ochraceous-buff to pale-brown with sandy tint; ventral hairs have slate bases and white tips. The skull of *griseus* has on average wider and deeper rostrum and narrower M^1 than *pseudogriseus* (Lebedev & Lisovsky 2008).

Cricetulus barabensis pseudogriseus Ishakova, 1974

Etymology. The epithet *pseudogriseus* is composed of 'pseudos' (Greek for 'false') and *griseus* which is a subspecific name for Chinese lesser hamsters (see above). When the name was coined, *griseus* and *pseudogriseus* were distinguished only karyologically.

Taxonomy. Iskhakova (1974) published *pseudogriseus* in a conference proceeding, while a detailed description was still in press (Orlov & Iskhakova 1975). Pavlinov & Rossolimo (1987: 167) condemned the name as *nomen nudum*, because it allegedly lacks a description. This is not so, since Iskhakova listed diagnostic traits. Regardless of this, subsequent authors nearly unanimously accepted the position of Pavlinov &

Rossolimo (*l. c.*) and quoted a subsequent paper by Orlov & Iskhakova (1975) as the first valid naming of *pseudogriseus*. We concur with Lebedev (2012) that naming of *pseudogriseus* in Iskhakova (1974) is valid.

Lebedev & Lisovsky (2008) stressed that *pseudogriseus* is likely predated by *Mus furunculus* Pallas, 1779, which would, in their view, necessitate designation of the neotype for *furunculus* in order to stabilize nomenclature. Furthermore, the type locality restricted by the neotype should be in the historic Dauriya, which is one of 3 localities quoted by Pallas for *furunculus*. Messerschmidt indeed reported *furunculus* (as *Furrunculus myodes*) from "Dalai Nor" [Lake Hulun, Nei Mongol, China] (Pallas 1779: 273, footnote) or "Dalaï Lacum Dauuriæ", as Pallas (*l. c.*) formulated it. As we stressed above (see Synonymy under *C. barabensis*), *furunculus* is a renaming of *barabensis*, and not a name for a new species (see also Chaworth-Musters 1933, and Allen 1940), hence no typification is needed for defining its scope. Even if this would not be the case, the type locality has already been restricted, *e. g.* the Baraba Steppe (Vinogradov 1933: 45) or "Altaisky Krai, Barnaul" (Pavlinov & Rossolimo 1987: 167). Such a restriction would satisfy the requirements of the Code (ICZN 1999), considering that among the 3 localities quoted by Pallas (1779: 273) there is also "arenoſa regione Barabenſium camporum, inter Barnaul & Kaſmala rivos, verſus Obum", *i. e.* "between the Kasmala and Barnaul [Barnaulka] Rivers" (Chaworth-Musters *l. c.*).

Since 2000, *pseudogriseus* is occasionally still classified as a species in its own right (Wang 2003, Vakurin et al. 2014, Bazhenov 2022).

Distribution. Southern Buryatia and Zabaikalsky Krai in Russia; provinces of Arhangay, Bulgan, Selenge, Töv, Ulaanbataar, Hentiy, Dornod, and Sühbaatar in Mongolia (possibly also Ovorhangay). In China known with certainty in central Nei Mongol (Poplavskaya et al. 2018a). Luo et al. (2000) did not include *pseudogriseus* into the list of Chinese mammals, while Wang (2003) reported it for north-eastern Nei Mongol.

The western and south-western borders tentatively follow the line Povorot (Buryatia, Russia) – Zuunburen (Selenge Province, Mongolia) – Saikhan (Bulgan Province) – Khashaat (Arhangay) – Bat Khaan Uul Mts.

(Töv) – Xilin Gol, Nei Mongol (China) (Poplavskaya et al. 2018a). The northern border stretches from Buryatia (Kiran) to Hentiy Province in Mongolia (Ulz Gol River), turning north to Zabaikalsky Krai where follows a wavy line Kubukhai – Karaksar – Kovyli – Kozlovo – Nerchinsky Zavod; further east, the range continues into Nei Mongol, but the details are not known.

Characteristics. Characterized by the nucleotide sequences of cyt*b* (Poplavskaya et al. 2018a), the karyotype (2n = 24), and colouration. Dorsal pelage is in general duller or with more reddish tinge then in *griseus* (Figure 32b & 37a–d). In comparison to *barabensis* group, the mid-dorsal stripe tends to be thinner and not so well defined or fades entirely. Back shows various shades of brown, with different admixture of dull, grey, reddish or ochraceous tints; ventral hairs have slate bases and occasionally white tips. The skull of *griseus* has on average narrower and shallower rostrum and wider M¹ than *griseus* (Lebedev & Lisovsky 2008).

Cricetulus sokolovi Orlov & Malygin, 1988 – Sokolov's Lesser Hamster

Cricetulus sokolovi Orlov & Malygin, 1988: 305. Type locality: "Баян-Хонгорский аймак МНР, на юго-

западном берегу оз. Орог-Нур" [Bayanhongor Province, Mongolian People's Republic, south-western shore of Lake Orog-Nur].

C[ricetulus] socolovi: Tembotova, 2015: 227. Incorrect subsequent spelling of *sokolovi* Orlov & Malygin.

Etymology. The species epithet is eponym for Vladimir E. Sokolov (1928–1998), a Russian mammalogist, Professor at the Moscow State University, Director of the Institute of Evolutionary Animal Morphology and Ecology, member of the Russian Academy of Sciences, and Vice-President of the Fauna and Flora International (Pavlov & Shishkin 1998).

Taxonomy. Early students of Mongolian mammals recognized Sokolov's lesser hamster under the name *obscurus* (Allen 1925, 1940, Howell 1929). Distributional map provided by Bannikov (1954) for *C. barabensis obscurus* accurately captured the geographic scope of *C. sokolovi* in Mongolia. Decisive information on the taxonomic rank of Sokolov's lesser hamster was provided by karyological research (Orlov et al. 1978) and translated into Linnaean taxonomy with a lag of the entire decade (Orlov & Malygin 1988). The new name *sokolovi* was readily accepted in the West and in Russia
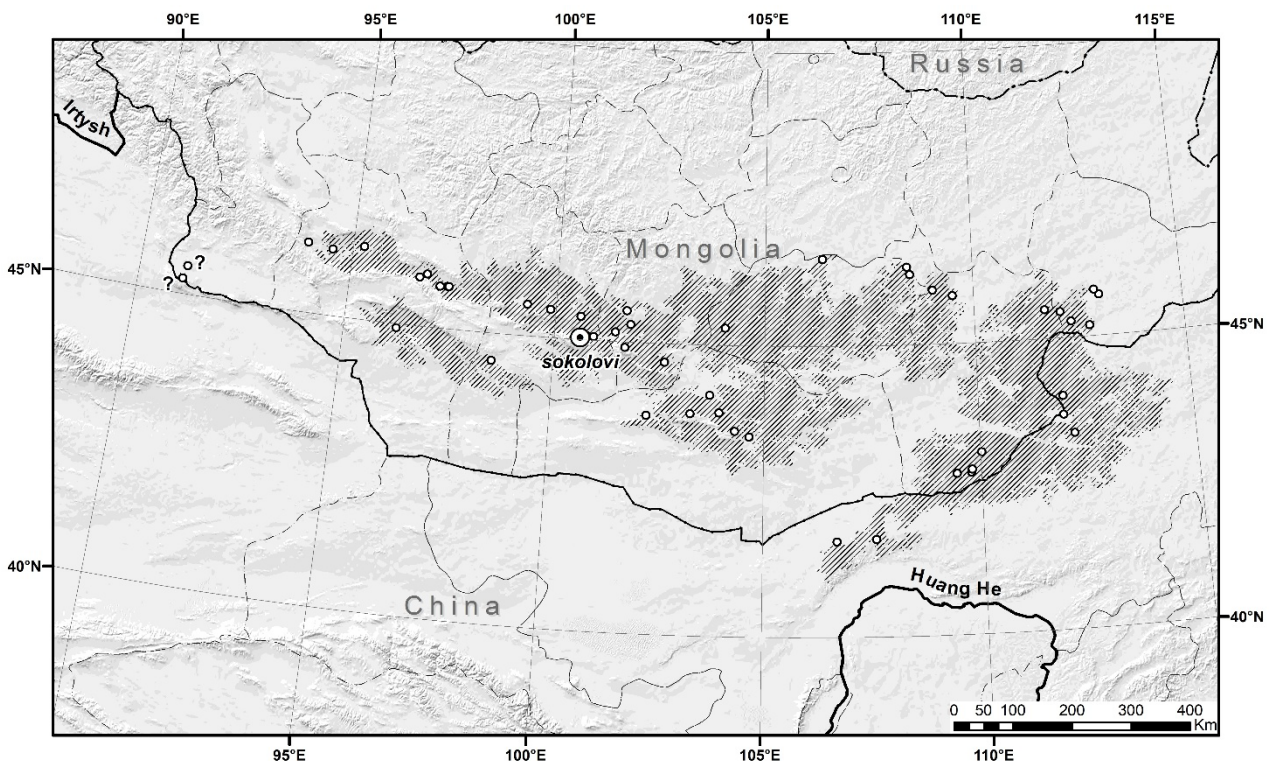
Figure 38: Distributional range of the Sokolov's lesser hamster *Cricetulus sokolovi*. The 2 records in Khovd require reconfirmation and are therefore interpreted by question mark.

(*e. g.* Musser & Carleton 1993). Chinese authors were at first hesitant (e. g. Zhang et al. 1997, Luo et al. 2000) and included Sokolov's lesser hamster into the list of Chinese mammals in the early 2000s (Wang 2003). A recent phylogenetic analysis based on cyt*b* gene confirmed the status of *sokolovi* as an independent species (Poplavskaya et al. 2017a) and its sister position against *C. barabensis*; time of divergence is estimated at 0.33 Mya (CI = 0.05–0.69 Mya; Lebedev et al. 2018a).

Distribution. Endemic to Mongolia and adjacent central Nei Mongol in China (Figure 38). The range covers an estimated 301,290 km². In Mongolia, *C. sokolovi* occupies the provinces of Govi-Altay, Bayanhongor, Ömnögovi, Övörhangay, Dundgovi, and

Sühbaatar; there is also an isolate in the extreme south-western Khovd (Mongolian Dzungaria), on the border with Xinjiang (China), which requires confirmation. Lesser hamsters, however, are scarce and localized there. *E. g.* during extensive field work performed in Khovd in 1978–2022 by Soviet (after 1998 the Russian)-Mongolian Complex Biological Expeditions which collected large samples of small mammals (housed in ZMMU), the only lesser hamsters were *C. longicaudatus*. Two occurrence points for *Cricetulus s. str.* are known from Khovd. One was dealt with in 1975 by German-Mongolian Biological expedition, which yielded 3 specimens originally identified as *C. barabensis* and subsequently lost. The other occurrence involved the Mongolian Expedition of the Museum of South-

Figure 39: Sokolov's lesser hamster *Cricetulus sokolovi* from Orog Nor. Note large scrotal testicles in inset (b) which reach dimensions 14 x 11 mm in adult males (*cf.* Orlov & Sokolov 1988). Photo courtesy of Klaus Rudloff

Figure 40: Skins of Sokolov's lesser hamster *Cricetulus sokolovi* in dorsal (a, b), ventral (a', b') and lateral (b") views: a – type of *C. sokolovi* (ZMMS S-110099); b – Orog Nur, Mongolia (SMG 15095).

Western Biology (MSB, Albuquerque, New Mexico, USA) which gained 4 specimens identified as *C. sokolovi*. Since the Khovd population may represent either an isolate of *C. barabensis* or *C. sokolovi* proper we call for reidentification of the MSB vouchers.

Contrary to *C. barabensis*, which is primarily a steppe-dweller, *C. sokolovi* is restricted to a semidesert zone. It occupies structurally simple habitats on rocky slopes, fixed sands, clay, and saline soils. Vegetation consists of needlegrass, nitre bushes, Siberian pea-tree, almond shrubs, feather grass, and halophytes. Abundance is higher around springs and in oases. Elevational range is 885–2,190 m (mean = 1,324 m).

Characteristics. Size and proportions are similar as in *C. barabensis*; tail accounts for 27–29% of head and body length. Dimensions: body mass = 17–25 g, length of head and body = 77–114 mm, length of tail = 18–32 mm, length of hind foot = 13–18 mm, length of ear = 13.0–18.5 mm, condylobasal length of skull = 22.7–26.0 mm, zygomatic width = 12.1–14.2 mm, length of maxillary tooth-row = 3.7–4.7 mm. Males are on average heavier (mean body mas ± SD = 39.4 ± 2.01 g) than females (32.9 ± 2.15 g; data from captivity;

Chernova et al. 2022a). Sokolov's lesser hamster is more sexually dimorphic (quotient of male-to-female body mass = 1.20) than *C. barabensis griseus* (1.13). Tail is furrier then in *C. barabensis* and hair largely conceal the underlying annulation (Figure 29b); terminal pencil is feeble (length < 1.5 mm). Soles are nude in summer but hairy during winter when hairs conceal the pads (Sokolov & Orlov 1980). Vibrissae are long (27–20 mm); fur is soft (7.5–13.5 mm) and dense, the sparse longer all-white or all-black hairs protrude by 1.5–2.5 mm. Colour varies from uniformly buff, lacking any dash of black hairs, to light reddish or to grey with brownish shade (Figures 39 & 40). The fur surrounding the eyes and ears is paler and some individuals have a white postauricular tuft. The nose, the buccal region and the lower part of the temporal region are white.

The underside is either cream or whitish-grey; ventral hair bases are grey, but slate (*i. e.* more blackish) in *barabensis*. Demarcation line along the flanks is distinct albeit not sharp; it is straight and set fairly high on the flanks, but descends towards the hips. Mid-dorsal stripe is blackish brown, up to 3 mm wide, and extends from the front region; on the posterior end it usually does not reach the tail base. The line is never sharp, but obscure

or even absent. Paws are white and ears are dull grey with contrasting white margin. Tail is whitish throughout (Figure 29b) or with a narrow blackish-brown stripe which fades towards the tip. Skull (Figure 34) and dentition (Figure 35c) are as in *C. barabensis* with few minor average differences; *C. sokolovi* has (1) wider alisphenoid region, (2) more caudally positioned posterior edge of the hard palate, (3) wider interorbital region, and (4) shallower braincase (Lebedev & Lisovsky 2008).

Karyotype (2n = 20, NF = 40) consists of 2 pairs of large metacentric, 3 pairs of medium metacentric, 3 pairs of small metacentric, and 1 pair of large subtelocentric chromosomes; the latter were also classified as sub-metacentrics (Poplavskaya et al. 2017a). Sex chromosomes are large (the X chromosome) and small (the Y chromosome) submetacentrics (Orlov et al. 1978, Poplavskaya et al. 2017a). The karyotype of *sokolovi* is highly rearranged, differing from the hypothetical ancestral condition by at least 4 Robertsonian events and a centromeric shift (Poplavskaya et al. 2017a).

Variation and subspecies. Monotypic.

SUBGENUS: *Ourocricetulus* new subgenus

Taxonomy. The new subgenus *Ourocricetulus* is a sister subgenus to subgenus *Cricetulus* (with *barabensis* and *sokolovi*); divergence time between the lineages is estimated at 1.06 Mya (CI = 0.50–1.64 Mya; Lebedev et al. 2018a). The new subgenus is monospecific.

Type species. *Cricetulus longicaudatus* (A. Milne Edwards, 1871).

Etymology. From 'oura' (Greek for tail) and *Cricetulus,* which is diminutive of *Cricetus* (*i. e.* the hamster). See also Etymology under *Cricetulus* and *Urocricetus*. Do not mismatch *Ourocricetulus* with *Urocricetus* (tribe Urocricetini).

Diagnosis and Comparison. The new subgenus is well defined by *mt*DNA nucleotide sequences (Lebedev et al. 2018a, Poplavskaya et al. 2018b). The X chromosome is the largest element in the complement

in *Ourocricetulus*, while it is of medium size in the subgenus *Cricetulus* (Orlov et al. 1978). *Ourocricetulus* lacks the mid-dorsal (spinal) stripe, which is nearly always present in *Cricetulus* s. str., and has decidedly longer tail (*cf.* Key to species above). The two subgenera differ in the overall cranio-dental morphology (Ross 1992). *Ourocricetulus* has narrower rostrum and less expanded zygomatica arches, broader palate, shorter maxillary tooth-row, and longer diastema. The coronoid and the articular processes of the mandible are less robust (Figure 30). The 2nd internal fold (*if*2) and 2nd primary fold (*pf*2) of M^1 are confluent in *Ourocricetulus* (Figure 44) while they are separated by metacone in *Cricetulus* s. str. (Figure 35).

Cricetulus longicaudatus (A. Milne Edwards, 1871) – Long-tailed Lesser Hamster

Cricetus (Cricetulus) longicaudatus A. Milne Edwards, 1871: 136. Not 1867 (See the account on Nomeclature under *Cricetulus barabensis*). Accompanying illustrations (Plate 12: Figure 2; Plate 13: Figures 3, 3^a, 3^b, 3^c), portraying a hamster from "Mongolie chinoise" (Figure 2), appeared in Milne Edwards & Milne Edwards (1868–1874). Type locality: "Mongolie chinoise"; subsequently restricted to "the vicinity of Saratsi [Lifen] in northern Shansi [Shanxi], China" (Allen 1940: 761).

Cric[etulus] longicaudatus: A. Milne Edwards, in David (1871: 93). First use of the current species name combination.

Cricetulus phaeus griseiventris Satunin, 1902: 566. Not 1903 (*e. g.* Ellerman & Morrison-Scott 1951: 624). Type locality: "Fluss Bis-shen-gol, Südabhang des Altain-nuru (Gobi-Altai)", currently Bugat Soum, Bij Gol, Govi-Altay Province, Mongolia.

Cricetulus dichrootis Satunin, 1902: 567. Not 1903 (e.g. Ellerman & Morrison-Scott 1951: 624). Type locality: "Fluss Gorban-angyr-gol, Nan-shan" [Gurban-Angyr-gol, Nanshan], Qinghai, China.

[Cricetus (Cricetulus)] dichrootis: Trouessart, 1904: 395. Name combination.

[Cricetus (Cricetulus)] phaeus griseiventer: Trouessart, 1904: 395. Incorrect subsequent spelling of *griseiventris* Satunin.

Cricetulus andersoni Thomas, 1908c: 642. Type locality: "100 miles N.W. of Tai-Yuen-Fu. 8000' [2,440 m]",

i. e. 161 km north-west of Taiyuanfu, Baode County, Shanxi, China.

Cricetulus andersoni nigrescens G. Allen, 1925: 2. Type locality: "Province of Chili, 100 miles [161 km] northeast of Peking, China."

Cricetulus kozhantscikovi Vinogradov, 1927: 36. Not 1928 (Ross 1992: 219). Type locality: "Тукеек-кем, б. Усинский пограничный округ, Саяны [Tukeek-kem, former Usonsky bordering districts, Sayan Mts.]". Amendment of the type locality to "Туксэль-Хэм [Tuksel-Khem]" (Pavlinov & Rossolimo 1987:168) is erroneous. Current name of the site is Talovka River (Kozhantschikov 1926), the left tributary of the Yenisei River in the Shushenskiy (formerly Minussinskiy) Rayon, Russian Federation. For detailed description of the locality see Djakonov (1926). The species epithet is eponym for a Russian entomologist В. Д. Кожанчиков (*cf.* Vinogradov's text) which was transliterated as V. D. Kozhantschikov or Kozhanchikov. The eponym was also spelled differently by various authors (*cf.* spellings listed below) and was emended as *kozhantschikovi*: Argyropulo, 1933b (see below).

Cricetulus griseiventris: Formozov, 1929: 48. New rank.

[Cricetulus (Cricetulus) longicaudatus] griseiventris: Argyropulo, 1933b: 246. Name combination.

[Cricetulus (Cricetulus) longicaudatus] dicrootis: Argyropulo, 1933b: 246. Name combination and new rank.

[Cricetulus (Cricetulus) longicaudatus] andersoni: Argyropulo, 1933b: 246. Name combination and new rank.

[Cricetulus (Cricetulus) longicaudatus] nigrescens: Argyropulo, 1933b: 246. Name combination.

[Cricetulus (Cricetulus) longicaudatus] kozhantschikovi: Argyropulo, 1933b: 246. Emendation of species epithet which was originally misspelled *kozhantscikovi*. New rank and name combination.

C[ricetulus] g[riseiventris] kozhantscikovi: Vinogradov, 1933: 45. Name combination.

C[ricetulus] l[ongicaudatus] kozhancikovi: Vinogradov & Argyropulo, 1941:170. Incorrect subsequent spelling of *kozhantschikovi* Vinogradov.

Cr[icetulus] l[ongicaudatus] kozhanscikovi: Kuznetzov, 1944: 320. Incorrect subsequent spelling of *kozhantschikovi* Vinogradov.

C[ricetulus] l[ongicaudatus] kozhanchikovi: Gromov, Gureev, Novikov, Sokolov, Strelkov & Chapskij, 1963: 489. Incorrect subsequent spelling of *kozhantschikovi* Vinogradov.
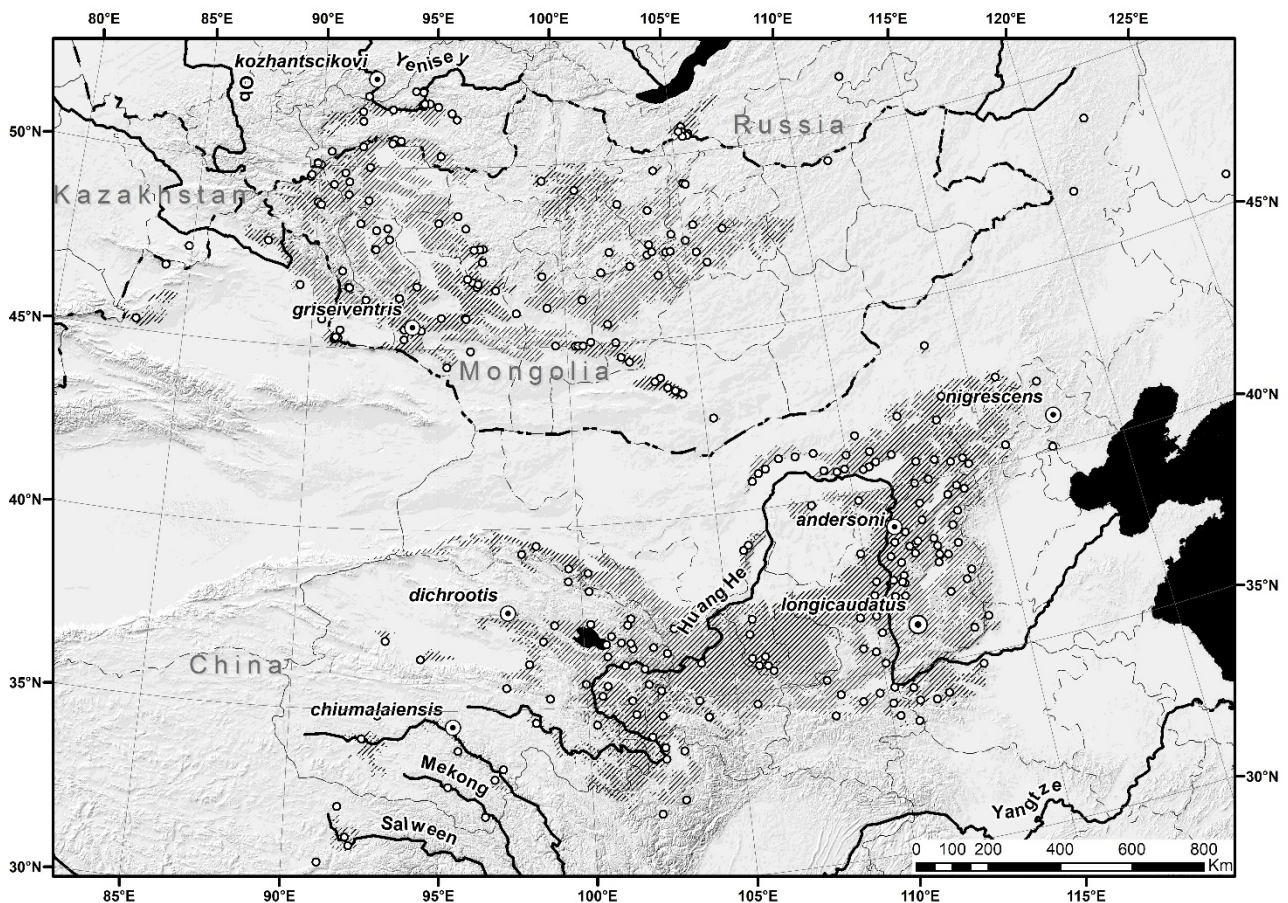
Figure 41: Distributional range of the long-tailed lesser hamster *Cricetulus longicaudatus.*

Cricetulus longicaudatus chiumalaiensis Wang & Cheng, 1973: 65. Type locality: "Chiumalai District (Sewukou Valley), Qinghai Province", China.

Etymology. The species epithet consists of two Latin words: 'longus' for 'long' and 'caudatus' for '-tailed' (from 'cauda' for the tail), *i. e.* a 'long-tailed' in allusion to the tail of *C. longicaudatus*, which is the longest in the genus.

Taxonomy. Throughout the 20th century, the majority of authors accepted *C. longicaudatus* as a species in its own right, though there were some nomenclatural inconsistencies. Therefore, *andersoni*, which was proposed as a full species (Thomas 1908c) and kept as such by Allen (1925) and Howell (1929), was synonymized with *longicaudatus* by Argyropulo (1933b, c). Argyropulo (*l. c.*) also included *dichrootis* into the scope of *longicaudatus*, but Allen (1940) synonymized it with *C. barabensis obscurus*. Chaworth-Musters (1933) suggested that *dichrootis* and *kozlovi* might be conspecific with *longicaudatus* and Flint (1966b) expressed a similar conjecture for *kamensis* and *kozlovi*. Formozov (1929) and Vinogradov (1933) elevated *griseiventris* to a species in its own right.

Throughout the first half of the 20th century, the length of tail relative to head and body was an important trait in the taxonomy of lesser hamsters above the species level. Hence, Trouessart (1904) classified *longicaudatus* into *Urocricetus* (as a subgenus of *Cricetulus*), along with *kamensis* (now in *Urocricetus*) and *triton* (*Tscherskia*). Subsequent authors continued keeping *longicaudatus* and *kamensis* in the same species group (Argyropulo 1933b, c, Ellerman 1941) until Ellerman & Morrison-Scott (1951) split the subgenus *Cricetulus* into two groups

Figure 42: Long-tailed lesser hamsters *Cricetulus longicaudatus* from Mongolia. Photo courtesy of Georgy Ryurikov

based on size of bullae. The *migratorius* group maintained current genera *Cricetulus* and *Nothocricetulus* and the *lama* group contained the current *Urocricetus*. This view was widely accepted, albeit with some modifications; for example, Pavlinov & Rossolimo (1987) classified *longicaudatus* and *barabensis* into the *barabensis* species group, as opposed to the *migratorius* group.

Distribution. The range of an estimated 1,060,000 km² is in 2 major fragments, one in Mongolia and the other in China (Figure 41). These fragments are separated by the irrigated flatland between the Gurvan Saikhan Mts. and Mt. Hörh Uul (Ömnogovi Province, Mongolia), and Yin Mts. (Nei Mongol, China). The Mongolian fragment encompasses eastern and central Mongolia as far east as the Khentii–Ömnogovi line (except for Dudngovi), and very marginally also the adjacent Russia (isolated populations in Altai Republic, Buryatia, Krasnoyarskiy Kray, Tuva, and Zabaykalskiy Kray), East Kazakhstan (Zaysan), and extreme northern Xinjiang (China). The fragment in China centres on the Huang-He valley, and extends from Hebei, Beijing, Tianjin, and Henan in the east, as far west as the Three Rivers Source Region (Sanjiangyuan) in the periphery of the Qinghai-Tibet Plateau and Gansu. The northern border is in central Nei Mongol and the southern-most records are from northern Sichuan. There are several isolated records in north-eastern Nei Mongol and western Heilongjiang.
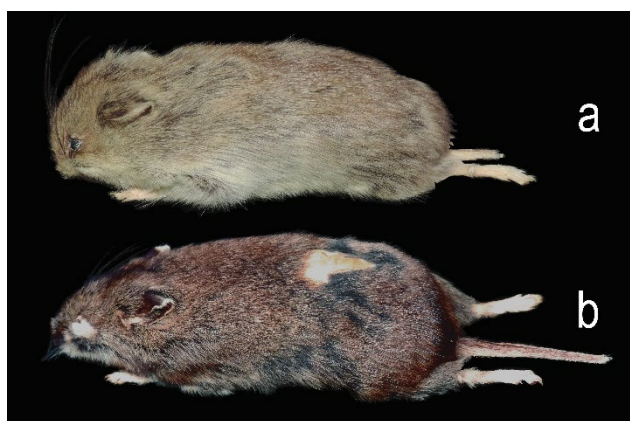
Figure 43: Extremes in fur colouration in the long-tailed lesser hamster *Cricetulus longicaudatus*: a – pale pelage (type of *griseiventris*; ZIN 10630); b – dark pelage (type of *kozhantscikovi*, ZIN 16909). The specimen in (b) lost some hair on the back.

The long-tailed hamster has rather narrow habitat requirements (Meyer & Skholl' 1977) and occupies rocky habitats in the steppe and semi-desert vegetation zones, particularly the eroded slopes with exposed rocks and screes. It is present also on slopes covered by brushes and around fields, and is locally abundant. Readily enters residential buildings (Flint 1966a). Elevational range is 140–5,150 m (mean = 1,770 m); the highest records are from Qinghai (Zheng 1986).

Description. Size and overall appearance are similar to *C. barabensis*, except for the lack of mid-dorsal stripe and longer tail in *C. longicaudatus* (Figure 42); tail accounts for 28–49% of head and body length (mean = 37%). Dimensions: body mass = 25–45 g, length of head and body = 83–126 mm, length of tail = 23–58 mm, length of hind foot = 14.5–19.0 mm, length of ear = 12.0–21.0 mm, condylobasal length = 22.3–27.6 mm, zygomatic width = 11.7–15.1 mm, length of maxillary tooth-row = 3.5–4.4 mm. The sexes are approximately of same size (*cf.* Luo et al. 2000: 52). Vibrissae are of comparable length to the remaining lesser hamsters (length = 26.5–32.5 mm). There are 5 palmar and 6 plantar pads; palms and soles are densely hairy to the pads. Fur is soft and long (length = 9–11 mm) with sparse longer hairs protruding by 1.0–2.5 mm; there is no difference between the summer and winter fur. Tail is moderately densely furred and the annulation is largely concealed; terminal pencil is feeble (Figure 29c). Ears are hairy on both sides, grey to blackish-brown, and usually narrowly edged white. The white circumference tends to be less extensive and contrasting than in *Cricetulus* s. str.; occasionally, the ear is grey throughout. Upper parts of head and body are uniform and darker in the centre of the back but without a definite dark line. Colouration varies from light buffy-grey to deep brown (Figure 43), but the majority of hamsters are drab or drab-grey with occasional darkening caused by denser black hairs (Figure 42). Ventral hairs have basal ⅔ slate-grey and white tips. Posteriorly, the flanks are often vaguely marked buffy. Delineation is distinct but only exceptionally sharp; demarcation line is set high, crossing the mystacial pad, the upper part of the humerus and femur, and the base of the tail. On the head, white marks are frequently present: a postauricular tuft, and a sub- or postauricular spot which may extend further back. Tail is bicolour; dorsal side is of same colour as back and the underside is white. The paws are pure white. Externally, *C. longicaudatus* resembles *Nothocricetulus migratorius* but has

ventral hairs with slate bases (in *migratorius*, bases are white at least on chin, throat and chests) and usually white-margined ears which are plain grey in *migratorius*.

Skull (Figure 34) is like in *C. barabensis*, but tends to be narrower across rostrum and zygomatic arches; zygomatic width account for 49.6–56.0% of condylobasal length (mean = 53.6%); in *C. barabensis*, the relative width is up to 59.5%. In comparison to *Cricetulus* s.str., *C. longicaudatus* has on average broader palate, shorter maxillary tooth-row, and longer diastema (Ross 1992). Dentition is like in *Cricetulus s. str.*; the only exception is that 2nd primary and 2nd internal folds are confluent (Figure 44).
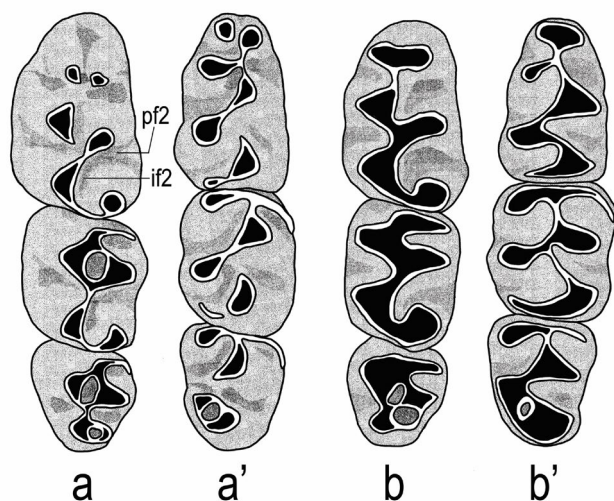
Figure 44: Grinding pattern of upper (a, b) and lower (a', b') molars in the long-tailed lesser hamster *Cricetulus longicaudatus* from Mongolia. Acronyms: *if2* – 2nd internal fold; *pf2* – 2nd primary fold.

Karyotype: 2n = 24, NF = 40. The autosomal set consists of 3 pairs of biarmed and 7 pairs of acrocentric chromosomes. The X chromosome is submetacentric and is the largest element in the set; the Y is metacentric or submetacentric and of slightly smaller size (Orlov et al. 1978). This report is consistent with Graphodatsky (2006a), though some authors gave different values: 2n = 28 (Sokolov & Orlov 1980) and NF = 40 (Král et al. 1984).

Variation and subspecies. Regional studies recognized a low number of subspecies, i.e. single one (*kozhantschikovi*) in Russia (Vinogradov & Argyropulo 1941, Kuznetzov 1944, Vinogradov & Gromov 1956, Kuznetsov 1965, Gromov & Baranova 1981, Gromov

& Erbajeva 1995) and Mongolia (the nominotypical subspecies; Bannikov 1954), and 2 subspecies in China (Allen 1925, 1940, Wang & Cheng 1973, Luo et al. 2000, Wang 2003). Synthesis of these views resulted in 3 subspecies recognized in Haslauer (2017b): *kozhantschikovi*, *chiumalaiensis*, and the nominotypical subspecies. Earlier global assessments listed higher numbers: 5 subspecies (Argyropulo 1933b, c, Ellerman & Morrison-Scott 1951) or 6 subspecies (Ellerman 1941).

Subspecific variation was so far addressed in 2 studies. Wang & Cheng (1973) split Chinese long-tailed lesser hamsters into 2 subspecies, the smaller nominotypical (with *dichrootis* and *nigrescens*), and the larger *chiumalaiensis*. This view was adopted by Chinese authors. Poplavskaya et al. (2018a) explored mitochondrial (cyt*b*) and craniometric variation and covered a significant part of distributional range. In their results, haplotypes from Qinghai and north-western Sichuan hold basal position in the phylogenetic tree but without forming a monophyletic lineage. A sample from Kham (western Sichuan) was also the most divergent in a phenogram derived from craniometric variation. While these results expose the north-eastern part of the Qinghai–Tibetan Plateau as the cradle of diversification for *C. longicaudatus* at ~ 150 kya (Poplavskaya et al. 2018a), they still do not facilitate a straightforward taxonomic conclusion. For the moment being, we tentatively distinguish 2 subspecies pending for further studies in China in general and in Qinghai and adjacent regions in particular.

Cricetulus longicaudatus longicaudatus (A. Milne Edwards, 1871)

Synonyms: *Cricetulus phaeus griseiventris* Satunin, 1902; *Cricetulus andersoni* Thomas, 1908; *Cricetulus kozhantscikovi* Vinogradov, 1927.

Taxonomy. The nominotypical subspecies is genetically fairly homogeneous, however, some of the marginal populations are divergent, most notably from central and eastern Tuva (Tyva), Greater Khingan and Buryatia (Poplavskaya et al. 2018b). Hamsters from Buryatia were classified as the nominotypical subspecies already in the past (Borisova et al. 2001).

Distribution. Its range is in Russia, Kazakhstan, Mongolia, and China: Beijing, Hebei, Shanxi, and Shaanxi. Heilongjiang, Henan, Nei Mongol, Ningxia, Shaanxi, Shanxi, Tianjin, and Xinjiang. The border against *dichrootis* has not been resolved.

Characteristics. Encompasses the cyt*b* lineage which is widespread in Mongolia (Poplavskaya et al. 2018b). Chinese authors (Wang & Cheng 1973, Luo et al. 2000) diagnosed the nominotypical subspecies by size: profile length of skull = 22.8–28.0 mm (mean = 25.7 mm), zygomatic width = 12.4–14.5 mm (mean = 13.4 mm). Interpopulation differences were reported for different morphological traits. Ross (1992) documented size trends in certain cranial structures, specifically an east-to-west decline in the length of incisive foramens and the concomitant increase in the breadth of interorbital constriction and of palate. Furthermore, hamsters are smaller in the south (Inner Mongolia, Shanxi, and Shaanxi) than in the Mongolian Plateau further north (Ross 1992). There are also differences in fur colouration between regions (Figure 43). Hamsters are darker in Beijing and along their northern border in Russia, and paler in Mongolia, Inner Mongolia, Shanxi, and Shaanxi.

Cricetulus longicaudatus dichrootis Satunin, 1903

Synonyms: *Cricetulus longicaudatus chiumalaiensis* Wang & Cheng, 1973.

Etymology. The species epithet *dichrootis* is a combination of two words in ancient Greek, the 'dikhrous' (two-coloured) and '-otis' (-eared) in allusion to the colouration of the ear which is dark in *C. longicaudus* and sometimes margined white.

Taxonomy. Luo et al. (2000) and Wang (2003) restricted *chiumalaiensis* to Ando and the Tanggula Mts. (Xizang) and southern Qinghai, while Wang & Cheng (1973) synonymized *dichrootis* with the nominotypical race. Furthermore, Zheng (1986) classified hamsters from northern Sichuan, Gansu, and eastern Qinghai as the nominotypical subspecies. This contradicts the results by Poplavskaya et al. (2018b) who showed that hamsters from Sichuan and Qinghai are outside the scope of the widespread lineage occupying Russia and

Mongolia (here classified as ssp. *longicaudatus*). Satunin's name *dichrootis*, described from Qinghai, predates *chiumalaiensis*, hence we use it as a senior synonym.

Distribution. The Three Rivers Source Region (Sanjiangyuan) in the periphery of the Qinghai-Tibet Plateau and Sichuan; putatively present also in Gansu. Distribution against the nominotypical subspecies has not been resolved.

Characteristics. Comprises a bunch of highly divergent cyt*b* lineages from Qinghai and Sichuan (Poplavskaya et al. 2018b). Chinese authors diagnosed *chiumalaiensis* by large size: profile length of skull = 26.5–30.7 mm (mean = 28.3 mm), zygomatic width = 13.4–15.5 mm (mean = 14.6 mm) (Luo et al. 2000). Large size, however, is perhaps typical only of the population in Xizang and southern Qinghai (Wang & Cheng 1973), whereas hamsters from the surroundings are of smaller size.

GENUS: *Nothocricetulus* Lebedev, Bannikova, Neumann, Ushakova, Ivanova & Surov, 2018 – Grey Hamsters

Nothocricetulus Lebedev, Bannikova, Neumann, Ushakova, Ivanova & Surov, 2018a: 342. Type species is *Mus migratorius* Pallas, 1773.

Cpicetullus: Kuznetsov, 1932: 119. Incorrect subsequent spelling of *Cricetulus* A. Milne-Edwards, in combination with *migratorius*.

Taxonomy. Monospecific genus.

Nothocricetulus migratorius (Pallas, 1773) – Grey Hamster

Mus migratorius Pallas, 1773: 703. Not 1794 (Trouessart 1897: 508). Type locality: "in graminofis Iaĭkum [steppes along the Yaik (now Ural) River]"; subsequently restricted to the "R. Ural, S.W. of Orenburg" (Thomas 1917: 452), Russian Federation.

Mus arenarius Pallas, 1773: 704. Type locality: "in auftralibus as Irtin [Lower Irtysh]"; Pallas (1779: 265) provided further details: "in arenofis

Barabenfium camporum ad Irtin fl. [fields of Baraba at Irtysh]" and "Primo inveni marem in fabulofis collibus Koptælye dictis". In old Russian maps, "Koptælye dictis" is spelled "Копьева - Copiewa", while the current spelling is Kopyevo [55.93° N, 75.02° E] in Omsk Oblast, Russian Federation. Thomas (1917: 454) restricted type locality to "Baraba Steppes, Lower Irtish, Siberia". Another restriction to "Gratchefskoi [Grachevskiy; N50.75°, E78.64°] on the Irtish River, below Semipalatinsk, Siberia" by Ellerman & Morrison-Scott (1951: 622) is erroneous because the site is located in the Middle (and not Lower) Irtysh and to the south of Baraba. Still further restriction (by Pavlinov & Rossolimo 1987: 168) was to "Павлодарская обл., Ермаковский р-он [Pavlodar Oblast, Yermakovskiy Rajon]" in Kazakhstan, which is on the left bank of the Irtysh, while Baraba is on its right bank.

Glis migratorius: Erxleben, 1777: 373. Name combination

Glis arenarius: Erxleben, 1777: 375. Name combination

Mus accedula Pallas, 1779: 257. Type locality: "a Rhymno fluvio adlatum […] in colliculosa regione inter rivos Irtek & Kindely", restricted to "Казахстан, Гурьевская обл., Индерский р-н" [Kazakhstan, Gur'evskaya (now Atyrauskajaya) Oblast, Inderskiy Rayon] (Pavlinov & Rossolimo 1987: 168). This name is possibly an unintentional typographic error for *acredula*; the later derives from Latin 'credulus' for 'credulous' or 'unsuspecting' which may be in allusion to a fearless behaviour of the grey hamster. If *accedula* is indeed due to typographic error, then the name was emended to *acredula* by Gmelin (1792: 242); see below. However, Pallas in his subsequent publications (e.g. Pallas 1831; see below) repeatedly used *accedula*, while Gmelin persisted with *acredula* (Gmelin 1805).

Mus phaeus Pallas, 1779: 261. Type locality: "in Aftrachanenfi deserto, circa Zarizynum [Tsaritsyn, now Volgograd] præfertim", restricted to "Lower Volga, near Sarepta [Old Sarepta]" (Thomas 1917: 452) which matches "окрестность Сталинграда" (Kuznetzov 1944: 320), in Latin spelling "Near Stalingrad [now Volgograd, Russian Federation]" (Ellerman & Morrison-Scott 1951: 622); Sarepta [since 1920 Krasnoarmeysk] is located 28 km south of Tsaritsyn [later renamed Stalingrad, now Volgograd], Russian Federation.

M[us] Cricetus Acredula: J. F. Gmelin, 1792: 242. Name combination and variant spelling of *accedula* Pallas.

M[us] Cricetus arenarius: J. F. Gmelin, 1792: 244. Name combination.

M[us] Cricetus phaeus: J. F. Gmelin, 1792: 245. Name combination.

Cricetus accedula: Pallas, 1831: 162. Name combination.

Cricetus arenarius: Pallas, 1831: 162. Name combination.

Cricetus phaeus: Pallas, 1831: 163. Name combination.

Cricetus acedula: Lessone, 1842: 119. Incorrect subsequent spelling of *accedula* Pallas.

Hypudaeus cinerascens Wagner, 1848: 184. Type locality: "Syrien" (p. 185). Trouessart (1897: 560) synonymized *cinerascens* with *Microtus socialis*. It is clear from Wagner's description, that *cinerascens* is not an arvicoline (cf. Ellerman & Morrison-Scott 1951: 622, Corbet 1978: 90).

Cricetus isabellinus Filippi, 1865: 344. Type locality: "Teheran", now Tehran, Iran.

Cricetus (Cricetulus) fulvus Blanford, 1875: 108. Type locality: "Plains of Eastern Turkestan, Pámir, and Wakhán"; restricted to "Kashgar [Qeshqer]", Tarim Basin, southern Xinjiang, China (Thomas 1917: 455).

Cricetus murinus Severtsov, 1873: 82. Based on 2 syntypes from "въ степной травы вершинъ Ори" and "в Сарепты"; in English version of the paper (Severtzoff 1876: 54), the localities are spelled "the Summit of Ori" and "Sarepta". Type locality was subsequently restricted to "Sarepta" (Trouessart 1897: 508). Although Zoological Record reported the 1873 naming of *murinus* (Alston 1873: 18), many authors quote 1876 as the year of first publication (e.g. Ellerman & Morrison-Scott 1951: 622, Musser & Carleton 2005: 1043). Obviously, they were familiar with the 1876 English translation of Severtsov's paper, while the Russian original from 1873 escaped their notice. For 1873 as the correct year see Pavlinov & Rossolimo (1987: 168).

Arvicola coerulescens Severtsov, 1879: 63. Type locality: "Kara-kul" (p. 64), *i. e.* Karakul Lake, Khokhiyi Murgob (former Murgabskiy rayon), Tajikistan.

Cricetus arenarius: Trouessart, 1897: 507. Name combination

Cricetus accedula migratorius: Trouessart, 1897: 508. Name combination and new rank.

Cricetus phaeus isabellinus: Trouessart, 1897: 509. Name combination and new rank.

Cricetus phaeus fulvus: Trouessart, 1897: 509. Name combination and new rank.

Cricetulus atticus Nehring, 1902: 3. Type locality: "Pentelikon in Attica", Greece.

Cricetulus kozlovi Satunin, 1902: 570. Not 1903 (e.g. Ellerman & Morrison-Scott 1951: 624). Type locality: "Oase Sa-tschou" (p. 571), spelled also "Sa-chou" (Allen 1925: 3); currently Oasis Satschou, Dunhuang, Nanshan, Gansu, China. Status follows Lebedev & Potapova (2008).

[Cr]icetulus phaeus: Satunin, 1902: 59. Name combination.

[Cr]icetulus arenarius: Satunin, 1902: 59. Name combination.

[Cricetus (Cricetulus)] atticus: Trouessart, 1904: 395. Name combination.

[Cricetus (Cricetulus)] arenarius: Trouessart, 1904: 395. Name combination.

[Cricetus (Cricetulus)] kozlovi: Trouessart, 1904: 395. Name combination.

Cricetulus tauricus Satunin, 1908: 140. Nomen nudum. Publication was not seen and is quoted from Pidoplitshka (1928: 426); see also Kuznetzov (1944: 247) and Pavlinov & Rossolimo (1987: 168).

Cricetulus migratorius atticus: Miller, 1912: 593. New rank.

Cricetulus arenarius bellicosus Charleman, 1915: 70. Type locality: "вблизи м. Степанцевъ въ Каневскомъ уѣздѣ Кіевской губерніи", i.e. Stepantsy, south of Kiev, Ukraine. Ellerman & Morrison-Scott (1951: 623) spelled the author's name as Sharleman, probably transliterating the Russian variant Шарлемань [or Шарлеманъ]. The family name Charleman is on the cover page (see also Pavlinov & Rossolimo 1987: 168).

Cricetulus phaeus neglectus Ognev, 1916: 81. Syntypes were from "Атманай, Мелитопул у. [Atmanay, County Melitopul]" and "Бурульча, пр. Салгира, Бешко [Burul'cha, Salgira, Beshko]", both on Crimea (p. 84). Invalid as infrasubspecific name (aberratio); validated by Pidoplitshka (1928: 426).

C[ricetulus] migratorius vernula Thomas, 1917: 453. Type locality: "Khotz [now Çosandere], near Trebizond [Trabzon]", northern Asia Minor, Turkey.

C[ricetulus] migratorius griseiventris: Thomas, 1917: 454. Thomas added to *griseiventris* an abbreviation "Sat." (for Satunin; *cf. Cricetulus phaeus griseiventris* Satunin, 1902; now a synonym of *Cricetulus longicaudatus*) and "from Gobi Altai"; the latter is the type locality of Satunin's name. Hence, Thomas evidently did not introduce *C. m. griseiventris* as a new taxonomic name. Ellerman & Morrison-Scott (1951: 622) commented *griseiventris* Thomas as "Probably not of Satunin, 1902", and synonymized it with *coerulescens* Severtsov. Musser & Carleton (2005: 1043) retained combination "*griseiventris* Thomas (obviously not an available name)" in the synonymy of *N. migratorius*; we concur that *giseiventris* Thomas is unavailable name.

C[ricetulus] migratorius arenarius: Thomas, 1917: 454. Name combination and new rank.

C[ricetulus] migratorius fulvus: Thomas, 1917: 455. Name combination and new rank.

[Cricetulus migratorius] accedula: Thomas, 1917: 453. Name combination and new rank.

Cricetulus falzfeini Matschie, 1918: 299. Type locality: "Ascania Nova [Askania-Nova]", "Taurien [Taurida Steppe, Kherson Oblast], Southern Russia [now Ukraine]" (Ellerman & Morrison-Scott, 1951: 623).

Cricetulus fulvus: Ognev, 1923: 89. Name combination.

Cricetulus fulvus fulvus Blanf. m. *pamirensis* Ognev, 1923: 89. Syntypes originated from "г. Мазарка, Памирь [Mazarka settlement, Pamir]" and "Памирский Пост [Pamir Post; now Murgab]". Invalid as infrasubspecific name; validated in Vinogradov (1931: 4).

Cr[icetulus] m[igratorius] bellicosus: Ognev, 1924: 24. Name combination.

Cricetulus migratorius (phaeus) griseus Kashkarov, in Kashkarov et al., 1923: 215. Type locality: "гор. Каратау, с верховьев речки Терс" [Karatau Mts., from the upper flows of the Ters River], Zhambilskaya (Dzhambulskaya) Oblast, Kazakhstan. Permanently invalidated as a primary homonym of *Cricetus (Cricetulus) griseus* Milne-Edwards, 1867 (= *Cricetulus barabensis*).

Cricetulus migratorius (phaeus) caesius Kashkarov, in Kashkarov et al., 1923: 215. Type locality: "Аулие-Ата" [Aulie-Ata], now Taraz, Zhambilskaya (Dzhambulskaya) Oblast, Kazakhstan.

Cricetulus migratorius pulcher Ognev, 1924: 22. Type locality: "бл. Ларса, Воено-Грузинская дорога, 25 верст от г. Владикавказа [near Lars, Military Georgian Road, 27 km from Vladikavkaz]", Northern Caucasus, Georgia.

Cr[icetulus] m[igratorius] bellicosus: Ognev, 1924: 24. New rank.

Cricetulus migratorius cinereus Kashkarov, 1926: 23. New name for *griseus* Kashkarov. Argyropulo (1933b: 247) cited type locality as "г. Пишпек, Семиречье [city of Pishpek (now Bishkek), Semirechye]", Kyrgyzstan; this act is not valid. The *nomen novum* retains the same type locality as was proposed for *griseus* Kashkarov, 1923.

Cricetulus migratorius zvieresombi Pidoplitshka, 1928: 421. Type locality: "Ростов над Доном [Rostov-on-Don]", Rostov Oblast, European Russia. The name is eponym to Ukrainian entomologist Yevgeny (Evgen) V. Zverezomb-Zubovskiy (in Russian alphabet Зверезомб-Зубовский) (1980–1967) whose name is spelled in Ukrainian as Zverozomb-Zubovskiy (Зверозомб-Зубовский) or Zvirozomb-Zubovskiy (Звірозомб-Зубовський). Both, the author's name and the eponym, were frequently incorrectly spelled (see below).

Cricetulus migratorius phaeus sviridenkoi Pidoplitshka, 1928: 424. Type locality: "Кізлярського пов., м. Арешевка, Терської Обл. [Kizlyar District, Areshevka, Terek Oblast, Daghestan]". Explicitly proposed as infrasubspecific taxon (natio) and hence invalid.

Cricetulus migratorius phaeus: Pidoplitshka, 1928: 423. New rank.

Cricetulus migratorius neglectus Pidoplitshka, 1928: 426. First appropriate use of *neglectus* Ognev. Type locality restricted to "Бурульчі, доплив р. Салгира в Криму [Burul'chi, valley of the Salgir River, Crimea]".

C[*ricetulus*] *m*[*igratorius*] *zrvieresombi:* Pidoplitshka, 1928: 417. Incorrect spelling of *zvieresombi* Pidoplitshka.

Cricetulus migratorius falz-feini: Flerov, 1929: 395. Variant spelling of *falzfeini* Matschie; *felzfeini* is eponym for Eduard Oleg Alexandrowitsch von Falz-Fein.

Cricetulus migratorius zwierezombi: Kalabuchow & Rajewskij, 1930: 144. Incorrect subsequent spelling of *zvieresombi* Pidoplitshka.

Cricetulus migratorius zwerezombi: Kalabuchow & Rajewskij, 1930: 144. Incorrect subsequent spelling of *zvieresombi* Pidoplitshka.

Cricetulus migratorius coerulescens: Vinogradov, 1931: 3. Name combination and new rank.

C[*ricetulus*] *m*[*igratorius*] *pamirensis* Vinogradov, 1931: 4. First use of *pamirensis* Ognev as trinomen (listed as a junior synonym of *coerulescens*). Syntypes were from two localities, Mazarka and Murgab (see above

under *pamirensis* Ognev). Mazar means a mausoleum in Arabic, hence the toponym possibly relates to a mountain or hill with a mausoleum. Since the precise site cannot be identified, we restrict the type locality to Murgab, Tajikistan.

[*Cricetulus migratorius*] *cinerascens:* Argyropulo, 1933b: 247. Name combination and new rank.

[*Cricetulus migratorius*] *coerulescens* natio *ognevi* Argyropulo, 1933b: 427. Type locality: "окр. Самарканда [neighbourhood of Samarkand]", Uzbekistan. Invalid as infrasubspecific name (natio). Validated in Vinogradov & Argyropulo (1941).

[*Cricetulus migratorius*] *murinus:* Argyropulo, 1933b: 247. Name combination and new rank.

[*Cricetulus migratorius*] *myosurus* Argyropulo, 1933b: 247. Nomen nudum (cf. Pavlinov & Rossolimo 1987: 169, Musser & Carleton 2005: 1043). Argyropulo (*l. c.*) credited "Severzov [Severtsov]" as the author of the name but without quoting the year. We could not trace *myosurus* in Severtsov's papers (1876, 1879); *myosurus* is neither mentioned in papers predating Argyropulo's 1933 naming (e.g. Trouessart 1897).

[*Cricetulus migratorius*] *zvierozombi:* Argyropulo, 1933b: 247. Incorrect subsequent spelling of *zvieresombi* Pidoplitshka.

Cricetulus koslovi: Chaworth-Musters, 1933: 222. Incorrect subsequent spelling of *kozlovi* Satunin.

C[*ricetulus*] *m*[*igratorius*] *ognevi* Vinogradov & Argyropulo, 1941: 171. Type locality: "окресности Самарканда [neighbourhood of Samarkand]", Uzbekistan. First use of *ognevi* Argyropulo as trinomen.

Cr[*icetulus*] *m*[*igratorius*] *zvierezombi:* Kuznetzov, 1944: 320. Incorrect subsequent spelling of *zvieresombi* Pidoplitschka.

Cr[*icetulus*] *m*[*igratorius*] *sviridenkoi:* Kuznetzov, 1944: 320. Incorrect subsequent spelling of *sviridenkoi* Pidoplitschka.

Cricetulus migratorius elisarjewi Afanasiev, 1953: 237. Type locality: "окресности с. Шемонаихи и разъезда Казахстан", i.e. the vicinity of village Shemonankha and railway station "Kazakhstan" (approximately 13 km north of Shemonankha, north-western foothills of the Altai Mts., East-Kazakhstan Region, Kazakhstan. Corbet (1978: 91) remarked that *elisarjewi* might be nomen nudum. Afanasiev, however, satisfied the provisions of Articles 11 and 13.1.1 of the Code (ICZN 1999), hence *elisarjewi* is available name.

C[ricetulus] m[igratorius] elesarjewi: Afanasiev, 1960: 55. Incorrect subsequent spelling of *elisarjewi* Afanasiev.

[Cricetulus longicaudatus] kozlovi: Flint, 1966b: 14. Name combination.

C[ricetulus] m[igratorius] caesius: Wang & Cheng, 1973: 62. Name combination.

C[ricetulus] kamensis kozlovi: Wang & Cheng, 1973: 64. Name combination.

C[ricetulus] m[igratorius] ceorulescens: Davydov, 1988: 119. Incorrect subsequent spelling of *coerulescens* Severtsov.

Cricetulus migratorius isbellinus: Zykov, 1991: 76. Incorrect subsequent spelling of *isabellinus* Filippi.

[Cricetulus migratorius] fernula: Zykov, 1991: 78. Incorrect subsequent spelling of *vernula* Thomas.

[Cricetulus migratorius] zvierezombi: Musser & Carleton, 1993: 538. Incorrect subsequent spelling of *zvieresombi* Pidoplitshka.

Cricetulus migratorius issabellinis: Kandaurov, Morgilevskaya & Bukhnikashvili, 1994: 132. Incorrect subsequent spelling of *isabellinus* Filippi.

Cricetulus migrodentorius: Wu, Fu, Yuan, Gao & Yue, 2015: 44. Incorrect subsequent spelling for *migratorius* Pallas.

Cricetulus migrates: Esfandiari, Nahrevanian, Pourshafie, Gouya, Khaki, Mostafavi, Darvish & Hanifi, 2017: no pagination; the name is consistently misspelled throughout the entire paper.

Nothocricetulus migratorius: Lebedev, Bannikova, Neumann, Ushakova, Ivanova & Surov, 2018a: 343. First current name combination.

Etymology. Generic name is composed of 'Nothos' (Latin for 'false'; Lebedev et al. 2018a) and *Cricetulus,* which is diminutive of *Cricetus* (i. e. the hamster). The name (false dwarf hamster) is allusion to a widespread classification of *migratorius* as *Cricetulus*. Since *Cricetulus* has *barabensis* as the type species, the inclusion of *migratorius* created paraphyletic group (see below). The species epithet *migratorius* (from Latin 'migrare', meaning 'to migrate') alludes to a presumed migratory nature of these animals, for which Pallas (1773: 703) reported to occur in steppes along the Ural River, but in certain years migrate in great numbers out of a desert ("Occurit graminoſis Iaĭkum, diciturque certis annis copioſiſſime e deſertis auentare …"). Johann F. Gmelin provided similar account: "The Cossacks say that [the species] migrates out of the deserts in vast multitudes;

but Dr Pallas suspects this to be a mistake" (Gmelin 1792: 243). There is no current evidence on mass migrations in this species.

Taxonomy. Throughout the 19th century, the grey hamster was classified as a member of the genus *Cricetus,* but was transferred into *Cricetulus* in the early 1900s (Nehring 1902, Satunin 1902, 1903) where it remained until recently (Ellerman 1941, Ellerman & Morrison-Scott 1951, Pavlinov & Rossolimo 1987, Musser & Carleton 2005, Haslauer 2017a). Molecular phylogenetics unanimously retrieved paraphyly of *Cricetulus* with respect to *migratorius; migratorius* holds sister position against *Cricetus* + *Allocricetulus* combined (Figure 1) (Lebedev et al. 2003, 2018a, Neumann et al. 2006, Ding et al. 2016a). The divergence time is estimated at 4.46 Mya (CI = 3.41–5.88 Mya), which places the event into the Early Pliocene (Lebedev et al. 2018a).

In the past, *Cricetulus* frequently included, in addition to the current *Nothocricetulus*, also *Allocricetulus, Tscherskia*, and *Urocricetus*, as they are defined in this volume. Some authors classified such a heterogenous species assembly into different subgenera or species groups. Therefore, Argyropulo (1933b, c) recognized 2 species groups, *migratorius* group which included also *lama* (now in *Urocricetus*), and *barabensis* group. The grey hamster was classified as the sole representative of the *migratorius* species group by Ellerman (1941), Pavlinov & Rossolimo (1987) and Pavlinov (2003, 2006). Ellerman & Morrison-Scott (1951) also allocated *barabensis* and *longicaudatus* into the *migratorius* group.

Fossil history of *Nothocricetulus* is rather puzzling. *Cricetulus migratorius* of earlier authors is not sharply delimited from the fossil *Allocricetus*. McKenna & Bell (1997) treated *Allocricetus* and *Cricetulus s. lat.* (i. e. with the inclusion of *migratorius*) to be congeneric, while Kowalski (2001) explicitly synonymized *Allocricetus bursae* with *migratorius*. The earliest records of broadly defined *Cricetulus* are from the Early Pliocene (Island of Rhodes, Greece; Turnbull 1975) and are succeeded by material from the Middle Pliocene from Russia (Topachevskiy & Skorik 1992) and the Lower Pleistocene from Europe (Maul 1990). The proper *migratorius* is stated for Anatolia since the Early Pliocene (Alpaslan et al. 2009); European records are reportedly

from the Late Pliocene (Villanyian), Biharian and Toringian (Kowalski 2001). There is considerable discrepancy among authors, however, and Toringian and older material is frequently classified as *Allocricetus bursae*. Vasileiadou & Sylvestrou (2022) still accept *Allocricetus* as a genus in its own right, and reported *A. bursae* until the Late Pleistocene of Europe and Turkey.

A high number of species of grey hamsters was admitted during the 19th century. Pallas already recognized 4 species (*migratorius, phaeus, accedula, arenarius*), and by early 1900s a further 6 species were added (*cinerascens, isabellinus, fulvus, murinus, coerulescens, atticus*). Taxonomy and nomenclature were revised by Thomas (1917) who relegated all these names to subspecies (or synonyms) of a single polytypic species *migratorius*. Thomas further concluded that "by a curious fatality, not unusual in nomenclature" (p. 452), *phaeus*, and not *migratorius*, was accepted as the oldest name for grey hamsters (Thomas 1917). Some early authors, however, synonymized *migratorius* with *acredula* (e.g. Gmelin 1788).

Particularly puzzling was the identity of *Cricetulus kozlovi* Satunin, 1902, from Gansu which was for long known only from the type which consists of skin (Figure 50h) and damaged skull (figured in Argyropulo 1933c: Figure 25, and Lebedev & Potapova 2008: Figure 5). The main source of confusion was a pseudo-sciuromorphous type of zygo-masseteric structure, which induced various authors to accept *kozlovi* as a species in its own right (Argyropulo 1933b, c). Alternatively, *kozlovi* was synonymized with *Cricetulus barabensis obscurus* (Allen 1940) or *Urocricetus kamensis* (usually ranked as one of its subspecies; Wang & Cheng 1973, Corbet 1978, Wilson & Reeder 1993, 2005, Zhang et al. 1997, Luo et al. 2000, Wang 2003, Smith & Hoffmann 2008, Haslauer 2017d); some authors shifted *kozlovi* to the *incertae sedis* section of *Cricetulus* (Ellerman 1941, Ellerman & Morrison-Scott 1951). Sokolov & Orlov (1980) suggested that *kozlovi* is close to *migratorius*, and Lebedev & Potapova (2008) showed that a presumably unusual type of zygomasseteric architecture in *kozlovi* was well inside the variation range for *migratorius*.

Distribution. The range is by far the largest of any hamster species, encompassing 7,129,600 km² and stretching from eastern Europe to eastern Nei Mongol (Figure 45). In the west, grey hamsters occupy Russia southward of the Volga and the Kama rivers; the northern-most occurrence is in Bol'shechernigovsky rayon (Samara District; Simak 2009). From the vicinity of Samara, the range border steadily declines southwards towards Ukraine where reaching the western extension in Vizhnitskiy Rayon (Tatarinov 1973) on the eastern foothills of the Carpathian Mts.; further south-east, the border follows this mountain arch until reaching eastern Romania (Simionescu 1966). South of the Danube River, there are 2 isolates on the Aegean-Black Sea shore (1) in south-eastern Bulgaria (Nedyalkov 2016) and adjacent Turkish Thrace (Kryštufek & Vohralík 2009), and (2) in Greece. The Greek isolate is further fragmented in Thessaly, Central Greece (Sterea Ellada), Attica, and Peloponnesus (Ondrias 1966, Bontzorlos 2009). Grey hamsters are excessively scarce in these fragments, and majority of records come from owl pellets both in Greece (Bontzorlos 2009, Bontzorlos et al. 2003) and Bulgaria (Nedyalkov 2016).

Between the Volga and Ob Rivers, hamsters do not move north of the 55th parallel; the most exposed occurrence is the Nizhneomsky district (Bakhrushev et al. 2005). The exposed records, however, are widely isolated in northern Kazakhstan and adjacent south-western Siberia; in Kazakhstan, the range becomes contiguous only south of the 50th parallel (Shubin 1977b). Eastward of the upper Irtysh River, the range is shaped by the western slopes of the Altai Mts.; further east, it is defined by the 45th parallel. The eastern-most range is in Mongolia (Bayanhongor, Dornogovi, Govi Altay, Hovd, Ömnögovi) and in China between Nei Mongol and the middle and upper reaches of the Huang-He; the exposed eastern record is in Ar Horqin Banner (Xu 2016). To the west of the Huang-He, the Chinese records are widely scattered across Ningxia, Qinghai, Gansu and Xinjiang (Zhang et al. 1997). To the west of Chinese Turkestan, the range sharply turns south reaching northern and western Pakistan (to the
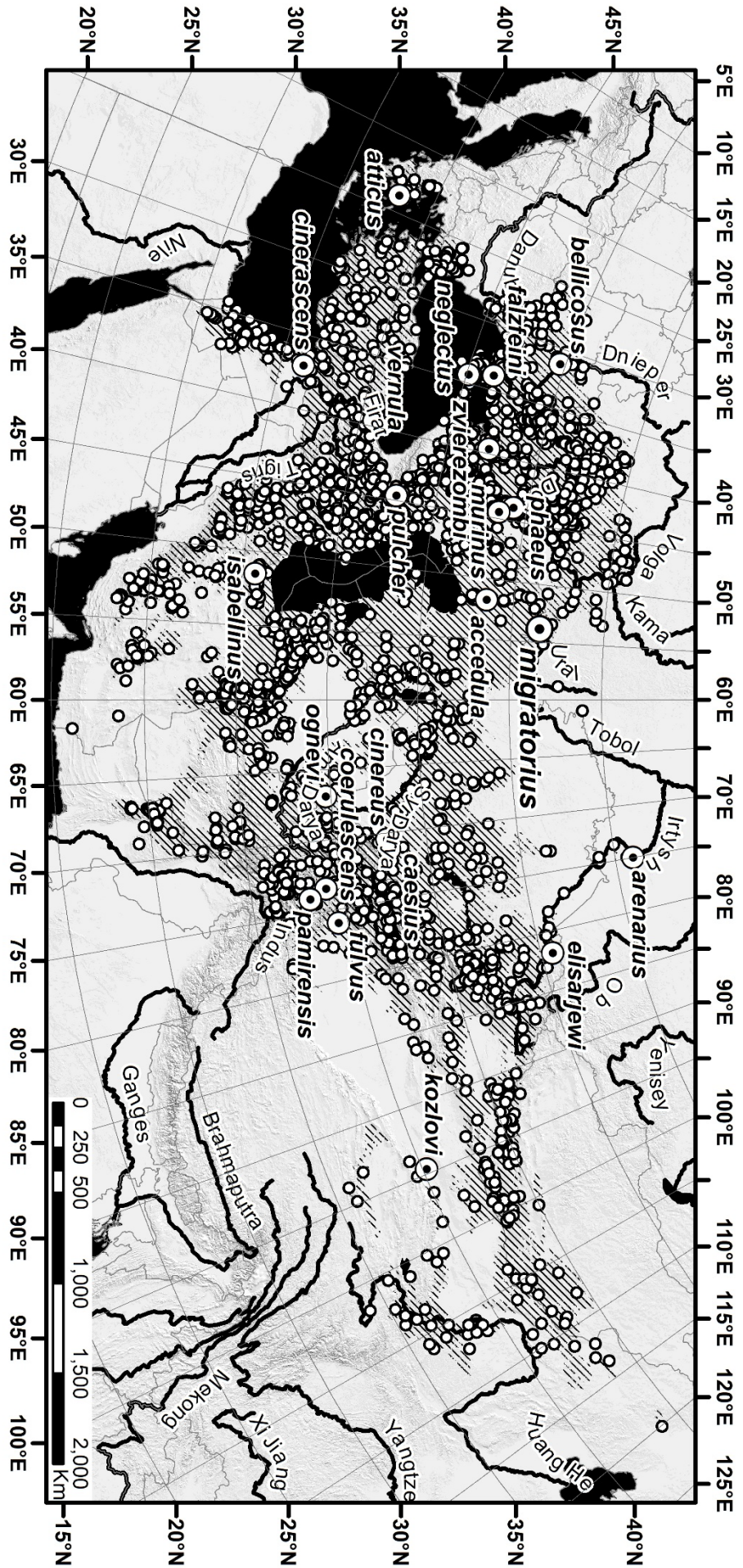
Figure 45: Distributional range of the grey hamster *Nothocricetulus migratorius*.

west of Indus) as far south as Sulaiman Mts. (Roberts 1977). Further west, the grey hamster is present in western and northern Afghanistan, the mountainous margins of the Iranian Plateau (Zagros, Alborz, Köpet Dag), northern Iraq (Al-Sheikhly et al. 2015), northern Syria (Aidek et al. 2025), the entire Levant coast (Tohmé & Tohmé 1985, Qumsiyeh 1996, Mendelssohn & Yom-Tov 1999, Amr et al. 2018) as far south as Ma'an (southern Jordan; Obuch 2018), the entire Anatolia (Kryštufek & Vohralík 2009), and the greater part of Trans-Caucasus in Azerbaijan, Armenia, and eastern Georgia (Dal' 1954, Shidlovskiy 1962, Alekperov 1966, Tembotov 1972, Bukhnikashvili 2004). Grey hamsters are present throughout Central Asia, *i. e.* in Kazakhstan (Shubin 1977b), Kyrgyzstan (Ayzin 1979), Tajikistan (Vinogradov 1935), Uzbekistan, and Turkmenistan (Marinina 2005), as long as suitable habitat is present. Hence, they are absent from large parts of the Karakum and Kyzylkum deserts in Uzbekistan and Turkmenistan (Marinina 2005), from coniferous forests in northern Kazakhstan, sandy substrate south of the Balkhash Lake in eastern Kazakhstan (Shubin 1977b), and Dzungarian Basin in Xinjiang (Zhang et al. 1997). Similarly, they are missing from hyper-arid deserts of Dasht-e Kavir and Dasht-e Lut in Iran (*cf.* Yusefi et al. 2019). The grey hamster is absent from the islands, but historically occupied the Island of Barsake'lmes in the former Aral Sea (Shubin 1977b). The Quaternary range exceeded the current one, stretching as far west as Spain and Great Britain (Kowalski 2001).

Grey hamsters occupy a wide range of open and dry habitats like forest steppe, mountain steppe with wormwood and juniper, steppe with cereal grasses, deserts and semi-deserts which frequently hardly provide any shelter. They were collected from various types of substrates, *e. g.* black and brown soils, fixed sands, saline soils, clay, and stony ground. On barren slopes and mountain peaks they hide in screes and among rocks and boulders. In Mongolian deserts they are frequently restricted to oases (Sokolov & Orlov 1980). Grey hamsters occupy cultivations, including gardens and old orchards. In parts of their range, grey hamsters inhabit dry forests or forest belts, specifically in Moldova (Lozan 1971), Crimea (Flerov 1929), Kabardino-Balkaria (Tembotov 1960), west Siberia (Bakhrushev et al. 2005), Kyrgyzstan (Ayzin 1979),

Kazakhstan (Afanasiev 1953), Tajikistan (Davydov 1988), and Pakistan (Roberts 1977).

Elevational range is from –25 in the Caspian Depression up to 4,800 m in the Pamir Mts. (Davydov 1988). There are considerable regional differences in occupied elevations. In Europe, grey hamsters are tied to lowlands but ascend up to 2,300 m high in Anatolia (Kryštufek & Vohralík 2009) and Caucasus (Dal' 1954, Alekperov 1966). Further east in Central Asia, their presence is common at 3,500–4,000 m of elevation (Vinogradov et al. 1936, Janushevich et al. 1972, Pavlenko & Allabergenov 1974, Ayzin 1979).

Grey hamsters were observed inside houses already by Pallas (1779). So far, synanthropic populations have been reported from European Russia (Minoransky et al. 1997), south-west Asia (Satunin 1905, Missone 1959), including Armenia (Dal' 1954), Azerbaijan (Alekperov 1966), the Caucasus (Vereschagin 1959, Tembotov 1960, Shidlovsky 1962), in Turkmenistan (Nurgel'dyev 1969), Kazakhstan (Afanasiev 1953, 1960, Shubin 1977b), Kyrgyzstan (Stogov 1951, Toktosunov 1958, Janushevich et al. 1972, Ayzin 1979), Uzbekistan (Mukhamedkulov 1964, Pavlenko & Allabergenov 1974), Tajikistan (Davydov 1988), Pakistan (Roberts 1977), and Mongolia (Sokolov & Orlov 1980). In some urban settlements, grey hamsters are as abundant as house mice (*Mus*) or rats (*Rattus*) (e.g. Shidlovsky 1962).

Description. Similar to the long-tailed lesser hamster *Cricetulus longicaudatus* (Figure 46). Dimensions: body mass = 25.5–70 g, length of head and body = 105–132 mm, length of tail = 22–41 mm, length of hind foot = 17.0–20.0 mm, length of ear = 15.8–22.0 mm, condylobasal length of skull = 25.4–31.2 mm, zygomatic width = 13.0–16.9 mm, length of maxillary tooth-row = 3.7–5.1 mm; captive hamster weight up to 75 g (Volf & Volf 1993). Sexes are of approximately the same size in Anatolia (Kryštufek & Vohralík 2009), though some populations are dimorphic. In Central Asia, males are heavier on average; the quotient of mean male / female body mass is 1.15 in Tajikistan (Davydov 1988) and 1.26 in Kyrgyzstan (Janushevich et al. 1972). Contrary to this, Cheesman (1921) found females to be on average larger than males in Shiraz (Iran). Tail is longer than hind foot, while its length is highly variable, accounting for 16–42% of length of head and body
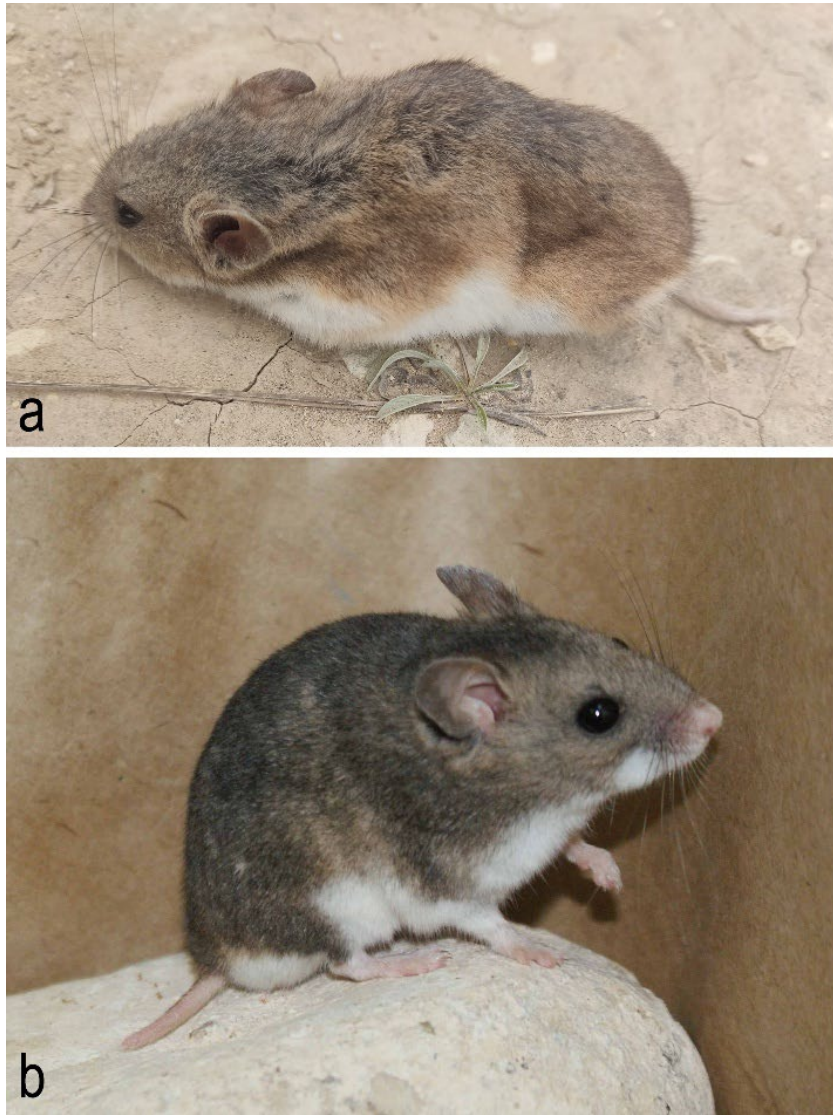
Figure 46: Grey hamsters *Nothocricetulus migratorius* from Levashinskiy Rayon, Dagestan (a), and Homs, Syria (b). Photo courtesy of Magomed Magomerasulovich Chunkov (a) and Alenka Kryštufek (b)

(usually ≈ 28%). Tail is parallel-sided and more densely clad than in *Cricetulus* (Figure 29d); terminal pencil is feeble (length ≈ 1 mm). Eyes are moderately large (diameter = 4.1–4.9 mm) and ears are long and circular; they are densely hairy on the outer side and nude to sparsely clad with hairs on the inner side. Whiskers are long (up to 35 mm), white, brown or blackish. Palms and soles have 5 and 6 pads, respectively. Plantar pads are of approximately the same size and the metatarsal pair is comparatively larger than in *Cricetulus* (Figure 33b). Fur is soft and dense, 7–11 mm long on mid-back and 5–6 mm on belly; protruding sparse hairs are particularly long at tail base (Figure 29d). Summer fur is shorter than winter hairs. Hamsters moult throughout the vegetation season (Davydov 1988). Feet are thickly covered by short white hairs. Hairs of dorsal pelage are typically tricoloured, with slate base, buffy subterminal

band and whitish or black tip. White-tipped hairs predominate in pale individuals and black-tipped hairs are more abundant, along with all-black longer hairs, in dark grey animals. Colouration of dorsal surface from muzzle to tail-base is either grey or buff. Grey hamsters vary from light grey to glaucus (bluish) grey and dim-grey, and buff animals have grey ground colour heavily admixed drab, buffy or brown (Figure 47). Black-tipped hairs became conspicuous on the crown and along the spine producing a fuzzy mid-dorsal streak (Figure 47). Hairs on the underside are either white-to-base or have grey bases and white tips. All-white hairs usually cluster into irregular patches on the chin, throat, chest, armpits and the inguinal region. As the result, belly is a mosaic of pure white and grey clouded patches; rarely, the underside is shaded pale buff. Line of demarcation is well defined or sharp; it is slightly serpentine with white

underside turning dorsally between the rib cage and the hip (Figure 47a–c). Outer surface of fore feet is white and that of hind feet is of same colour as the back. Hairs are frequently faintly tinged drab or light buff on the head, cheeks, on flanks and at tail base. Some individuals have a white postauricular tuft. Ears do not contrast much with surrounding parts; they are monochromatic grey and lack white rim which is characteristic of *Cricetulus*. The tail is usually indistinctly bicolour, darker above and paler below. Juvenile hamsters are usually duller and greyer.

Glans penis is wide, shallow and blunt at its peak; the width approximately equals the length. Dorsal base has no bump (present in *Cricetulus*) and the central belt of the glans has no spines. Spines cover the proximal and the distal parts of glans, and are present across the entire glans in *Cricetulus*. Both, *Nothocricetulus* and *Cricetulus*, have 2 ventral papillae but lack dorsal papilla. Central papilla is slightly wider than lateral papillae in *Nothocricetulus*, while the difference between these papillae is prominent in *Cricetulus* (Vorontsov 1982). Baculum has a heavy proximal part with expanded base and comparatively small distal baculum (Figure 17e). Dimensions (length): proximal baculum = 3 mm, lateral distal baculum = 1 mm, medial distal baculum = 0.5 mm (Argyropulo 1933c, Didier 1953).
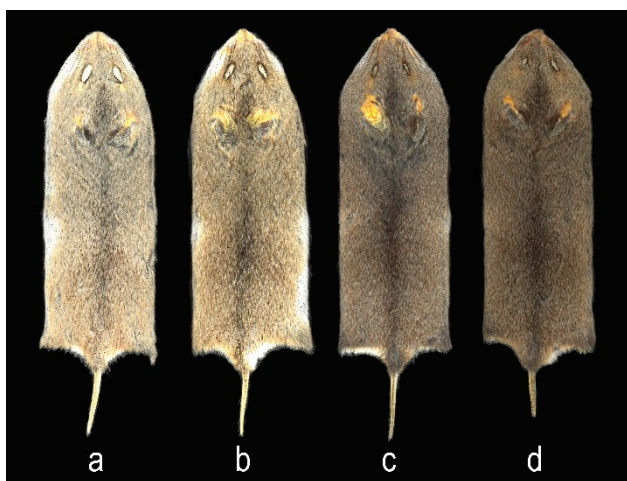
Figure 47: Skins of grey hamsters *Nothocricetulus migratorius* in dorsal view to show colour variation across a distance of 450 km in Anatolia (Turkey): a, b – Ermenek, Karaman Province; c, d – Şarkışla, Sivas Province. Note dark spinal stripe which terminates on the front as crown patch. Vouchers (a–c) show dorsad expansion of white fur between the rib cage and the hip (compare to *Urocricetuls lama* on Figure 102).

Skull (Figure 48) closely resembles *Cricetulus* in size and proportions; width across zygomatic arches accounts for 49.3–58.0% of condylobasal length (mean = 53.5%). The most obvious difference between the two genera is in (1) length of the squamosal suture and interparietal suture, and (2) in the morphology of the zygomasseteric structure. In *Nothocricetulus*, the squamosal suture (*sutura squamosa cranii*) is, in dorsal view, longer than in *Cricetulus* that comes from different position of the fronto-temporal angle of the parietals relative to the orbit. The interparietal (sagittal) suture is shorter in *Nothocricetulus* and does not reach the posterior level of the orbit, whereas it is normally at that level in *Cricetulus*. Secondly, the zygomasseteric structure is either myomorphous or pseudo-sciuromorphous (Figure 20d) in *Nothocricetulus*, but strictly myomorphous in *Cricetulus* (Figure 20g). The myomorphous conditions are characterized by a more extensive zygomatic plate with a straight vertical or oblique anterior margin. Besides, keel of zygomatic plate is prominent and zygomatic notch is deep; both are seen in dorsal view (Figure 48). The pseudo-sciuromorphous type, on the other hand, shows a reduced masseteric plate with emarginate margin, weak or no keel and absence of zygomatic notch. The infraorbital foramen is more of oval shape in pseudo-sciuromorphous type, but is expanded dorsally and constricted ventrally in the myomorphous type. All transitions exist between the two extremes in *N. migratorius*; besides, asymmetry in zygomasseteric type was also reported (Lebedev & Potapova 2008).

Molars show similar pattern as in *Cricetulus* with some important differences. Metalophule (the antero-mesial ridge of metacone) contributes to the X-pattern of enamel ridges between the protocone-paracone and hypocone-metacone in M^{1-2}. Mesolophid is present on the lingual side between the entoconid and metaconid of M_3 (Figure 49).

Karyotype: 2n = 22, NF_a = 40, NF = 44; the autosomal complement consists of 5 metacentric and 5 subtelocentric pairs. In the conventionally stained mitotic preparations, the sex chromosomes appear as isomorphic large subtelocentric elements but show a distinct internal structure, including slightly different centromere position. Various studies reported
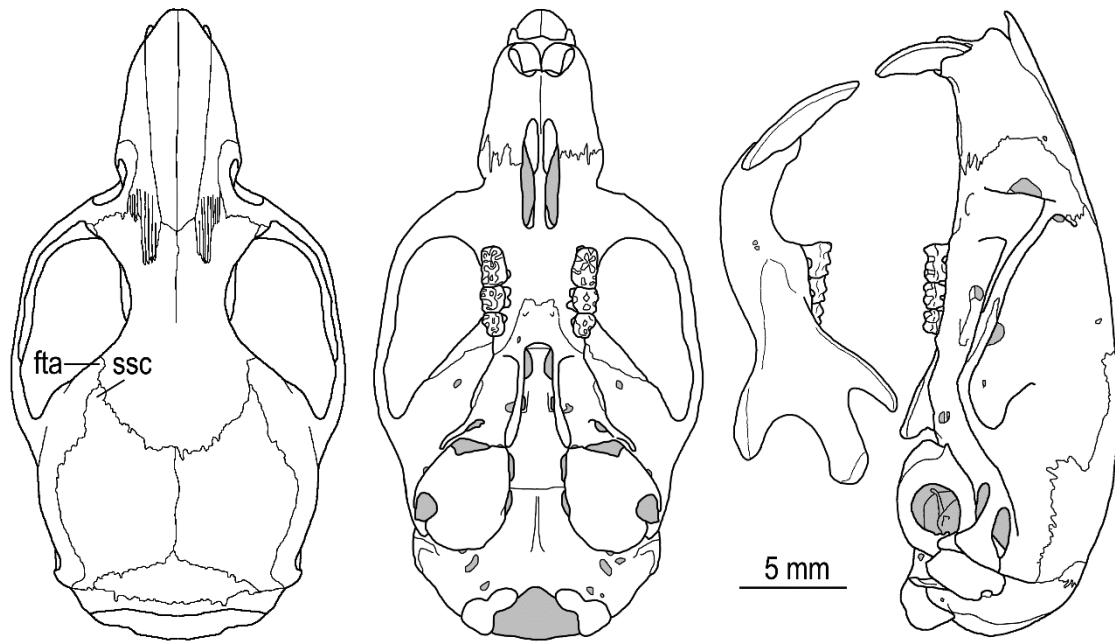
Figure 48: Skull and mandible of grey hamster *Nothocricetulus migratorius* from Sivas, Turkey. Abbreviation: fta – fronto-temporal angle of the parietals; ssc – *sutura squamosa cranii*.

differences in size of individual chromosomes and in the position of centromere in the small autosomal pair (reviewed in Arslan & Zima 2014). Besides, heteromorphy of homologous chromosomes was retrieved in at least two chromosomal pairs in several different populations (Yerganian & Papoyan 1965, Kartavtseva 1985, Brandler & Blekhman 2024). Brandler (1999) reported a population from the Tianshan Mts. with 2n = 24, NF = 46. The sex chromosomes are heteromorphic; the X chromosome is medium-sized submetacentric and the Y chromosome is acrocentric of similar size (Brandler & Blekhman 2024).

Variation and Subspecies. Phylogenetic analysis based on *mt*DNA retrieved 3 deeply divergent allopatric lineages, which presumably originated from trichotomy at the end of the Middle Pleistocene ~ 130–160 kya (Lebedev et al. 2018a). The West lineage contains hamsters to the west of the Volga River in Europe, the Caucasus and Asia Minor, while the East lineage comprehends samples to the east of the Volga in Eastern Europe and Asia, as far west as Iran. The West lineage is further structed into 4 allopatric sublineages, which evidently split during the early Last glacial cycle at ~ 80 kya: (1) the European sublineage, which is widespread to the north of the Sea of Azov–northern
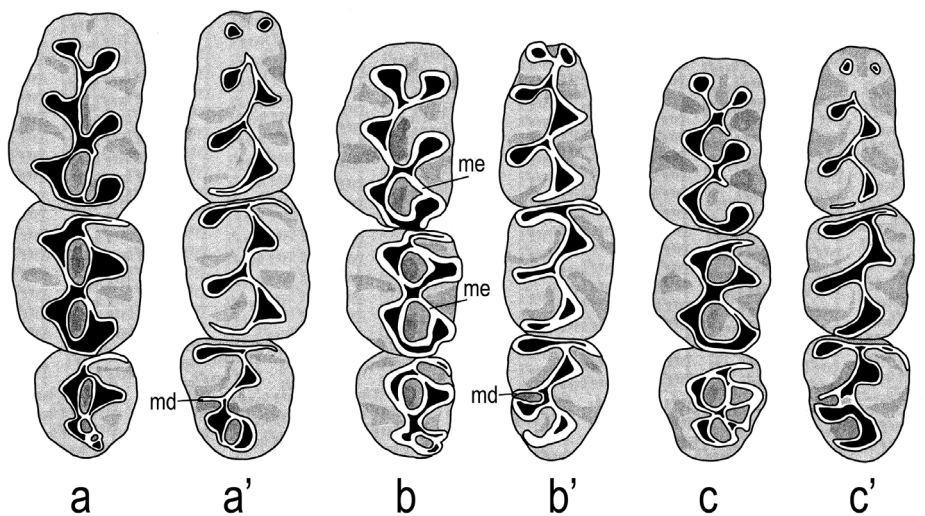
Figure 49: Grinding pattern of upper (a, b, c) and lower (a', b', c') molars in grey hamsters *Nothocricetulus migratorius*: a – Kochkor District, Kyrgyzstan; b – Mongolia; c – Sivas, Turkey. me – metalophule; md – mesolophid.

coast of the Caspian Sea line; (2) the cis-Caucasian sublineage from the steppes between foothills of the north-Caucasus and the Azov–Caspian line; (3) the Armenian sublineage, and (4) the Anatolian sublineage; the last holds sister position against the remaining West haplotypes. Contrary to this situation, the East lineage shows minimal structure. These 2 major lineages were originally identified by 2 putatively diagnostic allozyme loci out of 8 polymorphic loci studied (Lebedev et al. 1998, 2000, Mezzherin 2001). Furthermore, multivariate analysis of size-adjusted cranial measurements similarly retrieved 2 major population clusters, which were also separated by the Volga River (Lebedev et al. 1998, 2000). The 3rd major phylogenetic lineage from the Qurama Mts. (south-western end of the Tianshan range flanking north-western Fergana Valley, Uzbekistan) is also characterized by a distinct cytotype (2n = 24), but its morphology is not known at the time of writing.

Earlier authors recognized 12–15 subspecies of grey hamsters (Pidoplitshka 1928, Argyropulo 1933b, c, Ellerman 1941, Vinogradov & Argyropulo 1941,

Ellerman & Morrison-Scott 1951, Vinogradov & Gromov 1952, Gromov et al. 1963, Kuznetsov 1965); regional studies similarly returned high numbers of subspecific taxa, *e. g.* 5 subspecies for each, the Caucasus area (Shidlovskiy 1962) and Kazakhstan (Afanasiev 1960), 3 subspecies for Kyrgyzstan (Toktosunov 1958), 2 subspecies for a comparatively small area in northern Pakistan (Siddiqi 1969), and so forth. Subspecies were diagnosed by fur colouration and size. Grey hamsters tend to be paler where climate is arid and darker in more humid conditions (Figures 47 & 50). *E. g.* in Anatolia, dull-grey hamsters (classified as ssp. *vernula*) occupy the Black Sea coast, while buffy-greyish hamsters (*cinerascens*) live inland in regions receiving less rain (Kryštufek & Vohralík 2009).

Similarly, in Tajikistan, pale hamsters with ample sandy tints (*ognevi*) live at lower elevations, while darker hamsters (*coerulescens*) inhabit higher elevations (Davydov 1988). At large scale, pale sandy-buff hamsters (*caesius, coerulescens*) are typical of the mountains of Central Asia (Janushevich et al. 1972), while grey hamsters (*bellicosus, zvieresombi*) occupy black-
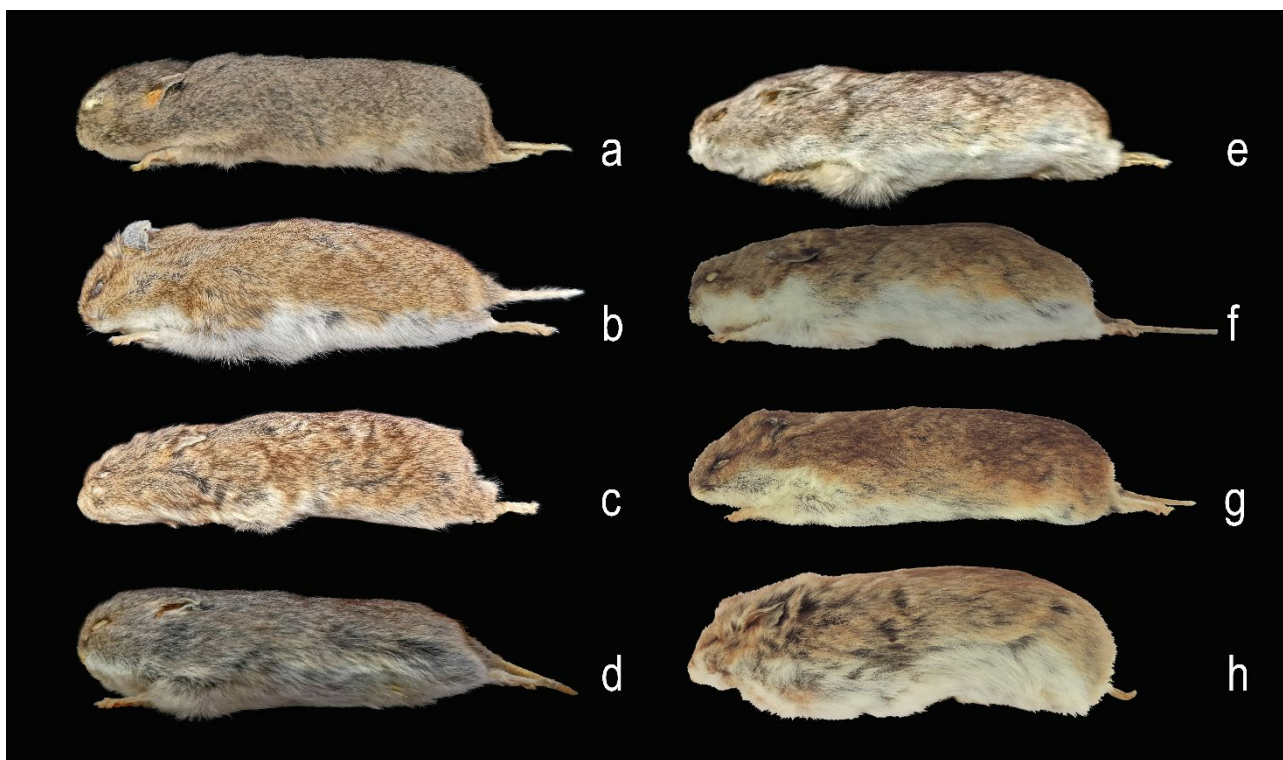
Figure 50: Skins of grey hamsters *Nothocricetulus migratorius* from different parts of their range to show variation in fur colouration. Parenthesized are subspecific names which were traditionally used to define the particular sample. a – Criulensk District, Moldova (*bellicosus*); b – Ankara, Turkey (*cinerascens*); c – Volgograd District, European Russia (*phaeus*); d – Ayagoz, eastern Kazakhstan (*caesius*); e – Ustyurt, Qoraqalpogiston, Uzbekistan (*migratorius*); f – Hisar Range, Tajikistan (*coerulescens*); g – Kopal'skiy Uezd, Semirechye, northern foothills of Dzungarian Alatau, south-eastern Kazakhstan (*cinereus*); h – Nanshan, Gansu, China (type of *Cricetulus kozlovi*; ZIN 5831). In line with subspecific taxonomy proposed in this volume, samples a–c classify as *phaeus* and samples d–h as *migratorius*.

soil regions of Ukraine (Pidoplitshka 1928). Size differences among populations and putative subspecies may be considerable. *E. g.* in Kazakhstan, body mass reaches 45 g around the Balkhash Lake and 65 g in southern Kazakhstan (Shubin 1977b).

Gray hamsters are on average the largest (mean condylobasal length of skull >27 mm) in the mountainous regions of Central Asia (Lebedev 2000), specifically in Turkmenistan (Zykov 1991, Marinina 2005), Afghanistan (Niethammer 1982), eastern Kazakhstan (Shubin 1977b), northern India (Agrawal 2000) and China (Luo et al. 2000). Hamsters living northward and westward are smaller on average (mean condylobasal length <26.5 mm). Outliers, however, were reported; *e. g.* grey hamsters occupying Ukraine and adjacent Russia have larger skulls (condylobasal length > 27.0 mm) (Pidoplitshka 1928, Migulin 1938) than expected from their geographical position. Ellerman (1961) stressed variation in the length of upper tooth-row. Indeed, hamsters from the mountainous regions of Central Asia also have longer molars (mean length >4.15 mm) than those from Siberia, western Kazakhstan, the Middle East and Europe (<4.20 mm). The overlap is considerable; *e. g.* the range in Kazakhstan is 4.1–4.5 mm on the east of the country *v.* 4.0–4.3 elsewhere (Shubin 1977b). External and cranial ratios similarly show variation at various spatial scales. Length of tail relative to length of head and body varies individually (Kryštufek & Vohralík 2009) and regionally (*e. g.* Janushevich et al. 1972). Similarly, width-to-length of skull changes both within the same population (Kryštufek & Vohralík 2009) and between regions (Ellerman 1961). The west-to-east trend is also seen in the zygo-masseteric structure. More than 35% of grey hamsters from Mongolia have pseudo-sciuromorphous structure *v.* <12% of those occurring westward (Lebedev & Potapova 2008). Many authors stressed great variation in morphological traits (Toktosunov 1958, Ondrias 1966, Davydov 1988) and loose subspecific diagnoses (Bannikov 1954, Shubin 1977b, Sokolov & Orlov 1980). As traditional subspecies are frequently at odds with morphologically diagnosable populations, no subspecies are recognized in recent reviews (*e. g.* Haslauer 2017a). In spite of this, we subsequently propose a crude subspecific division, which is mainly based on the results of Lebedev and coworkers (Lebedev 2000, Lebedev et al. 2018b). As suggested by Lebedev et al. (2018b), the 2 major subspecies (*migratorius* and *phaeus*) are more likely subspecies groups or semi-species (Lebedev 2012). In any case, refinement of subspecific taxonomic remains a task for further taxonomic revision.

Nothocricetulus migratorius migratorius (Pallas, 1773)

Synonyms: *Mus arenarius* Pallas, 1773; *Mus accedula* Pallas, 1779; *Cricetus isabellinus* Filippi, 1865; *Cricetus fulvus* Blanford, 1875; *Arvicola coerulescens* Severtsov, 1879; *Cricetulus kozlovi* Satunin, 1902; *Cricetulus migratorius griseus* Kashkarov, 1923 (replaced by *cinereus* Kashkarov, 1926); *Cricetulus migratorius caesius* Kashkarov, 1923; *Cricetulus migratorius pamirensis* Vinogradov 1931; *Cricetulus migratorius ognevi* Vinogradov & Argyropulo, 1941; *Cricetulus migratorius elisarjewi* Afanasiev, 1953.

Distribution: Eastern Europe (to the east of the Volga River); Iran (border against ssp. *phaeus* not resolved), and the rest of range in Asia.

Characteristics: Diagnosed by cyt*b* and cytochrome oxidase I (*coI*) gene sequences and by 2 fixed alleles for *Ck-2* and *s-Ord* loci (Lebedev et al. 1998, 2000). Karyotype: 2n = 22, NF = 44; sex chromosomes are isomorphic (Arslan & Zima 2014). Rostrum is more gracile, longer and shallower, upper incisors are narrower, nasals are longer, tympanic cavity is more swollen, interorbital region is wider, and braincase is shorter and narrower (Lebedev 2000).

Nothocricetulus migratorius phaeus (Pallas, 1779)

Synonyms: *Hypudaeus cinerascens* Wagner, 1848; *Cricetus murinus* Severtsov, 1873; *Cricetulus atticus* Nehring, 1902; *Cricetulus tauricus* Satunin, 1908 (nomen nudum); *Cricetulus arenarius bellicosus* Charleman, 1915; *Cricetulus arenarius vernula* Thomas, 1917; *Cricetulus falzfeini* Matschie, 1918; *Cricetulus migratorius pulcher* Ognev, 1924; *Cricetulus migratorius neglectus* Pidoplitshka 1928; *Cricetulus migratorius zvieresombi* Pidoplitshka, 1928; *Cricetulus migratorius phaeus sviridenkoi* Pidoplitshka, 1928 (invalid as infrasubspecific taxon).

Distribution: Europe to the west of the Volga River; the Caucasus, Anatolia and the Levant coast; border against the nominotypical subspecies not resolved.

Characteristics: Diagnosed by cyt*b* and cytochrome oxidase *I* (*coI*) gene sequences and fixed alleles for *Ck-2* and *s-Ord* loci (Lebedev et al. 1998, 2000). Karyotype: 2n = 22, NF = 44; sex chromosomes are isomorphic (Arslan & Zima 2014). Rostrum is more robust, shorter and deeper, upper incisors are broader, nasals are shorter, tympanic cavity is less inflated, interorbital region is narrower, braincase is longer and wider (Lebedev 2000).

Nothocricetulus migratorius unnamed subspecies

Distribution: Known from the Angren Plateau (Qurama Mts.) in south-western end of the Tianshan range, Uzbekistan.

Characteristics: Diagnosed by cyt*b* and cytochrome oxidase *I* (*coI*) gene sequences (Lebedev et al. 2018b). Karyotype: 2n = 24, NF = 46; sex chromosomes are heteromorphic (Brandler & Blekhman 2024). Morphology is not known (Lebedev et al. 2018b).

GENUS: *Allocricetulus* Argyropulo, 1933 – Eversmann's hamsters

Allocricetulus Argyropulo, 1933b: 242. Type species by original designation is *Cricetulus eversmanni* Brandt. Argyropulo proposed *Allocricetulus* as a subgenus of *Cricetulus*.

Etymology. The name *Allocricetulus* was coined from 'allos' (Ancient Greek for 'other' or 'strange') and *Cricetulus*, which is diminutive of *Cricetus* (the hamster), *i. e.* a 'strange small hamster'.

Taxonomy and Nomenclature. *Allocricetulus* has no vernacular name in English. By using 'Eversmann's hamsters' as generic name we follow Russian authors (Gromov et al. 1963, Flint 1966b, Shubin 1977d, Sokolov & Orlov 1980, Gromov & Baranova 1981, Gromov & Erbajeva 1995).

The year of publishing *Allocricetulus* is sometimes stated as 1932 (Pavlinov & Rossolimo 1987: 170, Lebedev 2012: 215), although the issue of the Proceedings of the Zoological Institute in Leningrad for 1932 with 2 papers by Argyropulo (1933a, b) was seemingly released in 1933 (Baranova & Gromov 2003: 48). Besides, Argyropulo (1933b: 243) himself dated his *Cricetus cricetus fuscidorsis,* which was published in the same volume of the Proceedings, as being released in 1933. Gromov et al. (1963: 503) erroneously gave the year of publishing *Allocricetulus* as 1937.

Allocricetulus was established as a subgenus of *Cricetulus* (Argyropulo 1933b). Prior to this, Eversmann's hamsters were classified in the genus *Cricetulus* without further subgeneric ranking (Trouessart 1910, Martino & Martino 1916, Beljaev 1933). Less often, *Allocricetulus* was synonymized with *Nothocricetulus migratorius* (Thomas 1917, Allen 1925) or included into *Mesocricetus* (Ogneff 1925, Pidoplitshka 1928, Kouznetzof 1928, Argyropulo 1931). Vinogradov & Gromov (1952, 1956) classified Eversmann's hamsters into *Cricetus*; Stroganova (1954) and Popov (1960) kept *Allocricetulus* as a subgenus of *Cricetus*. Ellerman (1941: 429) classified Eversmann's hamsters into the *eversmanni* group within *Cricetulus*, though subsequently (p. 435) accepted *Allocricetulus* as a valid subgenus.

Allocricetulus was elevated to a genus in its own right already in the early 1940s (Vinogradov & Argyropulo 1941). This was widely accepted by Russian and some Eastern authors (Flint et al. 1965, Stubbe & Chotolchu 1968, Vorontsov & Krjukova 1969a, Yudin et al. 1979, Sokolov & Orlov 1980, Gromov & Baranova 1981, Kartavtseva & Vorontsov 1992, Gromov & Erbajeva 1995, Gromov et al. 1963, Pavlinov & Rossolimo 1987), while part of Russian authors (Shnitnikov 1936, Kuznetzov 1944, Kuznetsov 1948, 1975, Afanasiev 1953, Bannikov 1954, Stroganova 1954, Vorontsov 1960, Karaseva 1963) and the majority of Western (Corbet 1978, Corbet & Hill 1980, 1986, Honacki et al. 1982, Zima & Král 1984) and Chinese authors (Zhang et al. 1997, Luo et al. 2000, Fu et al. 2005, Wu & Fu 2005) continued to report Eversmann's hamsters as part of *Cricetulus*, thought frequently at a subgeneric rank. The concept of *Allocricetulus* as a genus independent from *Cricetulus* has been widely accepted

since 1990 (Kowalski 2001, Wang 2003, Jiang et al. 2015).

The actual phylogenetic position of Eversmann's hamsters is contested (Figure 1). Gromov et al. (1963) exposed a mosaic nature of their morphology. In the shape of limb bones, *Allocricetulus* is intermediate to *Cricetulus* and *Cricetus*, while its cranial shape resembles "small *Mesocricetus*". Morphology of bullae suggests a sister position against the clade of *Cricetulus* + *Nothocricetulus* (Potapova 2005). In *Allocricetulus* and part of *Nothocricetulus*, the anterior portion of lateral masseter (*masseter lateralis anterior*) reaches rostrum, hence the zygomasseteric structure is of pseudosciuromophous type (Lebedev & Potapova 2008). Ross (1992) suggested for Eversmann's hamsters to hold a sister position against *Cansumys* + *Tscherskia* + *Cricetus* + *Mesocricetus*, while chromosomal data clustered *Allocricetulus* inside *Cricetulus* + *Nothocricetulus* + *Cricetus* (Romanenko et al. 2007). Sequence data retrieved a sister position of *Allocricetulus* and *Cricetus* (Lebedev 2018a, Ding et al. 2020). In spite of the obvious differences in external and cranial morphology between *Allocricetulus* and *Cricetus*, these genera have several characteristics in common: (1) well developed *torus linguae* and *sulcus semilunaris*, (2) medial sulcus which ends before the tip of the tongue; (3) the borderline fold (*margo plicatus*) of the stomach is convoluted, and the corneous epithelium extends into the glandular portion, but not beyond the isthmus; (4) 3 *ampullae coli*, (5) comparatively short intestine (ratio of intestine to head and body is less than 4.5), (6) a postponed exposure of dentin on enamel ridges which separate 2nd internal fold (*if2*) from 2nd primary fold in M$^{1-2}$, (7) pterygoid platform is below (i.e. dorsad to) the level of palate (Ross 1992), (8) coronoid processus of the mandible is powerful, and (9) karyotype is characterized by low diploid number and specific pattern of differentially stained chromosomes (Romanenko et al. 2007).

Several authors argued that living Eversmann's hamsters are closely related to the fossil *Allocricetus* Schaub, 1930. Thus, Gromov & Baranova (1981) suggested that *Allocricetus* is the most probable direct ancestor of *A. eversmanni* and might be congeneric with *Allocricetulus*; this was categorically rejected by Ross (1992). McKenna & Bell (1983), Kowalski (2001) and Horáček & Lebedová (2022) synonymized *Allocericetus*

with *Cricetulus,* and simultaneously treated *Allocricetulus* as a genus in its own right. From cladistic analyses based on molar cuspidation in fossil taxa (which did not include *Allocricetulus*), Bescós (2003) concluded that *Allocricetus* includes fossil species *Allocricetus jesreelicus* Bate, 1943, and *Allocricetus teilhardi* Zheng, 1984, which clustered with *Nothocricetulus* and *Cricetus*, rather than with *Allocricetus bursae* (as the genotype). From the results of Bescós (*l. c.*) one can conclude that *Allocricetus* is a crown cluster in the phylogenetic tree of hamsters and also a composite of several genera. Stuart (1991), on the other hand, suggested conspecificity between *Allocricetus bursae* Schaub, 1930, and *Cricetiscus sungorus*. In any case, the identity and scope of *Allocricetus* is loosely understood; for a detailed discussion on its status, see Horáček & Lebedová (2022). Fossils of *A. eversmanni* are reported from the Middle (Gromov & Baranova 1981) and Late Pleistocene (Kowalski 2001); McKenna & Bell (1983) quote no fossils at all.

Number of species in *Allocricetulus* was still disputed in recent times. The main source of disagreement is the position of Eversmann's hamsters from Zaysan Basin (east Kazakhstan), which are referred to as *pseudocurtatus*. These hamsters externally resemble *curtatus,* but have the karyotype of *eversmanni*, and were in the past either interpreted as conspecific with *eversmanni* or transitional between the two species. Depending on this view, different authors considered *Allocricetulus* either as a monotypical (sub)genus (Kuznetsov 1932, 1965, Allen 1940, Kuznetzov 1944, Mitina 1959, Bannikov 1954, Ellerman & Morrison-Scott 1951, Ma et al. 1987, Zhang et al. 1997, Fu et al. 2005, Wu & Fu 2005) or to contain 2 species (Argyropulo 1933b, c, Ellerman 1941, Vinogradov & Argyropulo 1941, Gromov et al. 1963, Flint 1966b, Stubbe & Chotolchu 1968, Kuznetsov 1975, Corbet 1978, Sokolov & Orlov 1980, Gromov & Baranova 1981, Honacki et al. 1982, Corbet & Hill 1986, Pavlinov & Rossolimo 1987, Musser & Carleton 1993, 2005, Gromov & Erbajeva 1995, Wang 2003, Lebedev 2012). Strong evidence in support of a 2-species solution of *Allocricetulus* emerged already from chromosomal studies by Matthey (1960) and Vorontsov (1960). Musser & Carleton (2005: 1040), however, called for fresh perspective to validate the specific status of *curtatus*, which is summarized in Gureeva (2022). Based on her results, we accept 2 species of Eversmann's

hamsters: *eversmanni* and *curtatus*. They differ in diploid number and the morphology of chromosomes (2n=20 in *curtatus* and 2n=26 in *eversmanni*; Romanenko et al. 2013), cranial morphology (Gureeva et al. 2020), morphology of glans penis and baculum (Vorontsov 1982), and in nucleotide sequences of mitochondrial and nuclear genes (Neumann et al. 2006, Gureeva 2022, Meschersky et al. 2024). Their ranges are allopatric as they are separated by the Dzungarian Govi and Mongol Altai Mts. (see distributional maps below). Evolutionary divergence between the two species is estimated at 120 kya, however, the confidence interval is wide (CI = 50–212 kya).

Contrary to earlier views on a complete reproductive isolation between *eversmanni* and *curtatus* (Vorontsov 1982), these species did hybridize in captivity, though pregnancy frequently failed. Next, the F1 hybrids were by 15–35% smaller than parental species and yielded no litters. Meiosis in hybrids has been disrupted during pachytene (prophasis I). Some spermatocits did develop into spermatozoa, however, the fertility in F1 males has been reduced (Gureeva et al. 2016). Relationships between *eversmanni* s. str. and *pseudocurtatus* are further discussed below in the account of A. *eversmanni*.

Distribution. Steppes and semideserts between the Volga River and eastern Gobi Desert at 117°E in China; the eastern-most records are in Hebei. In the north, Eversmann's hamsters reach the 56th parallel in Russia; the southern border is tentatively set by deserts of Central Asia in Kazakhstan, the Mongol Altai Mts. and Gobi Altai Mts. (Mongolia) and the Huang He River (north China).

Characteristics. Medium-sized hamsters with moderately long snout (Figures 51, 56, 59); the tail which accounts for approximately $1/5$ of head and body length (tail relative to head and body = 14–22%) is proportionally longer in juveniles. In both species, males are on average by 20% heavier than females (Gureeva et al. 2016). Ears are of modest length, rounded and covered by short hairs (Figure 8). Hind foot is short, only slightly longer than the ear; the toes are comparatively shorter than in the remaining Cricetina. There are 4 fingers on the front paws, equipped with comparatively weak claws; the thumb is rudimentary. The 5 palmar pads are comparatively large; interdigital pads are about ½ size of metacarpal pads. The posterior thumb does not differ appreciably in size from finger V, and fingers II–IV are of approximately same length. Hind claws are slightly
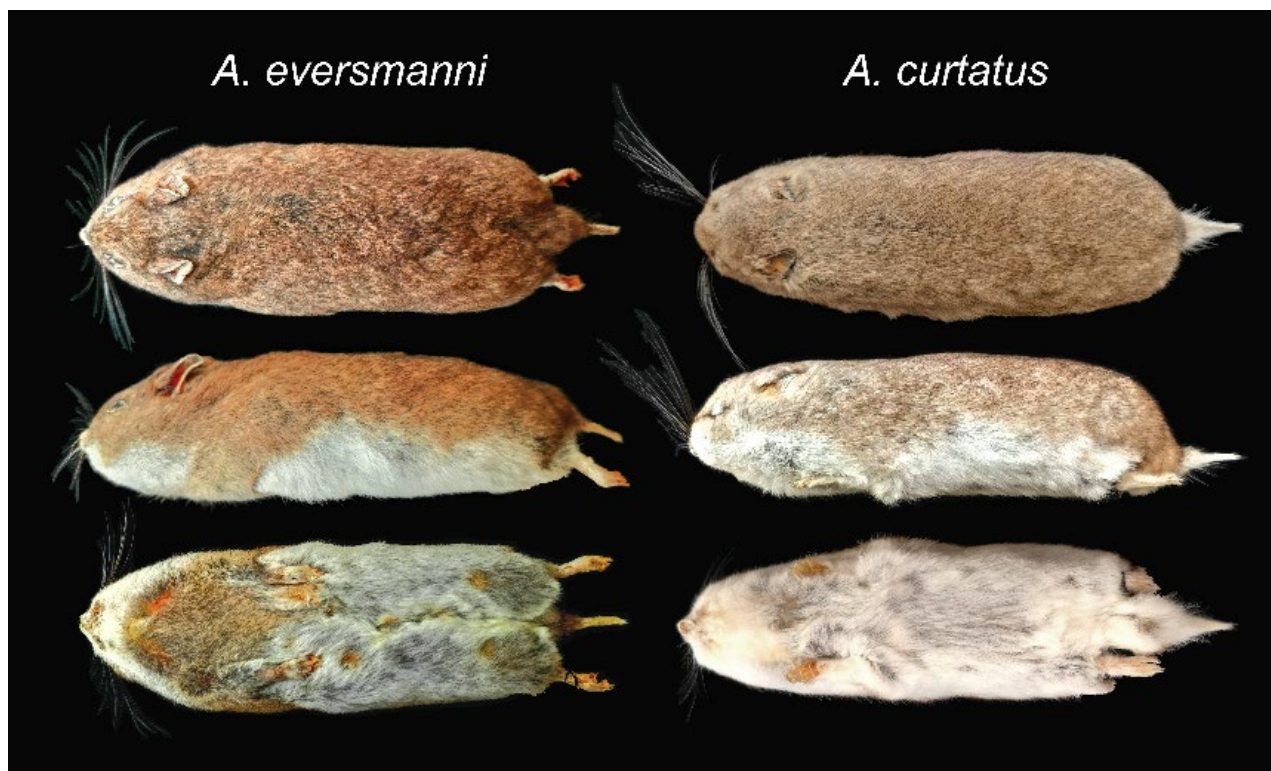
Figure 51: Skins of Eversmann's hamsters *Allocricetulus*: *A. eversmanni* (Saratov, Lower Volga, Russian Federation) and *A. curtatus* (south of Nomgon sum, Mongolia) in dorsal, lateral and ventral views. Photo: B. Kryštufek

Allocricetulus curtatus
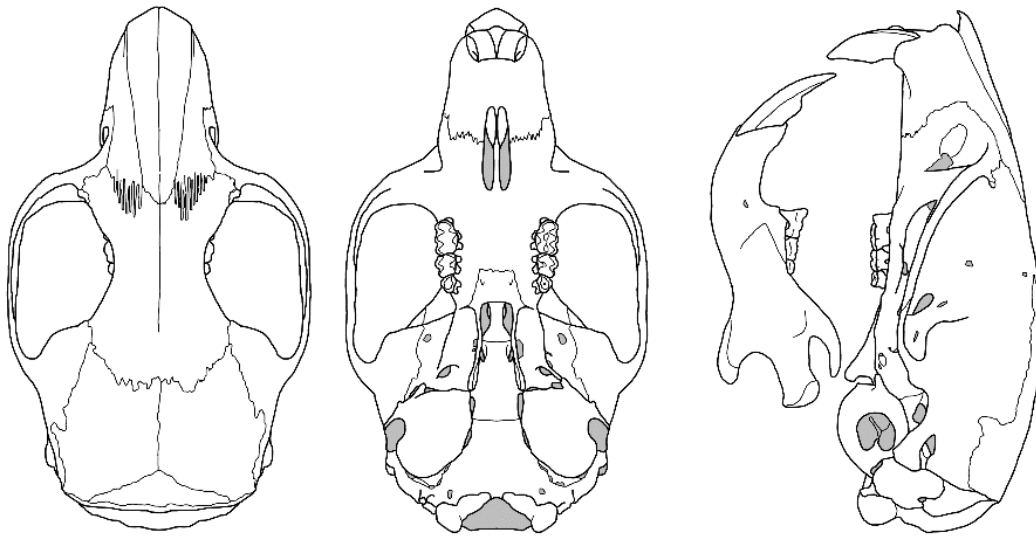
Allocricetulus eversmanni
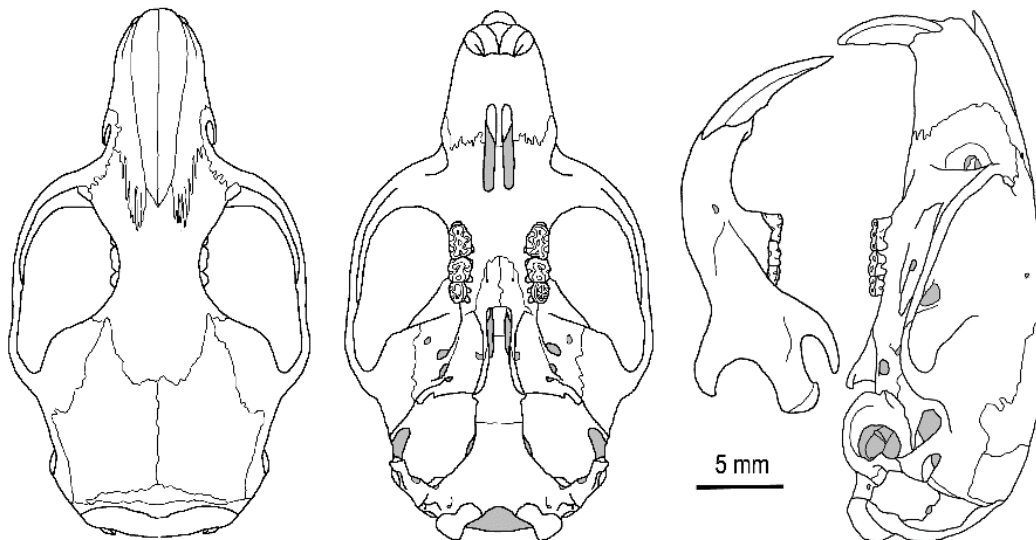
Figure 52: Skull and mandible in Eversmann's hamsters *Allocricetulus*: *A. eversmanni* (Volga Region, Russian Federation) and *A. curtatus* (Lake Orok-nor, Mongolia) in dorsal, lateral and ventral views.

heavier than the front ones. Plantar pads are small, particularly so the metatarsal pair and the interdigital pad III. Plants are hairy posterior to pads (Figure 33c). Fur is soft and fairly short, interspersed with numerous all-black hairs which usually protrude by 0.5–2 mm. The long protruding hairs are numerous at the tail base, producing a conical appearance (Figure 51); the tail, however, is sparsely hairy and with no real terminal tuft. The dorsum is uniformly brown to sandy-buff, belly is white and the demarcation is sharp.

Females have 8 nipples each (2 pairs of pectoral and 2 pairs of inguinal nipples). Glans penis is barrel-shaped and covered for the major part by furrows, ridges and

papillae; horny spines are restricted to the apex. The central and the 3 ventral papillae are prominent and visible from the outside (Vorontsov 1982). Baculum is ossified but tips of the trident remain cartilaginous (Figure 17f, g); distal trident is proportionally long (65–76% of the length of proximal shaft). Manubrium is expanded both laterally and ventrally, and can be notched basally; width across the lateral expansions of the shaft's base accounts for 72–94% of its length. The central digit of trident is usually shorter than the lateral ones (Vorontsov 1982, Ross 1992).

The skull is rather robust, though it lacks prominent bony ridges (Figure 52); zygomatic arches are rounded

and moderately expanded (zygomatic width accounts for 53–59% of condylobasal length), braincase is short and circular, rostrum is rather short and stout. Occipital condyles only slightly project beyond occiput and are therefore hardly seen in dorsal projection. The palate is proportionally long; the incisive foramina terminate well before reaching the level of M¹, and interpterygoid fossa does not extend to the level of M³; the pterygoid platform is below (i.e. dorsad to) the level of palate. Bullae are fairly small and rounded; the interparietal is wide but reduced in length. Anterior margin of masseteric plate is straight or emarginated; the infraorbital foramen, zygomatic notch and the keel of zygomatic plate are not visible in dorsal view; the zygomasseteric structure is of pseudo-sciuromophous type (Lebedev & Potapova 2008). In frontal view, the infraorbiral foramen resumes oval shape (Figure 20e). Some authors (Popov 1960, Ross 1992) cite a W-shaped coronal suture as diagnostic for *Allocricetulus*. Indeed, this suture frequently displays irregular anteriorly oriented projection at the anterior margin of interparietal, therefore giving the impression of the letter 'W'. Shape of coronal suture is, however, highly variable and the bulge is sometimes absent (Figure 53). Bullae are of moderate size. Mandible is long and shallow with well-developed processes; the coronoid process is prominent and extends back to the anterior margin of mandibular condyle; the blunt alveolar process is present on the outer wall of mandibular ramus at the level of *caput mandibulae* (Figure 54).
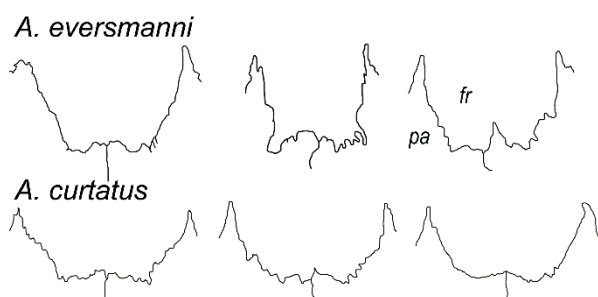
Figure 53: Variation in shape of coronal suture in *Allocricetulus eversmanni* (top) and *A. curtatus* (bottom). Abbreviations: *fr* – frontal bone, *pa* – parietal bone. Anterior is to the top; not to scale.

Upper incisors are orthodont and on the anterior side embedded in orange enamel. M¹, and frequently also M², have internal fold 2 (*if2*) isolated from primary fold 2 (*pf2*) by enamel ridge; the ridge, however, is shallow, hence the abrasion of its dentin is significantly

postponed relative to the lingual side of *if2* (Figures 57 & 60).
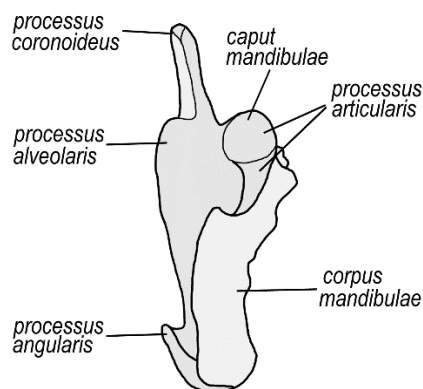
Figure 54: Caudal view of mandibulae of Mongolian Eversmann's hamster (*Allocricetulus curtatus*).

Key to species

1a) Dorsal fur usually brownish (Figure 56), ventral side usually with a sternal streak which is of same colour as the back[1] (Figure 51); glans penis is parallel-sided in dorsal view (width-to-length ratio = 0.63), without ventral medial groove; central *papilla ventralis* smaller than *papillae laterales*; *papilla lateralis* without lateral expansion; distal baculum with central digit obviously shorter than lateral digits (Figure 17f); interorbital width ≤ 4.9 mm; interparietal ≥ 4-times as wide as long; 2n = 26; present to the west of the 89th meridian in Russian Federation, Kazakhstan and northern Xingjian (China) …..…………………..…..…*eversmanni*

1b) Dorsal fur greyish-sandy (Figure 59), ventral side plain white (Figure 51); glans penis in dorsal view with rounded body and narrowed base and tip (width-to-length ratio = 0.80), ventrally with a shallow medial groove; central *papilla ventralis* approximately of same size as *papillae laterales*; *papilla lateralis* with lateral expansion (Γ-shaped); distal baculum with central digit nearly as long as lateral digits (Figure 17g); interorbital width ≥ 4.9 mm; interparietal < 4-times as wide as long; 2n = 20; present to the east of the 89th meridian in Mongolia, China (absent in northern Xingjian), and marginally in Russian Federation (Tyva) …………………………………....… *curtatus*

[1] Population from the eastern Zaysan Basin is of same colouration as *A. curtatus*

Allocricetulus eversmanni (Brandt, 1859) – Common Eversmann's hamster

Cricetus eversmanni Brandt, 1859: 210. Type locality ("in provincia Orenburgensi") was subsequently restricted to "Окресности г. Оренбурга к северу от города [Neighbourhood of Orenburg to the north of the city]", Russian Federation (Mitina 1959: 1870).

[Cr]icetulus eversmanni: Satunin, 1905: 340. Name combination.

[Cricetulus migratorius migratorius] eversmanni: Thomas, 1917: 453. Name combination and new status.

Mesocricetus eversmanni Ogneff, 1925: 13. Name combination.

Mesocricetus microdon Ogneff, 1925: 14. Type locality: "бл. Пономаревки Бугурусланского у Самарской губ" [near Ponomarevka, Buguruslanskiy uezd (Distict), Samara Governorate]", Russian Federation.

Cr[icetulus] ev[ersmanni] microdon: Kuznetsov, 1932: 94. Name combination.

Cr[icetulus] (Allocricetulus) eversmanni: Argyropulo, 1933b: 245. Name combination. For 1933 as the year of publication (instead of 1932) see the generic account above.

Cr[icetulus] (Allocricetulus) eversmanni microdon: Argyropulo, 1933b: 245. Name combination.

Cr[icetulus] (Allocricetulus) eversmanni beljaevi Argyropulo, 1933b: 245. Type locality: "Зайсан [Zaysan]", also spelled "Saissan" (*e. g.* Argyropulo, 1933c: 137, Ellerman 1941: 435). In the account on Nomenclature (below) we argue that Argyropulo's statement of the type locality is erroneous. The name *beljaevi* was based on the same type specimen as Selewin's *belajevi* (see below). Correct type locality is provided in Selewin (1934: 77): "Бассейн р. Токрау, б. Каркаралинского округа" (in the original Russian version) and "Wasserbecken des Flusses Tokrau des Bezirks von Karkaralinsk" (German text; Selewin 1934: 87), *i. e.* River Tokrau in the Karkaray (Karkaralinsk) District in the Karaganda (Qaraghandy) Region, Kazakhstan.

Cr[icetulus] (Allocricetulus) eversmanni beljavi: Argyropulo, 1933c: 137. Incorrect subsequent spelling of *beljaevi* Argyropulo. 1933b. Argyropulo (1933c) correctly spelled the name (as *beljaevi*) on p. 149 of the same work. See also comments below in the account on Taxonomy and nomenclature.

Cricetulus eversmanni belajevi Selewin, 1934: 77. For type locality ("Бассейн р. Токрау, б. Каркаралинского округа") and spelling see comments under *belajevi* Argyropulo, 1933b (above), and the account on Nomenclature below. The two names, *beljaevi* and *belajevi,* are based on the same voucher (ZIN 78702) and are therefore objective synonyms.

Allocricetulus eversmanni: Vinogradov& Argyropulo, 1941: 168. First use of the current name combination.

A[llocricetulus] e[versmanni] microdon: Vinogradov & Argyropulo, 1941: 169. Name combination.

A[llocricetulus] e[versmanni] beljaevi: Vinogradov & Argyropulo, 1941: 169. Name combination.

Cricetus (Allocricetus) eversmanni: Stroganova 1954: 63. Name combination.

Cricetulus eversmawni: Karaseva, 1963: 211. Incorrect subsequent spelling of *eversmanni* Brandt.

Allocricetulus eversmanni beljaevi pseudocurtatus Vorontsov & Krjukova, 1969a: 99. Type locality: "Восток Зайсанской котловины, пески Айгыр-Кум в 10 км к северу от с. Улькен-Каратал [eastern Zaysan Basin, Aygyr-Kum sands, 10 km north form the village Ul'ken-Karatal]", eastern Kazakhstan. Invalid as infrasubspecific taxon (natio); validated in Kartavtseva & Vorontsov (1992; see below).

C[ricetulus] e[versmanni] beljewi Zhang et al. 1997: 215. Incorrect subsequent spelling of *beljaevi* Argyropulo.

All[ocricetulus] ev[ersmanni] pseudocurtatus Kartavtseva & Vorontsov 1992: 10. Type locality not specified, however, the only karyotyped individual was from "Agir Kum sands in the east Zaissan hollow (the North-West of the Zungaris [typographic error for Dzungaria])". First appropriate naming of *pseudocurtatus* Vorontsov & Krjukova.

Etymology. The species epithet is eponym to Russian physician and naturalist of German ethnicity Alexander Eduard Friedrich Eversmann (1794–1860). Eversmann was the first to describe *A. eversmanni* (as *Cricetulus phaeus*). Brandt based his 1859 description on vouchers collected and reported by Eversmann (1850).

Nomenclature. Baranova & Gromov (2003: 48) designated lectotype of *A. eversmanni* (voucher ZIN 4578; Eversmann's collection No. 2998), which reportedly originates from "Караульная гора, Оренбург [Mt. Karaul'naya gora, Orenburg]". This locality cannot be precisely located because during the
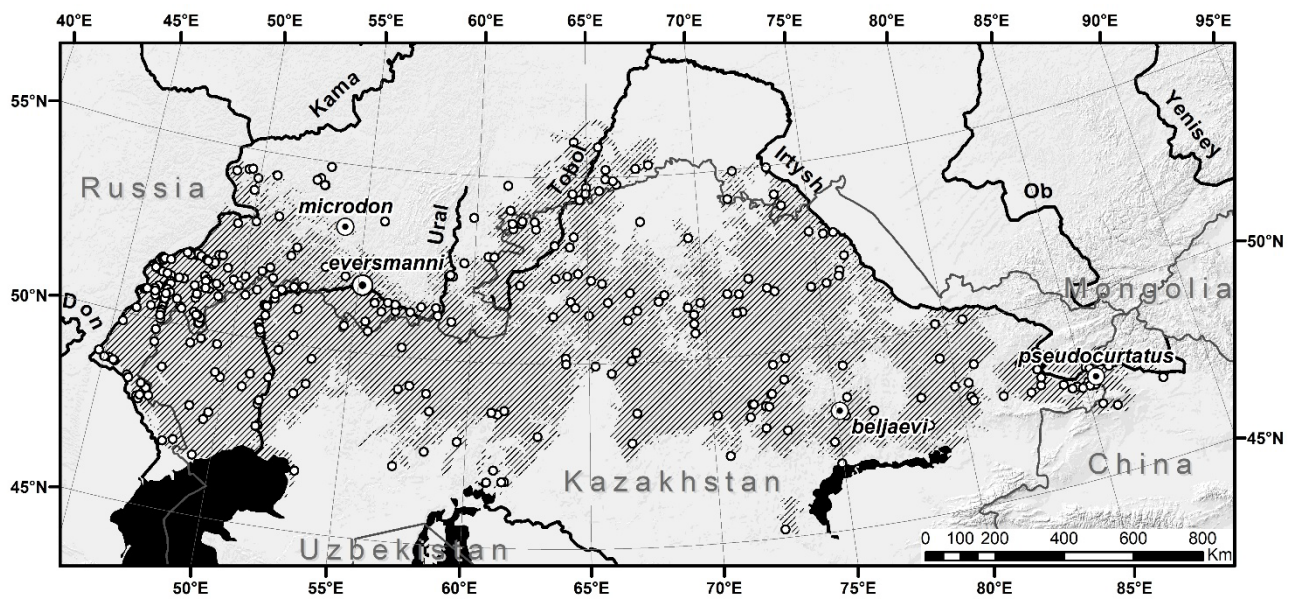
Figure 55: Distributional range of the common Eversmann's hamster *Allocricetulus eversmanni.*

18th and early 19th centuries, the toponym Karaul'naya gora was frequently used around Orenburg for any hill or flat-top mountain. Eversmann (1850: 147) stated for his vouchers that they originated from the vicinity of Orenburg. This is also inscribed in the original label of the lectotype (Baranova & Gromov 2003: 48) and was reported already by Brandt (1859: 210).

Type locality of *A. eversmanni* was frequently reported as "Киргизская степь (Казахстан) [Kyrgyz Steppe, Kazakhstan]" (Argyropulo 1933b, 1936), "Kirgisensteppe" (Argyropulo 1933c), "степь сев. Казахстана [steppes of northern Kazakhstan]" (Kuznetzov 1944: 322), "Northern Kazakhstan Steppes" (Ellerman & Morrison-Scott 1951: 626), and "Khirgis Steppe" (Ross 1992: 257). "Kyrghiz" ("Kirghiz") is an old Russian word for the Kazakh Steppe which currently defines a vast grassland in northern Kazakhstan and adjacent Russia; Orenburg is situated on the north-western edge of the region.

In the English abstract of her paper, Mitina (1959: 1875) restricted the type locality to "environs of the town of Samara". This contradicts her conclusion in the main Russian text and is obviously due to an error.

There is a great deal of confusion around the names *beljaevi, beljawi* and *belajevi*. All these names are eponyms for A. M. Beljaev hence the correct spelling is *beljaevi*. This is how the name was firstly published by Argyropulo (1933b) and used shortly afterward by Beljaev (1933: 36) himself; see also Argyropulo (1936:

120) and Mitina (1959: 1872). In German edition of Argyropulo's paper (1933c), the name was incorrectly spelled *beljawi*. It therefore happened that the misprinted name *beljawi* entered the mainstream literature while the name *beljaevi* was erroneously attributed to Kuznetzov (1944) (*cf.* Ellerman & Morrison-Scott 1951: 626, Musser & Carlton 2005: 1040). The correct spelling is *beljaevi* as published in Argyropulo (1933b) and not in Kuzyakin (1944), while *beljawi* is an incorrect subsequent spelling of *beljaevi,* which was erroneously introduced by Argyropulo (1933c).

Relations between *beljaevi* Argyropulo and *belajevi* Selewin have never been properly resolved. Pavlinov & Rossolimo (1987: 170) claim that *beljaevi* Argyropulo and *belajevi* Selewin are based on different types, each with its own type locality: Zaysan for *beljaevi* and Tokrau for *belajevi*. Hence, Pavlinov & Rossolimo did not consider these names to be homonyms "although they represent different Latin transliterations of the same family name [Beljaev]". We disagree with this interpretation. Firstly, Argyropulo (1933b, c) did not designate the type or the type locality for *beljaevi*. He claimed, however, that his research was conducted "in the Zoological Institute of the USSR Academy of Sciences (ZIN), using its collections" (our translation from Russian; Argyropulo 1933b: 239). Pavlinov & Rossolimo (1987: 170) concluded, presumably on this ground, that the type of *beljaevi* is kept in ZIN. Their presumption, however, was categorically rejected by Baranova & Gromov (2003: 48) who further showed

that in the early 1930s ZIN was not in possession of a single voucher of *A. eversmanni* collected in Zaysan. With *A. e. beljaevi*, Beljaev (1933: 36) referred to "Agr. [obviously a misspelled abbreviation of Argyropulo] in litt [*in litteris*]", therefore he evidently received the information on a new taxon from Argyropulo, while the publication was still in press. More importantly, Beljaev was aware of a single locality for *beljaevi*, *i.e.* "б. Каркаралинский у." (former Karkaralinskiy region). Noteworthy, Karkaralinsky is the type locality for *belajevi* in Selewin (1934), who further identified Beljaev as the collector of the type specimen. Selewin's type was obtained on 21 August 1928 and is indeed deposited in ZIN (Baranova & Gromov *l. c.*). We therefore conclude that both, Argyropulo and Selewin, based their names on the same voucher which makes *belajevi* Selewin, 1934, an objective synonym of *beljaevi* Argyropulo, 1933. Beljaev (1933) reported *A. eversmanni* for Central and Western Kazakhstan, and for Karkaralinsk, but not for Zaysan.

Distribution. Endemic to southern Russia in Europe and Asia, northern and central Kazakhstan and northern China in Xingjian (Figure 55). The distribution area is estimated at 1,401,017 km². The western and eastern borders are set sharply by the rivers Volga and Irtysh, respectively. The southern border tentatively follows the northern shore of the Caspian Sea – northern Aral – central Betpak-Dala Desert – Lake Balkhash; the southernmost record is from the Baykara Mt. (Jambyl Province, Kazakhstan), while all the remaining localities lay to the north of the 46th parallel. In China, the common Eversmann's hamster is restricted to northern Xingjian, where known from the counties of Fuhai, Habahe, and Hoboksar. The northern border is in southern European Russia and southern Siberia. All the northward expansions tentatively follow the major rivers reaching the provinces of north-eastern Ulyanovsk, southern Tatarstan, and southern Bashkortostan (along the Volga), Omsk and Kurgan (along the Tobol), and the Omsk Province (along the Irtysh). The range segment in eastern Zaysan and adjacent Xingjian is presumably an isolate.

During the Late Pleistocene, *A. eversmanni* expanded its range westward across the Lower Don River into Romania and Moldova (Kowalski 2001) and endured there into the Neolithic and Chalcolithic (Lozan 1971). Since 1950, a decline was reported from European Russia (Oparin 2005) and at present the species is of conservation concern in 7 administrative districts of the Russian Federation: Bashkhortostan, Tatarstan, Astrakhan, Kurgan, Samara, Ulyanovsk, Chelyabinsk (Vakhrushev & Sidorov 2011); all districts except Kurgan are from the European part of the Federation.

The common Eversmann's hamster prefers semidesert and dry steppic habitats at low elevations; the range is between –26 m and 2,020 m (mean = 198 m). Specimens were recorded in various types of virgin steppe, a fallow and cultivated land, and *Artemisia* thickets; they thrive also on fixed sands and saline soils, providing there is some vegetation cover available (Modorov & Polyakov 2021). This hamster penetrates into the forest steppe however avoids humid environments (margins of woodland belts and depressions). The abundance is significantly higher in grain fields as opposed to pristine steppe (Danini & Olschwang 1936, Oparin 2005). Occasionally, common Eversmann's hamsters enter buildings (Afanasiev 1953, Afanasiev 1960, Shubin 1977d, Shlyakhtin et al. 2009, Shenbrot 2017f).

Characteristics. Dimensions: body mass = 61–93.5 g, length of head and body = 136–151 mm, length of tail =18–29 mm, length of hind foot = 15–21 mm, length of ear = 13–18 mm, condylobasal length of skull = 27.4–33.6 mm, zygomatic width = 15.3–19.8 mm, maxillary tooth-row length = 4.0–4.7 mm (Afanasyev 1953, Popov 1960, Shubin 1977d); tail is short and accounts for 17–22% of head and body length (mean = 19%; Danini & Olschwang 1936). Fur is short (length = 5.5–6.5 mm) and velvety; scarce black-tipped hairs protrude by approximately 2 mm and become more abundant on the rump and around the base of the tail. Vibrissae measure 33–35.5 mm. Colour is polymorphic (Vorontsov & Krjukova 1969a) and varies from buffy brown to grey-shaded pinkish buff or cinnamon buff.

Underside (lips, chin, lower side of mystacial pads, and feet) is white with slate hair bases; short hairs on the chin are white to bases. Belly is occasionally dirty-white, cream-grey, or light grey. Demarcation line is sharp and straight posterior to the arms; on the head, the white

Figure 56: *Allocricetulus eversmanni eversmanni* from Saratov, European Russia. Photo courtesy of M. Kabanov

underside forms re-entrants below the ear and on the posterior edge of mystacial pad (Figure 56). Brown dorsal pelage extends down the forearm to the wrist and is contiguous with the sternal streak between the forelegs (Figure 51). The streak is up to 3–4 cm long but is frequently shorter; it is entirely absent in the east. Rarely, the streak is medially split into two by white hair. Dorsal side of the tail, which is of same colour as the back, is frequently interspersed by more numerous all-black hairs; underside is white. Ears are grey and darkened towards their tip, with a post-auricular tuft of whitish or buff hairs. Juveniles are duller than adults.

Glans penis is parallel-sided. It is narrower than in *A. curtatus* and also lacks a shallow medial groove on its ventral side. The central *papilla ventralis* is smaller than *papillae laterales*; the lateral ones are not expanded terminally. Shaft of the baculum is wider than in *A. curtatus*; greatest width > 80% of shaft's length as opposed to < 80% in *A. curtatus*; the central digit of the distal baculum accounts for ¾ of the length of lateral digit (*c.* 90% in *A. curtatus*) (Argyropulo 1933c, Vorontsov 1982, Ross 1992).

In comparison to *A. curtatus*, the skull of *A. eversmanni* has narrower rostrum and palate, more constricted interorbital region (mean width = 4.63 mm), smaller bullae (average length × width = 5.2 × 5.8 mm), less expanded zygomatic arches, longer orbit, neurocranium, molars, incisive foramina, and diastema, and broader incisors (Figure 52). Interparietal is

comparatively shorter and longer (≥ 4-times as wide as long) (Allen 1940, Ross 1992, Gureeva et al. 2020). Molars show no peculiarities (Figure 57).

Karyotype: 2n=26, NF=38–40; 4 autosomal pairs are metacentric of different sizes, 5–6 pairs are submetacentric or subtelocentric, and 2–3 pairs are acrocentric. Sex chromosomes are subtelo-, submeta- or metacentric; depending on the subspecies, they are either isomorphic or heteromorphic (Kartavtseva & Vorontsov 1992, Kartavtseva & Surov 2005).

Variation and subspecies. Over the past century, the number of subspecies recognised in *A. eversmanni* varied between 2 (*eversmanni* and *beljaevi*; Kuznetsov 1965, Mitina 1959, Afanasiev 1960, Gromov et al. 1963, Corbet 1978, Shenbrot 2017f) and 3 (*microdon, eversmanni* and *beljaevi*; Beljaev 1933, Argyropulo 1941a, Ellerman 1941, Vinogradov & Argyropulo 1941, Kuznetsov 1944, Ellerman & Morrison-Scott 1951, Vinogradov & Gromov 1952, Vorontsov & Krjukova 1969a, Vorontsov 1982). Some of these authors ranked *curtatus* as the palest and the easternmost subspecies of *A. eversmanni*. Ross (1992), on the *other* hand, recognized no subspecies.

Subspecies were defined according to fur coloration; *microdon* is the darkest, *beljaevi* the palest, and the nominotypical subspecies is intermediate. The darkest individuals have the most distinct sternal streak between the forelegs, gradually fading in pale hamsters.
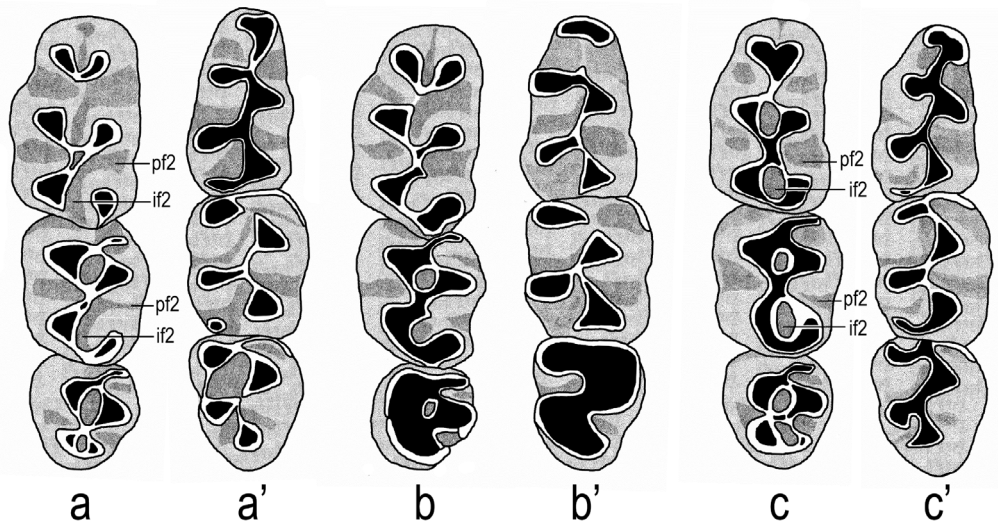
Figure 57: Grinding pattern of upper (a, b, c) and lower (a', b', c') molars in Common Eversmann's hamster *Allocricetulus eversmanni*. a, b – Ural River, Kazakhstan, c – eastern Zaysan Basin, Kazakhstan. if2 – internal fold 2, pf2 – primary fold 2. Scale bar = 1 mm.

The most detailed subspecific classification was provided by Mitina (1959). She distinguished 2 subspecies, the darker nominotypical which was mapped for northern steppes on black soils (chernozem) and the paler *beljaevi* from southern dry steppes and semideserts. Vorontsov (1982) concluded that colour is adaptive and depends on a small-scale steppe–desert mosaic; despite this, he still recognized 3 subspecies, claiming that differences between them are clearly seen in series. Lebedev (2012) stressed, however, that subspecific taxonomy does not correspond to the observed pattern of phylogeographic variation.

The most divergent lineage of *A. eversmanni* occupies the extreme eastern portion of the species' range in the Zaysan Basin (eastern Kazakhstan), displaying a confusing mixture of the *curtatus*-type external morphology (greyish-buff dorsal pelage and no sternal strike) and the *eversmanni*-type of karyotype (Vorontsov & Krjukova 1969a). This population is frequently referred to as *pseudocurtatus* and does not include *beljaevi*. The Zaysan hamsters were at first diagnosed by karyotype (Kartavtseva & Vorontsov 1992) and subsequently by mitochondrial markers (Gureeva 2022). Based on molecular clock, Gureeva (2022) estimated divergence between the Zaysan hamsters from the remaining *A. eversmanni* at 102 kya (CI = 50–212 kya), which postdates the divergence between *A. eversmanni* and *A. curtatus* (~ 120 kya) for merely 18 ka; pairwise genetic (K2P) distances are 2.0 (Zaysan–*eversmanni s. str.*) and 2.3 (Zaysan–*curtatus*).

Allocricetulus eversmanni eversmanni (Brandt, 1859)

Synonym: *Mesocricetus microdon* Ogneff, 1925 (Mitina 1959); *Cr[icetulus] (Allocricetulus) eversmanni beljaevi* Argyropulo, 1933.

Taxonomy. The nominal subspecies is further sub-structured in 3 phylogeographic lineages, which supposedly separated 67–79 kya (CI = 28–142 kya). One lineage is widespread and further 2 lineages are restricted to northern Kazakhstan and south-eastern Kazakhstan, respectively. The most distinct lineage occupies western East Kazakhstan and eastern Qaraghandy. Denser sampling is needed, however, to properly understand the geographic scope of these lineages (Gureeva 2022).

Distribution. The entire range of the species except for Zaysan Depression in eastern Kazakhstan and the north-western part of Dzungarian Basin in China.

Characteristics. Autosomes: 5 pairs are telocentric + 3 pairs are acrocentric elements (in addition to 4 pairs of metacentrics). Sex chromosomes are isomorphic and submetacentric; fundamental number of chromosomal arms NF = 40 (Kartavtseva & Vorontsov 1992, Kartavtseva & Surov 2005). Fur colouration is highly variable; the sternal streak is present though occasionally inconspicuous and sometimes split medially into 2. The overall skull shape is on average

more similar to *A. curtatus* than is *A. e. pseudocurtatus* (Gureeva et al. 2020).

The darkest hamsters, which were occasionally classified in the past as a subspecies *microdon*, occur between the Volga and Ural Rivers and in the Ural Mts. Dorsal fur is tawny-olive, hairs have long dark terminal band, and the sternal streak is distinct and long; ventral hairs have long and dull grey basal band. Hamsters occupying the black soils eastward of the Ural Mts. and northward of the 55th parallel have bright sayal-brown back, a comparatively long dark bands on dorsal hairs and distinct sternal streak, which is in some individuals medially split into 2. These animals were classified as the nominotypical subspecies and were occasionally referred to as of intermediate colouration. The transition between the darkest and the intermediate populations was reported for the Orenburg region (south European Russia; Kuznetsov 1932). Hamsters living to the south of the 55th parallel are the lightest and were in the past usually classified as subspecies *beljaevi*. They are dorsally light fawn grey to wood-brown, with distinct buffy and grey tint; dorsal hairs have short dark terminal bands. The sternal streak is inconspicuously light-fawn, and frequently split in 2. Ventral hairs have the shortest and palest grey basal band (Kuznetsov 1932, Mitina 1959, Vorontsov & Krjukova 1969a). The palest hamsters occupy sands of Aral (Mitina 1959). Transition between the intermediate and pale hamsters was reported from Naruzum and Semiozernoe in the Qostanay Region (north Kazakhstan; Mitina 1959).

There is little morphological variation among populations besides colouration. In Kazakhstan, hamsters living in the south display larger size and more pronounced secondary sex dimorphism (Shubin 1977d).

Allocricetulus eversmanni pseudocurtatus Kartavtseva & Vorontsov, 1992

Etymology. The name is composed of 'pseudos' (Greek for 'false') and *curtatus*, which is the species epithet for Mongolian Eversmann's hamster. The name (false Mongolian Eversmann's hamster) is allusion to a combination of the external appearance of *Allocricetulus curtatus* and the karyotype of *A. eversmanni*.

Taxonomy. The majority of authors followed Mitina (1959) and labelled all pale *A. eversmanni* occurring to the south of the 55th parallel as *beljaevi*. More rarely was *beljaevi* restricted to Zaysan (Kuznetzov 1944, Vinogradov & Gromov 1952, Afanasiev 1953, 1960). The Zaysan population was also named *pseudocurtatus* (Kartavtseva & Surov 2005, Romanenko et al. 2013, Gureeva 2022) or was treated as transitional between *A. e. eversmanni* and *A. e. curtatus* (Kuznetsov 1932). The entire isolate in Zaysan shows footprints of mitochondrial introgression from two phylogenetic lineages of *A. eversmanni s. str.* occupying Kazakhstan.

Distribution. Restricted to the Zaysan Basin in eastern Kazakhstan and north-western China.

Characteristics. Autosomes: 6 pairs are telocentric + 2 pairs are acrocentric (in addition to 4 pairs of metacentrics). Sex chromosomes are heteromorphic; the Y chromosome is submeta- or subtelocentric and is smaller than the meta- or submetacentric X chromosome; fundamental number of chromosomal arms NF = 38 (Kartavtseva & Vorontsov 1992, Kartavtseva & Surov 2005). Colouration is as in pale individuals of the nominal subspecies. Dorsal side is pinkish cinnamon to cinnamon buff with admixture of grey; dorsal hairs have short dark terminal band. The sternal streak is inconspicuous light-fawn and frequently split in 2; hamsters occupying Aygyr-Kum and the Dala sandy desert (eastern Zaysan Basin) have no sternal stripe and are externally indistinguishable from *A. curtatus* (Vorontsov & Krjukova 1969a). Ventral hairs have short pale-grey basal band.

Allocricetulus curtatus (Allen, 1925) – Mongolian Eversmann's hamster

Cricetulus migratorius curtatus G. Allen, 1925: 3. Type locality: "Iren Dabasu [Ehrlien], Mongolia"; subsequently emended to "Inner Mongolia" (Allen 1940: 764), China.

Cricetulus curtatus: Formozov, 1929: 50. Name combination and rank change.

Cr[icetulus] ev[ersmanni] curtatus: Kuznetsov, 1932: 95. Name combination.

Cr[icetulus] (Allocricetulus) curtatus: Argyropulo, 1933b: 245. Name combination.

A[llocricetulus] curtatus: Vinogradov & Argyropulo, 1941: 169. First use of the current name combination.

Etymology. Species name *curtatus* (masculine) is Latin for 'short-tailed', in allusion to the short tail of the species. While naming this taxon, Allen believed that *A. curtatus* is a subspecies of *Nothocricetulus migratorius* with apparently shorter tail.

Taxonomy. Originally described as a subspecies of *Nothocricetulus migratorius* (Allen 1925); subsequently classified as a subspecies of *A. eversmanni* (Allen 1940, Kuzntzov 1944, Mitina 1959, Kuznetsov 1932, 1965, Ellerman & Morrison-Scott 1951, Ma et al. 1987, Zhang et al. 1997, Luo et al. 2000) or a species in its own right (Argyropulo 1933b, c, Ellerman 1941, Vinogradov & Argyropulo 1941, Flint 1966b, Stubbe & Chotolchu 1968, Corbet 1978, Corbet & Hill 1980, 1986, Gromov & Erbajeva 1995, Musser & Carleton 1993, Pavlinov & Rossolimo 1987, Wang 2003, Musser & Carleton 2005, Lebedev et al. 2016, Shenbrot 2017g). For further details, see the account on Taxonomy and nomenclature under *A. eversmanni* (above).

Distribution. The entire range covers 766 thousand km². The core distribution covers Mongolia and central Nei Mongol (China), reaching the southernmost Tuva (Tyva; Russian Federation) in the north and northern China in the south: eastern Gansu, Ningxia, eastern Xinjiang (as far west as Yiwu and Mori), and marginally Hebei. Several Chinese records transgress the Ordos loop and occur on the right bank of the Huang He River (Figure 58). Mongolian range, which closely coincides with the biome of desert and xeric shrubland (Olson et al. 2001), extends from the Uvs Nuur Basin in the north-west further southward and eastward. In its western part, the range is squeezed between the Khangai Mts. from the north, Mongol Altai from the west, and Gobi Altai from the south. Further east, the northern range border is set by temperate grasslands reaching the western Sühbaatar Province. Mongolian hamster occupies gravel semideserts, saline soils and fixed sands with geophytes, cereals, halophytes, shrubland and cereal cultivations (Bannikov 1954, Chugunov 1962, Sokolov & Orlov 1980, Fu et al. 2005). Elevational range is 750–2,455 (mean = 1,330 m).

Characteristics. Slightly smaller than *A. eversmanni* but of identical body proportions (Figures 51 & 59).
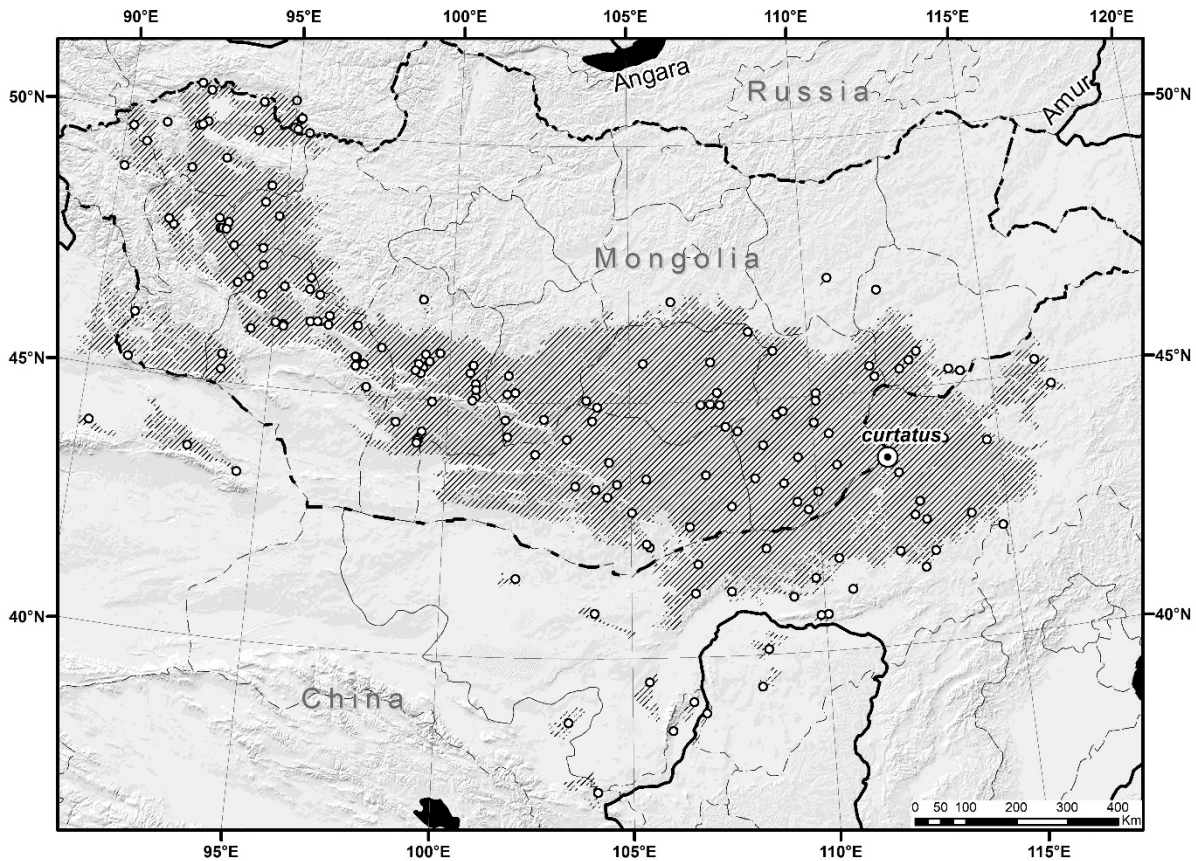
Figure 58: Distributional range of the Mongolian Eversmann's hamster *Allocricetulus curtatus.*

Figure 59: Mongolian Evresmann's hamster *Allocricetulus curtatus* from Republic of Tyva, Russian Federation. Photo courtesy of M. Kabanov

Dimensions: body mass = 35–70 g, length of head and body = 112–146 mm, length of tail = 14–27 mm, length of hind foot = 14–20 mm, length of ear = 13–19 mm, condylobasal length of skull = 26.6–31.6 mm, zygomatic width = 15.0–19.0 mm, maxillary tooth-row length = 4.0–4.9 mm (Bannikov 1954, Luo et al. 2000); tail accounts for 14–22% of head and body length (mean = 19%). Fur is softer and longer than in *A. eversmanni* (length = 7–10.5 mm); scarce black-tipped hairs protrude for ~ 1–3.5 mm. Vibrissae measure up to 27–37 mm. Tail is densely haired; hairs at its base are longer and produce a rather conical appearance (Figure 51); terminal pencil is ~ 3.5 mm long. Dorsal fur is pale buff to cinnamon buff and evenly lined with black-tipped hairs; some individuals show brown streak across shoulders posterior to the cheek-pouch. Underside (lips, chin, the lower portion of mystacial pads, and feet) is white with slate-grey bases; hairs on the chin, throat and sometimes between the fore legs are white to bases. Demarcation is less sharp than in *A. eversmanni*. Sternal streak is absent in the great majority of animals; occasionally, light-fulvous to rusty hairs, or more extensive grey hair bases form a just noticeable patch on the throat. Tail is white all-round, sometimes with darker medial stripe; feet are white. Ears are of same shade as the back and thinly clad by short whitish and dusky brown hairs; there is an extensive post-auricular tuft of whitish hairs. Juveniles are greyish-brown.

When viewed from above, the glans penis is barrel-shaped; it is comparatively wider than in *A. eversmanni* and has a shallow medial groove. *Papillae ventrales* are of approximately same size; the 2 *papillae laterales* have lateral expansion that gives a Γ-shaped appearance. Shaft of the baculum is less expanded than in *A. eversmanni*; the greatest width < 80% of shaft's length; the central digit of distal baculum accounts for approximately 90% of length of lateral digits (Argyropulo 1933c, Vorontsov 1982, Ross 1992).

Figure 60: Grinding pattern of upper (a) and lower (a') molars in Mongolian Eversmann's hamster *Allocricetulus curtatus* from Mongolia. *if*2 – internal fold 2, *pf*2 – primary fold 2. Scale bar = 1 mm.

The skull (Figure 52) has more massive rostrum and wider palate than in *A. eversmanni*; the interorbital region is wider (mean width = 5.05 mm), and zygomatic arches are more expanded; bullae are more swollen (average length × width = 5.56 × 6.19 mm), the orb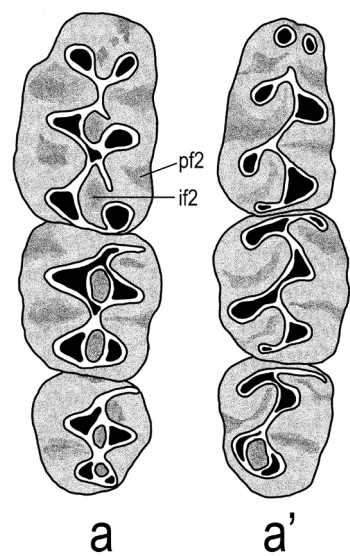it, neurocranium, molars, incisive foramina, and diastema are shorter, and incisors are narrower. Interparietal is comparatively shorter (< 4-times as wide as long) (Ross 1992, Gureeva et al. 2020). Molar pattern shows no peculiarities (Figure 60).

Karyotype: 2n=20, NF=38; 5 autosomal pairs are metacentric of different sizes, 3 pairs are submetacentric and subtelocentric, and 1 pair is acrocentric. Sex chromosomes are medium sized submetacentrics, which are heteromorphic with respect to the position of the centromere (Orlov et al. 1978).

Variation and subspecies. Phylogenetic analysis based on *mt* markers retrieved 2 weakly divergent (divergence ≈ 1%) allopatric lineages with a contact at the Valley of the Lakes and the Gobi Altai Mts. (Gureeva 2022). Mongolian Eversmann's hamsters tend to be paler along the southern distribution edge (Chugunov 1962). Despite all this, the species is classified as being monotypic (Shenbrot 2017g).

GENUS: *Cricetus* Leske, 1779 – Common Hamsters

Cricetus Zimmermann, 1777: 343. Not used as Linnean binominal, hence invalid (Nehring 1898c: 493, Palmer 1904: 203, Kryštufek et al. 2020: 10).

Cricetus Leske, 1779: 168. Type species is *Mus cricetus* Linnaeus, 1758, by tautonomy.

Hamster Lacépède, 1799: 10. Type species is *Hamster nigricans* Lacépède, 1799, by monotypy.

Heliomys Gray, 1873: 417. Type species is *Heliomys jeudei* Gray, 1873 (= *Mus cricetus* Linnaeus, 1758), by monotypy.

Hellomys: Shubin, 1977c: 249. Incorrect subsequent spelling of *Heliomys* Gray.

Taxonomy. The common hamster of Germany was named (as 'Cricetus' or 'hamester Germanicae') and briefly described already by Albertus Magnus (*c.* 1200–1280) in his 2nd treatise on quadrupeds (pp. 1374–1375 in Stadler 1920) and was frequently referred to by the pre-Linnean authors, including Gesner (1602), Topsel (1658) and Ray (1693) (reviewed in Buhle 1821). Leske (1779) established the genus *Cricetus* for 3 rodents which possess internal pouches: *Mus cricetus* of Linnaeus and 2 ground squirrels (*Spermophilus* and *Marmota*). At about same time, Zimmermann (1777) used the name *Cricetus* exclusively for the common hamster, although not as a binomial name. Towards the end of the 18th century, *Cricetus* was usually understood to contain true hamsters (current Cricetinae), *i. e.* the Linnean *cricetus* and taxa named by Pallas (1773, 1779), which are now in *Cricetulus, Nothocricetulus*, and *Cricetiscus*. Rodents other than hamsters were exceptionally also classified as *Cricetus*, *e. g. Chinchilla* (Geoffroy 1803) and *Hesperomys s. lat.* (Flower & Lyddeker 1891, Thomas 1888). On the other hand, a broad definition of *Cricetus* (with the inclusion of *Cricetulus s. lat.* and *Mesocricetus* as subgenera) still prevailed at the start of the 20th century (*e. g.* Winge 1887, Trouessart 1904). Following the generic segregation of *Cricetulus* and *Mesocricetus* (Satunin 1900, Trouessart 1910, Miller 1912), *Cricetus* was nearly universally understood as a monospecific taxon (Vinogradov 1933b, c, Ellerman 1941, Kuznetzov 1944, Vorontsov 1958, and subsequent authors). The only noteworthy deviation was the incorporation into *Cricetus* of *Mesocricetus* (Argyropulo 1933b, c, 1941a, Kuznetsov 1965), or *Allocricetulus* (Stroganova 1954, Popov 1960) or of both (Vinogradov & Gromov 1952, 1956).

Although the external (Figure 61) and cranial morphology (Figure 67) clearly separates *Cricetus* from other hamsters, it obscures its phylogenetic position within Cricetinae. Different phylogenetic reconstructions therefore yielded conflicting results on intergeneric relationships (*cf.* Figure 1). Two of these attempts (Ross 1992, Potapova 2005) suggested close proximity of *Cricetus* with *Mesocricetus*. This view was already suggested by Argyropulo (1933b, c) who stressed a colourful pelage and a ridged skull in both genera. Fahlbusch (1969) speculated that *Cricetus* diverged from *Cricetulus + Phodopus* lineage during the Miocene. Chromosomal (Romanenko et al. 2007) and molecular evidence (Lebedev et al. 2018a, Ding et al. 2020), however, safely placed *Cricetus* inside Cricetina, as is defined here, and close to *Allocricetulus*. For comparison between *Allocricetulus* and *Cricetus,* see generic account of the former.

The extant common hamster populations are uniformly classified as monospecific. In the past, *Cricetus* was only exceptionally split taxonomically; *e. g.* Matschie (1901) recognized 4 allopatric species (*cricetus, canescens, rufescens, nehringi*). Taxonomic scope of fossil hamsters is more ambiguous on both the generic and the species levels. *Cricetus* is hypothesized to originate anywhere between the middle Miocene and early Pleistocene, and the extant *C. cricetus* supposedly evolved between the late Pliocene–early Pleistocene and the late Pleistocene,

depending on the authority (reviewed in Kryštufek et al. 2020).

Etymology. The name *Cricetus* was used as early as in the 13th century by Albertus Magnus (Weissenborn 1839). It originates from Italian 'criceto' for hamster (Palmer 1904) and presumably originates from Greek κριξω meaning 'I scream' (Weissenborn *l. c.*). Ross (1992: 287) suggested that *Cricetus* "was probably derived from the Illyrian 'skrzeczieck' (Gesner 1602),

Figure 61: Common hamster *Cricetus cricetus* from Austria. Photo courtesy of Frank Zachos

and refers to the cheek-pouches which characterize the hamsters." The tag 'Illyrian', although frequently quoted in the pre-Linaean literature (*cf.* Topsel 1658), is perhaps misleading in this context (Kryštufek & Pozdnyakov 2018: 217). 'Skrzeczieck', however, is undoubtedly of Slavic origin being in use, historically, currently, or both, in Polish (Skreczecz, Skrezéczek), Czech (Sskrecek, Skřeček, Křeček, Křeč) and Slovak (Skrečok, Škrček, Skreček, and Škrečok). Its derivatives 'křeček', 'hrček', 'hârciogul' etc. predominate in 5 linguistic groups in the Pannonian and Carpathian Basins of Central Europe and are presumably onomatopoeia, imitating the hamster's vocalization 'khr' and 'gr' (Kryštufek & Pozdnyakov 2018). Nehring (1898c) explained *Cricetus* as "a medieval Latinization of the vulgar name Krietsch".

Cricetus cricetus (Linnaeus, 1758) – Common Hamster

[Mus] cricetus Linnaeus, 1758: 60. Type locality "Germania [Germany]", with reference to Ray (1693: 221) and Gesner (1602: 738). Type locality was restricted to "Thüringen [Thuringia]" (Thomas 1911: 147), following Ray (*l. c.*) who reported *C. cricetus* for "Turingia & Miſnia [Miśnia = Miessen, Saxony]".

Glis cricetus: Erxleben 1777: 363. Name combination

M[us] Cricetus germanicus Kerr, 1792: 243. Type locality "Germany."

M[us] Cricetus german[icus] niger Kerr, 1792: 243. Type locality "Siberia, the south of Russia, Poland, Sclavonia, Hungary, Silesia, Bohemia, and Germany beyond the Rhine, especially in Thuringia."

Mus Cricetus niger Schreber, 1792: Plate CXCVIII B. Without type locality. Homonym of *niger* Kerr, 1792, however, we could not ascertain which of these names holds priority.

Hamster nigricans Lacépède, 1799: 10. Type locality unknown; stated as "Germany" by Ellerman and Morrison-Scott (1951: 628).

Cricetus Germanicus: Leske, 1779: 506. Name combination.

Cricetus german[icus] niger: Leske, 1779: 506. Name combination.

M[us] C[ricetus] variegatus Bechstein, 1801: 1009. Type locality is "in Thüringen, so wie im Uralischen Gebiete [= in Thuringia (Germany), as well as in the area of the Ural Mts. (Russian Federation)]."

M[us] C[ricetus] albus Bechstein, 1801: 1009–1010. Type locality is "in Thüringen, so wie im Uralischen Gebiete [=in Thuringia (Germany), as well as in the area of the Ural Mts. (Russian Federation)]."

M[us] C[ricetus] fulvus Bechstein, 1801: 1010. Type locality is "Thuringia", Germany.

Cricetus vulgaris Geoffroy, 1803: 196. Type locality is "L'Europe septentrionale et orientale [= northern and eastern Europe]."

Cricetus frumentarius Pallas, 1811: 161. New name for *Mus cricetus* Linnaeus, 1758 (Miller 1912: 602), presumably to avoid tautonymous combination *Cricetus cricetus* (Kryštufek et al. 2020: 11).

Cricetus fuscatus Brandt, 1835: 435. Not 1832 (Ross 1992: 291). Geographic origin not known. A member of *Cricetus* (*cf.* Trouessart 1910: 160), though regarded as unidentifiable by Ellerman & Morrison-Scott (1951: 625) and Pavlinov & Rossolimo (1987: 174).

[Cricetus vulgaris] varius Fitzinger, 1867: 98. Type locality is "Eur. Österreich, Böhmen, Mähren, Ungarn, Deutschland [Europe. Austria, Bohemia, Moravia, Hungary, Germany]."

[Cricetus vulgaris] albus Fitzinger, 1867: 98. Type locality is "Eur. Deutschland [Europe. Germany]." Homonym of *albus* Bechstein, 1801.

[Cricetus vulgaris] niger Fitzinger, 1867: 98. Type locality is "Eur. Österreich, Ungarn, Deutschland. – As. Sibirien, Simbirsk, Usa [Europe. Austria, Hungary, Germany. – Asia. Siberia, Simbirsk (= now Ulyanovsk), Usa (either the Usa River, which is the right tributary of the Volga River in the Samara Oblast', or the settlement Usa, now Usinskoye, in the lower reaches of the Usa]." Homonym of *niger* Kerr, 1792.

Cricetus frumentarius niger Bogdanov, 1871: 171. Type locality is "въ Казан. губ. [in Kazan Governorate]," Russian Federation. Homonym of *niger* Kerr, 1792.

Heliomys jeudei Gray, 1873: 418. Type locality is not known.

Cricetus cricetus: Dahl, 1894: 130. First use of the current name combination.

Cricetus vulgaris var. *canescens* Nehring, 1899b: 1. Type locality is "Belgien, vom linken Ufer des Maas [Belgium, from the left bank of the Maas River];" restricted to "Near Fexhe-Slins, banks of the Maas, Belgium" (Miller 1912: 603).

Cricetus vulgaris var. *rufescens* Nehring, 1899b: 2. Type locality is "bei Tjubuk im dem Ural-Gebiete [near Tjubuk in the area of Ural]," Chelyabinsk Oblast, Kasli Rayon (Pavlinov & Rossolimo 1987: 173), Russian Federation.

Cricetus nehringi Matschie, 1901: 232. Syntypes were from "Slobosia, Cernavoda und Barza [Slobozia, Cernavodă and Barzâ];" Miller (1912: 605) restricted type locality to "Slobosia [Slobozia]", Ialomiţa County, Romania.

Cricetus vulgaris babylonius Nehring, 1903: 360. Type locality, which is given as "südöstlich von Bagdad [southeast of Baghdad]", is evidently erroneous considering that the common hamster does not occur in the Middle East (*cf.* Figure 62). Nehring purchased the type voucher from a certain Schlüter, a dealer in natural history objects, who had obtained it from his supplier from "Babylonia". Wepner (1934: 438) suggested that Nehring's voucher originated from the Caucasus, and not from the Tigris River. In Wepner's view, the locality was perhaps "Bagdat südöstlich von Kuteis in den südlichen Ausläufern des Kaukasus" [Bagdati near Kutaisi in Georgia]; *C. cricetus,* however, does neither occur in Georgia or elsewhere to the south of the Caucasus. Wepner further speculated that the collector could possibly be from Kutasi, while the hamster was actually captured in "Gebiet nördlich des Kaukasus [the area north of the Caucasus]." She concluded that "It seems certain that *babylonicus* (*sic*) designates the Caucasian hamster" ("Jedenfalls aber scheint sicher, daß der Name *babylonicus* (*sic*) den Kaukasushamster bezeichn") and therefore predates *stavropolicus* Ognev.

[Cricetus cricetus] canescens: Trouessart, 1904: 394. Name combination.

[Cricetus cricetus] rufescens: Trouessart, 1904: 394. Name combination.

[Cricetus cricetus] nehringi: Trouessart, 1904: 394. Name combination and new rank.

[Cricetus cricetus] babylonicus: Trouessart, 1904: 394. Name combination and emendation of *babylonius* Nehring, 1903.

Cricetus vulgaris niger Simroth, 1906: 337. Type locality was not given; Miller (1912: 602) reported it as "Saaltale [=Valley of the Saale, Germany]". Homonym of *niger* Kerr, 1792.

Cricetus vulgaris stavropolicus Satunin, 1907: 122. Type locality: "Сел. Предтеча, Ставропольской губерніи;" (Russian version), "Dorf Predteča, Gouv. Stavropol [= Village Predtecha, Governorate Stavropol]" (German summary on p. 162), Stavropol Krai, Russian Federation.

Cricetus vulgaris stawropolicus: Satunin, 1908: 11. Incorrect subsequent spelling of *stavropolicus* Satunin, 1907.

Cricetus vulgaris stauropolicus: Lydekker 1909: 64. Incorrect subsequent spelling of *stavropolicus* Satunin, 1907.

Cricetus cricetus niger: Trouessart, 1910: 394. Name combination. Trouessart referred to *niger* of several authors; the only identifiable combination is *niger* Simroth, 1906.

Cricetus cricetus stavropolicus: Trouessart, 1910: 395. Name combination.

Heliomys jeudii: Miller, 1912: 602. Unjustified emendation of *jeudei* Gray, 1873 (Kryštufek et al. 2020: 11).

Cricetus frumentarius polychroma Krulikovsky, 1915: 6. Replacement name for *Cricetus frumentarius niger* Bogdanov, 1871.

Cricetus cricetus latycranius Ognev, 1922: 110. Type locality is "Николаевский у. Самарской губ., Черемушка [Nikolaevskiy uezd, Samara Governorate, Cheremushka]," now Samara Oblast, Russian Federation.

Cr[icetus] cr[icetus] rufescens: Ognev, 1922: 111. Name combination.

Cr[icetus] cr[icetus] stawropolicus: Ognev, 1922: 111. Name combination and incorrect subsequent spelling of *stavropolicus* Satunin, 1907.

Cricetus c[ricetus] tauricus Ognev, 1924: 19. Type locality is "окрестности Симферополя [= vicinity of Simferopol]," Crimea, Ukraine.

Cricetus c[ricetus] tomeniss Ognev, 1924: 19. Type locality is "дер. Круглихина, Томской губ. около г. Томска [= village Kruglikhina, Tomsk Governorate, vicinity of the city of Tomsk]," Tomsk Oblast, Russian Federation. Incorrect spelling of *tomensis* Ognev, 1924.

Cricetus c[ricetus] tomensis: Ognev, 1924: Table V on p. 21. Correct spelling of *tomeniss* Ognev, 1924.

Cricetus cricetus nehringii: Călinescu, 1931b: 34. Incorrect subsequent spelling of *nehringi* Matschie, 1901.

Cricetus cricetus fuscidorcis Argyropulo, 1933a: 235. Correct spelling is *fuscidorsis* (see p. 236). Type locality is "окр. с. Ново-Антоновского, Черкасской вол.,

Лепсинского у., Джетысуйской губ. [=neighbourhood of the village of Novo-Antonovsky, Cherkasy volost, Lepsinsky uyezd, Dzhetysu province].” An abbreviated transliteration in Argyropulo (1933a: 235) reads: “Novo Antonovskoje, Distr[ict] Lepsinsk, Semiretshje [Semirechye, now Zhetysu],” Almaty Province, Kazakhstan. The year of publication is frequently stated as 1932 (Ellerman 1941: 440, Ellerman & Morrison-Scott 1951: 629); for 1933 see Argyropulo (1933b: 243) and comments in the account on *Allocricetulus*. Pavlinov & Rossolimo (1987: 173) condemned ‘*fuscidorsis* Argyropulo, 1932: 243 [actually Argyropulo, 1933a]’ nomen nudum due to lack of description. They seemingly referred to Argyropulo’s revision of Cricetinae (Argiropulo 1933b), which is indeed without a description, but overlooked the Argyropulo’s (1933a) article in which *fuscidorsis* was properly diagnosed.

Cricetus cricetus polychroma: Ellerman, 1941: 440. Name combination.

C[ricetus] polychromata: Popov 1960: 323. Incorrect subsequent spelling of *polychroma* Krulikovsky, 1915.

C[ricetus] c[ricetus] laticranius: Gromov, 1963: 497; in Gromov et al. (1963). Incorrect subsequent spelling of *latycranius* Ognev, 1924.

C[ricetus] c[ricetus] latieranius: Gromov, 1963: 497; in Gromov et al. (1963). Incorrect subsequent spelling of *laticranius* Ognev.

Hellomys sendii: Shubin, 1977c: 249. Incorrect subsequent spelling of *Heliomys jeudei* Gray.

C[ricetus] c[ricetus] pannonicus Neumann, 2013: 13. Nomen nudum.

Distribution of *C. cricetus* (Figure 62) covers a wide belt extending longitudinally for 5,500 km from northwestern and Central Europe, across Russia and Kazakhstan, as far east as the River Yenisei and Xinjiang (Niethammer 1982, Kryštufek et al. 2020). During the 20th century, when the range was at its largest, the species occupied eastern Belgium (Libois & Rosoux 1982), eastern France (Louarn & Saint Girons 1977), southern Netherlands (Saint-Girons 1973), Germany (Meinig et al. 2014), Switzerland (vouchers in NHMBa), Czech Republic (Anděra & Gaisler 2019), northeastern Austria (Spitzenberger & Bauer 2001), Slovakia (Krištofík and Danko 2012), Hungary (Zoltán 2007), northeastern Slovenia (Kryštufek 1991),

northern Croatia and northern Serbia (Ružić 1978), southern and central Poland (Surdacki 1983), southern Belarus (Serzhanin 1961, Lemyanchik 2006), Ukraine (Mezhzherin & Lashkova 2013), Romania (Murariu 1998), Moldova (Lozan 1971), northern Bulgaria (Popov 2007), Russian Federation (Berdyugin & Bolshakov 1998), northern Kazakhstan (Shubin 1977c), and extreme northwestern Xinjiang in China (Zhang et al. 1997). Report for Luxemburg (Saint-Girons 1973: Figure 91) is obviously erroneous (Schley & Herr 2018).

The entire range covered an estimated 2,370,500 km². The western border is on the left bank of the River Rheine, and the eastern border on the right bank of the Yenisei River, the western ends of the Minussinsk Steppe and the edges of Betpak-Dala Desert (Shubin 1977c). In the northwest, the range closely approaches the Atlantic and North Sea coasts; further east in Poland, the border sharply turns south and follows the line Brest–Rovno–Gomel’–Smolensk–Rzhev–Yaroslavl’–Vyatka–Perm–Ekaterinburg–Tjumen–Tobol’sk–Kolpashevo–Krasnojarsk (Berdyugin & Bolshakov 1998, Sidorov et al. 2009). The southern border is roughly set by the Alps, the River Danube and its southern tributary the Drava (Niethammer 1982), the Black Sea coast and the Caucasus (Tembotov 1972). Further east, the range border runs to the north of the Caspian coast but descends south along the Ural River and reaches the estuary of the Emba River into the Caspian Sea. From the northeastern corner of the Caspian, the range roughly follows the line to the north of the Aral Sea–Balkhash Sea, encompasses Semirechye (Shnitnikov 1936) and reaches Dzungarian Alatau and the extreme northwestern Xinjiang (Kuznetsov 1965, Shubin 1977c, Zhang et al. 1997).

The abundance of the common hamster and the expansion of its range varied over the last centuries to a degree far greater than in any other hamster. Range dynamic was seemingly not synchronous across the entire range. In short, common hamsters benefited from deforestation and land use change for agriculture (Grulich 1978), however, industrialization in food production drastically affected the carrying capacity of their habitat and precipitated sharp decline. In Germany, abundances were locally high in the late 17th century at the latest (Weissenborn 1839); the species remained abundant throughout the 18th century and
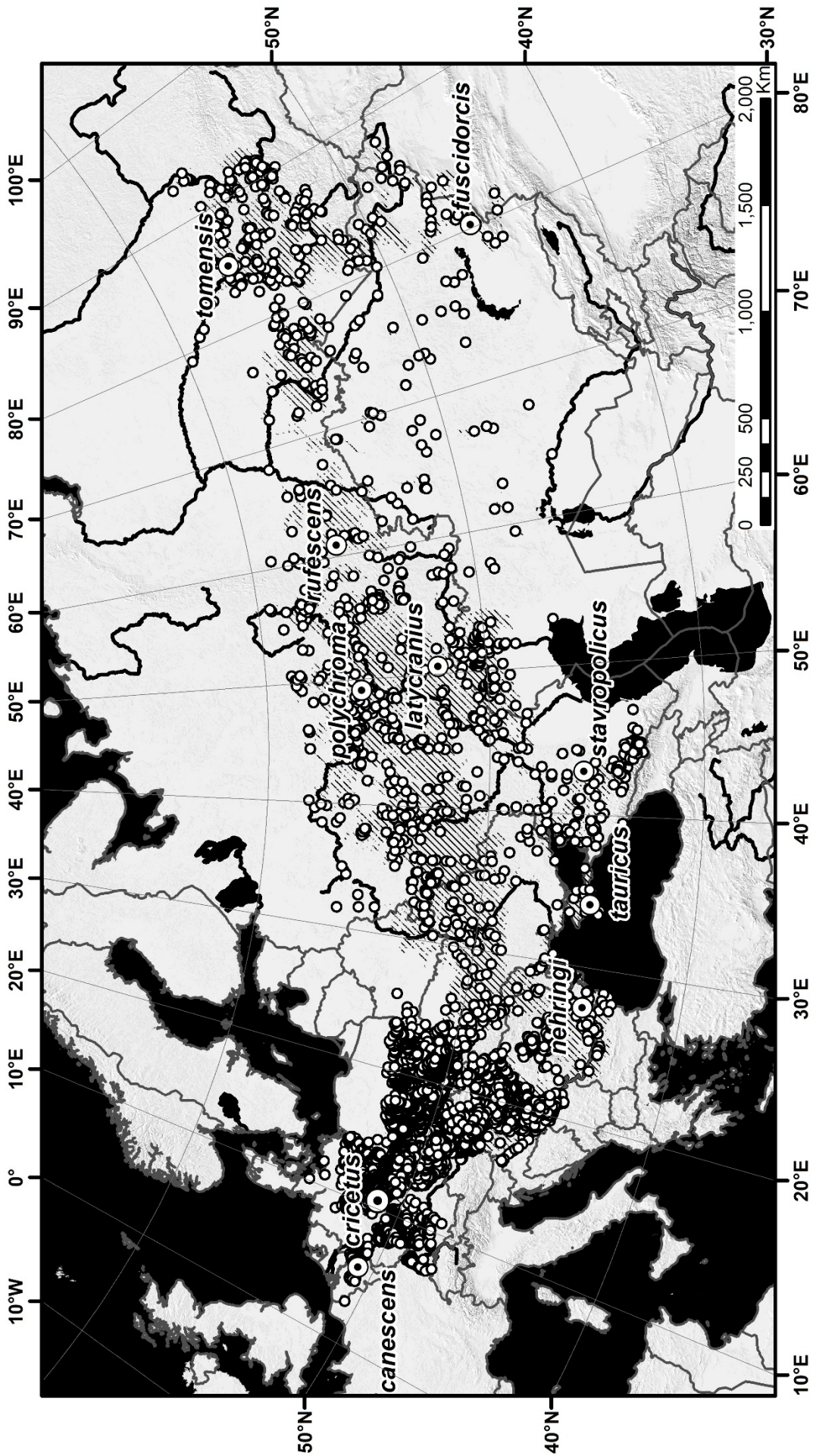
Figure 62: Distributional range of the common hamster *Cricetus cricetus*.

continued spreading its range during the 19th century (Nehring 1894a). A major expansion in the west started during the 2nd half of the 19th century. From Belgium, where hamsters were still uncommon prior to 1850 (Sélys 1842), they expanded after 1870 into France (Trouessart 1910) and Holland (Lenders & Pelzers 1985). The species reached pest proportions in the 1880s, spread to the outskirts of Brussels in 1930–1940s and stretched its range to the maximum around 1950 (Bont 2021). In southern provinces of European Russia, hamsters were "moderately frequent" at the turn of the 18th–19th centuries (Rumyantsev et al. 2018). Other reports corroborate hamster's rarity in various regions of Russia and Kazakhstan during the 19th century (Berdyugin & Bolshakov 1998). In the steppes of Ciscaucasia, where hamsters were always rare (Tembotov 1960, 1972), they invaded Kabardino-Balkaria shortly before 1900 (Satunin 1901). Abundances increased in the late 1920s and during 1930s in many parts of Russia (Viktorov & Istomin 2002, Rusinov 2004, Bobrov et al. 2008) and during the 1940s in Kazakhstan (Berdyugin & Bolshakov 1998). Hamsters reached the city of Moscow around 1970 (Sudeikin et al. 1972) and the easternmost Minussinsk Basin in the 2nd half of the 20th century (Gromov & Erbajeva 1995). In Semirechye, first hamsters were recorded in Dzungarian Alatau in 1910 and some 3 decades afterwards they occupied also the Balkhash-Alakol Depression (Afanasiev 1953). Southern Altai was colonized after the advent of soil ploughing (Kuznetsov 1932); e. g. hamsters were observed in the area of Lake Teletskoye in the mid-1930s (Jurgenson 1938).

Population decline was recorded throughout the 20th century in various parts of hamster's range (cf. Berdyugin & Bolshakov 1998, Nechay 2000). In The Netherlands, hamsters reached pest abundance merely a decade since their first appearance in the 1870s, but population plagues ceased already after 1915 (Lenders & Pelzers 1985). Population decline was noted since the 1950s in Russia and the Altai (Minoransky et al. 1997, Oparin 2005, Stakheev 2008). Contrary to this, Sutcliffe & Kowalski (1976: 85) concluded that hamsters were "gradually increasing expansion" in West Europe still in the 1970s. At about same time (1972), eastern Slovakia marked a sudden major outbreak (Grulich 1978). France continued to control hamsters as late as 1990

(Nechay 2000) and at about same time the animal was still classified as "a significant pest" in central and eastern Europe (Nechay et al. 2000). Population recovery was noted in Crimea since the mid-1980s (Evstafiev 2016) and in some parts of European Russia in the 1990s (Poplavskaya et al. 2016). Despite all this, the overall recent trend was a decline, which was particularly rapid in the west. In Central and Western Europe, >75% of the original range has been lost (Surov et al. 2016). What is left is heavily fragmented (cf. Figure 2 in Meinig et al. 2014) and marginal populations (in Switzerland, Holland and Slovenia) have already vanished. In Asia, the decline was less severe than in Europe (Moskvitina et al. 2022).

Original habitats are perennial grasslands and forest steppes on thick soil layer, however, hamsters promptly adapted to cultivated areas where they attained the highest abundances. They occupy various open habitats as well, like orchards, thickets, and forest edges, but are largely absent from dry steppe. In eastern Europe, the Urals and the mountains of Asia (Tarbagatai, Dzungarian Alatau, Altai, and Sayan), hamsters occasionally occupy open deciduous and mixed woodland (Kulik 1962, Berdyugin & Bolshakov 1998). Hamsters are primarily inhabitants of low elevations. Mean altitude is 232 m a.s.l. and in Central Europe hamsters mainly remain at <500 m a. s. l. (Kryštufek et al. 2020). They ascend into higher altitudes along the southern range border, i. e. up to 1,150 m in the Caucasus (Tembotov 1972) and up to 2,000–2,200 m in Dzungarian Alatau (Shubin 1977c).

C. cricetus has for long been known to occupy urban settlements (Bogdanov 1871), however, the process of synurbanization accelerated in the early 20th century (Serebrennikov 1929, Afanasiev 1953). Hamsters are now present in cities from Prague and Vienna in the west to Novosibirsk and Omsk in the east. In many regions, hamsters are known primarily as synanthropic animals (Poplavskaya et al. 2016); in Crimea, common hamsters occur inside the buildings with house mice and brown rats (Evstafiev 2016). Triggers towards synanthropisation are contested. While Grulich (1978) observed a switch towards synanthropy during the population outbreak, Evstafiev (2015) considers the phenomenon to be related to population decline.

Characteristics. *Cricetus* is the largest extant hamster of a robust and heavy-set form (Figure 61). Dimensions: body mass = 146–860 g, length of head and body = 165–320 g, length of tail = 28–68 mm, length of hind foot = 26.0–46.0 mm, length of ear = 17.0–41.0 mm, condylobasal length of skull = 36.8–58.9 mm, zygomatic width = 20.5–34.7 mm, maxillary tooth-row length = 6.6–8.9 mm (Grulich 1987a). Secondary sex dimorphism in size is pronounced (Figure 67); in Central Europe, males are on average by 31–44.6% heavier than females, but this differs among populations. Males have by 3.7–14% longer head and body, and by 1.56–7% longer skull (Grulich 1987b). Moving eastward, the secondary sex dimorphism is diminishing (Kryštufek et al. 2016); *e. g.* dimensions, which Shubin (1977c) published from Kazakhstan, suggest no significant dimorphism in body mass.

Length of tail accounts for 22–25% of head and body length (mean = 23%). Head is heavy and powerful, with comparatively small eyes. Ears are long and circular, densely clothed on both sides with fine hairs. Feet are broad and fingers are comparatively the longest in the subtribe Cricetina (Figure 33d); the central digit (digit III) is the longest in both, the front and hind feet. The front thumb is reduced but still prominent and equipped with a fairly large nail. Claws are usually thick and prominent, more elongate on the hind foot and broader on the front paw. There are 5 plantar and 6 palmar pads. The former are of unequal size; the medial and the central interdigital pads are small, while the outer pad and the metacarpal pads are evidently larger. Plantar pads are of small size; the medial interdigital pad (pad no. 1 in Figure 33) and the metatarsal pads are the smallest. The metatarsal pads are set further back compared to other species of Cricetinae. Feet are hairy posterior to pads (*cf.* Figure 33d).

Fur is thick and pretty rough; back hairs are 25–30 mm long (Chernova et al. 2022b); those at the base of tail are longer, reaching ½ of tail length. Colour pattern is specialized and the common hamster is one of the most colourful Palaearctic muroid rodents. Upper parts are brownish buff, belly is black and there are contrasting light patches on the contact between the brown and black areas (Figures 61 & 63). Besides this standard (tricolour) colouration, black individuals (Figure 64) are locally common, while other variants occur at very low frequencies (*e. g.* <0.01% in Central Germany; Keyser & Stubbe 2000). Colour polymorphism is further detailed in the Variation and subspecies section.

Figure 63: Standard museum skin of *Cricetus cricetus* (from western Siberia) in dorsal (top), lateral (middle) and ventral view (bottom). Light patches: I – cheek, II – neck, III – axillary, IV – thigh; c. – antebrachial cuff; c.s. – chin streak; f.g. – flank gland.

The tricolour pelage is brownish buff across much of the back, but is rusty on the head, muzzle and frequently also on the rump. The dorsum is clouded by sprinkling of black-tipped hairs. Flanks are lightly tinged reddish and the belly is uniformly black; the anal region and the tail are rusty. There are 4 contrasting light patches along the side, specifically (anterior-to-posterior) the cheek, neck, axillary, and thigh patches (Figure 9a & 63). These patches are either whitish, yellowish, cream or light buff; the anterior-most patches are frequently more buffy, and the posterior patches tend to be more whitish. The cheek patch which is the most extensive, covers the cheeks, lips, chin and the snout. The roundish neck spot, which is located just in front of the fore legs, and the axillary spot behind it, are separated by a dusky upward expansion of black hairs from the upper arms (Figure 63). The axillary patch tends towards medial expansion which restricts the black area of the belly (Figure 65). Such a constraint is seen in ~ 60% of individuals within the population and is more common in the west. The thigh patch is the smallest and is prone to obliteration; its

Figure 64: Black (melanistic) morphotype of the common hamster *Cricetus cricetus* from Thuringia, Germany. Note white snout and paws. Photo courtesy of Wolfgang Hock

Figure 65: Ventral side of common hamsters *Cricetus cricetus* to show variability in the extent of the axillary light spot (III) and the consequent restriction of the black belly colouration. Light colour on the right side of abdomen in specimen (d) is caused by hair loss. Origin of vouchers: a – Tomsk Region, western Siberia, Russian Federation; b, c – Bashkortostan, Russian Federation; d – Hortobagy National Park, Hungary. Photo: B. Kryštufek.

presence and size are occasionally asymmetric. Light (white to buff) spots and patches are present behind the ears, on throat (chin streak) and on the chest between forelegs (chest spot); their frequency and size vary among populations (Figure 66). Ears are of same colour as the head and are margined white. Paws are similarly white; white area on the antebrachium, which is of varying length, is usually called the cuff (Figure 63). Young hamsters are of similar pattern, but are darker; in very young individuals, the light patches are less prominent.

The penis is approximately 30 mm long when erected; dorsal surface is flat and ventral side is deeply grooved by *sulcus urethralis* (Reznik et al. 1979). Glans penis is cylindrical with a truncate tip; the width of glans equals approximately ⅓ of its length. The urethral crater is surrounded by 1 central and 2 lateral papillae which are of equal size (Figure 16). *Papilla ventralis* is flattened and bicuspid; dorsal papilla is absent (Bittera 1918). Baculum is robust with well ossified distal digits and heavily expanded base (Figure 17h). Proximal stalk measures 3.6 mm; the central and lateral digits of distal trident are of approximately same length (2.5 mm; Didier 1953). Females have 2 pairs of each, the pectoral and the inguinal nipples (8 nipples in total; Popov 1960).

The skull is robust, heavy-built and well ridged in adults (Figure 67). The dorsal profile is slightly bent, which is most evident anterior to the naso-frontale suture. Zygomatic arches are moderately to widely expanded and zygomatic width accounts for 56–58% of condylobasal length of skull. Old individuals with fully spread arches reach maximum width just in front of glenoid region. Masseteric plate is well developed; the infraorbital foramen is wide above, narrow and slit-like below (Figure 20a). Rostrum is robust and decidedly wider than the interorbital region. The latter is well constricted with distinct median furrow and raised edges. Temporal ridges merge posterior to the frontals, but do not fuse into sagittal crest. Frontals are postero-medially much constricted and wedge deeply between the parietals. Braincase is diamond shaped, with characteristically small and triangular interparietal; a powerful lambdoidal crest forms a prominent medial concavity. The occiput is oblique and is clearly seen in
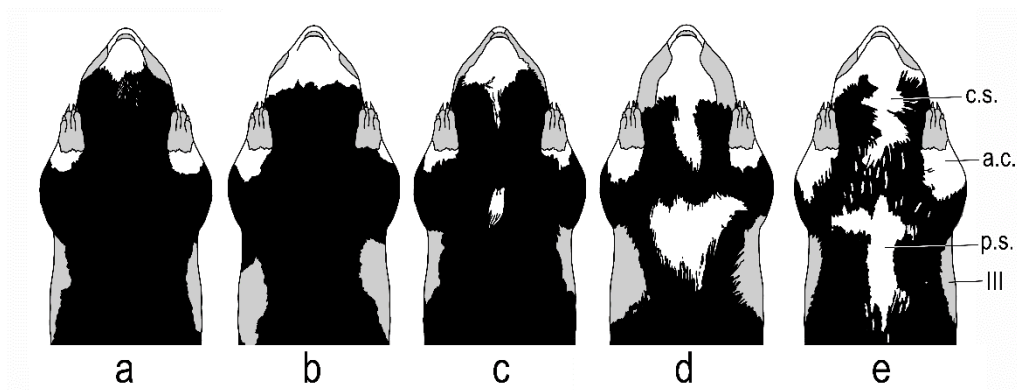
Figure 66: Variation in colour pattern of the ventral side of *Cricetus cricetus*: a.c. – antebrachial cuff, c.s. – chin streak, p.s. – pectoral spot, III – axillary light spot. Vouchers originate from: (a) – Kozhevnikovo, Tomsk Oblast, Siberia, Russian Federation; (b) – Kostanay Province, Kazakhstan; (c) – Dunaszeg, Hungary; (d) – Rhine-Westphalia, Germany; (e) – Belgium (modified from Husson 1959).
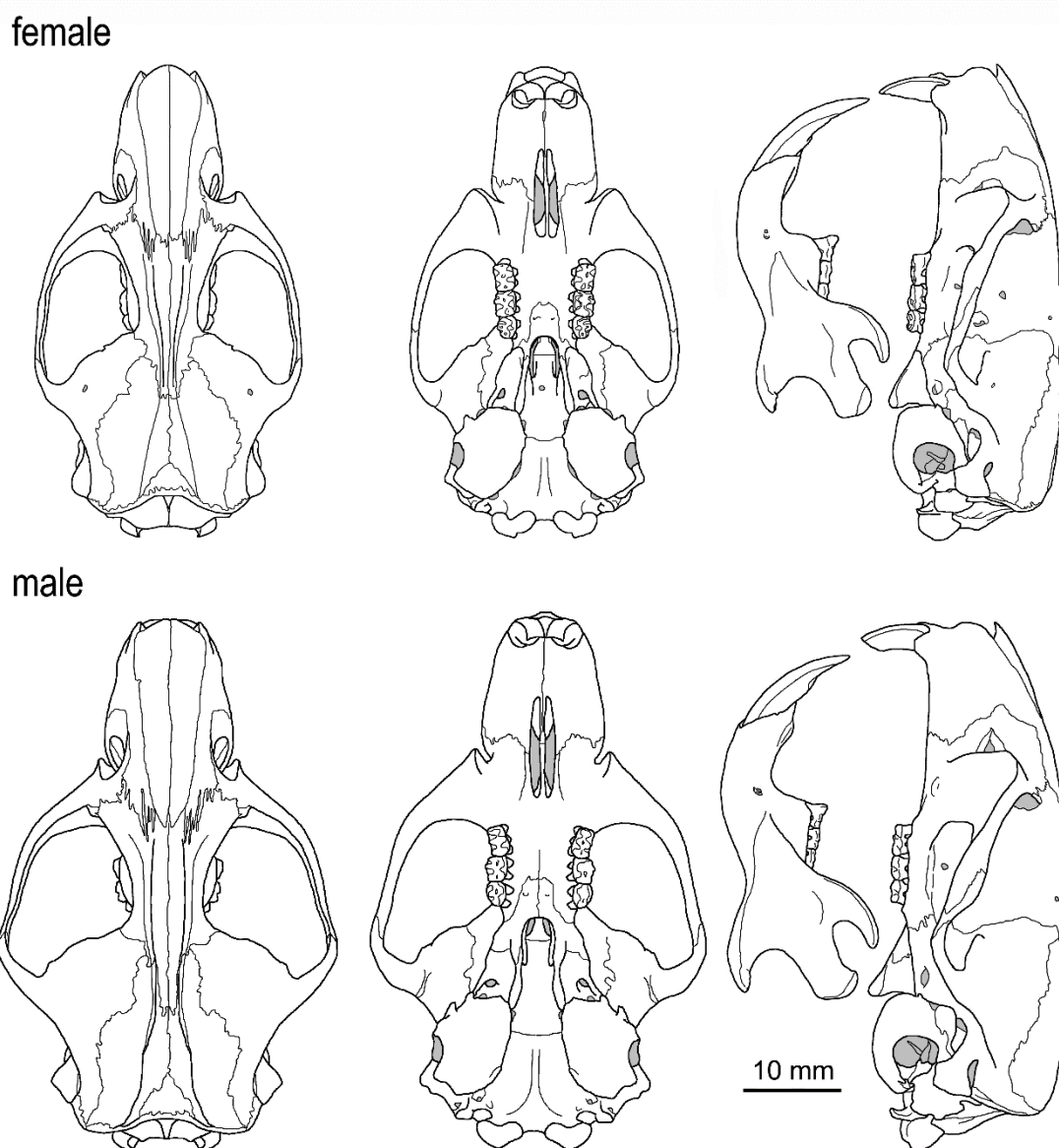
Figure 67: Adult female (top) and male (bottom) common hamster *Cricetus cricetus* skulls from Dunaszentpal, northwestern Hungary. Note dimorphism in size and shape.

dorsal view, along with condyles. Bullae are circular and rather large; paroccipital process is well developed and shifted posterior. Incisive foramina are quite long but still terminate well in front of the molars. Pterygoid processes are high and the interpterygoid vacuity is spacious; hard palate terminates at the posterior margin of the molars. Mandible is slender, with high recurved coronoid process; angular process is slim and bent outwards; articular process is robust. The root of the lower incisor forms an evident bulge on the outer wall of ramus slightly above the level of molars. The root of the upper incisor nearly reaches the posterior level of the infraorbital foramen, where forms a swelling. Number of roots in molars is 4 (M^{1-2}), 3 (M^3), and 2 (M_{1-3}). Molar pattern shows no peculiarities (Figure 68).

Karyotype (2n = 22) consists of 7–9 pairs of biarmed chromosomes (metacentrics and submetacentrics) of various sizes; the remaining autosomes are subtelocentric and acrocentric. Sex chromosomes are biarmed; the X is large and the Y is a rather small element. Fundamental number of chromosomal arms is NF = 42 (Ivanov 1969b, Zima & Král 1984). The karyotype is characterized by high amount of centromeric heterochromatin (Gamperl et al. 1978). Heterochromatic arms are restricted to sex chromosomes (Vistorin et al. 1976).

Variation and subspecies. Individual variation is excessive and blurs interpopulational variation. Size varied historically throughout the Pleistocene (Kowalski 2001, Horáček & Lebedová 2022),

presumably in response to the changing climatic conditions and in accordance with the Bergmann's rule (e.g. Smirnov & Popov 1979). Size classes have been classified as distinct taxa, either subspecies or species. They are currently synonymized with *C. cricetus*, largely due to their uniform dental morphology, which is identical to that in the current species (Sutcliffe & Kowalski 1976, Kowalski 2001). Dimensions (length of maxillary tooth-row; in mm) of the large fossil *C. cricetus praeglacialis* Schaub, 1930 (= 7.3–9.0) and the small *C. cricetus nanus* Schaub, 1930 (= 6.0–7.4; Pradel 1985) are largely within the variation range for central-European hamsters (= 6.6–8.9; see also account on Characteristics). Besides, size varies between years even in the same population; hamsters are on average the largest in the year following the population peak and the smallest 2 years after the peak. Furthermore, interpopulation size differences can be prominent even in populations separated by small geographical distance (Grulich 1987a). On the other hand, no obvious trend in size variation has been evident in recent hamsters both at large (Berdyugin & Bolshakov 1998) and locally (Stefen 2013).

Frequency of light colour marks vary among populations. Hamsters occurring to the west of the river Rhine have higher incidence of white crown and chest spots; the chest spot, chin streak and white antebrachial cuff are also larger (Figure 66). The crown spot which is present in 12.5% of hamsters from The Low Countries is still present in the Pannonian Basin (Husson 1959), but is largely absent elsewhere. The chin
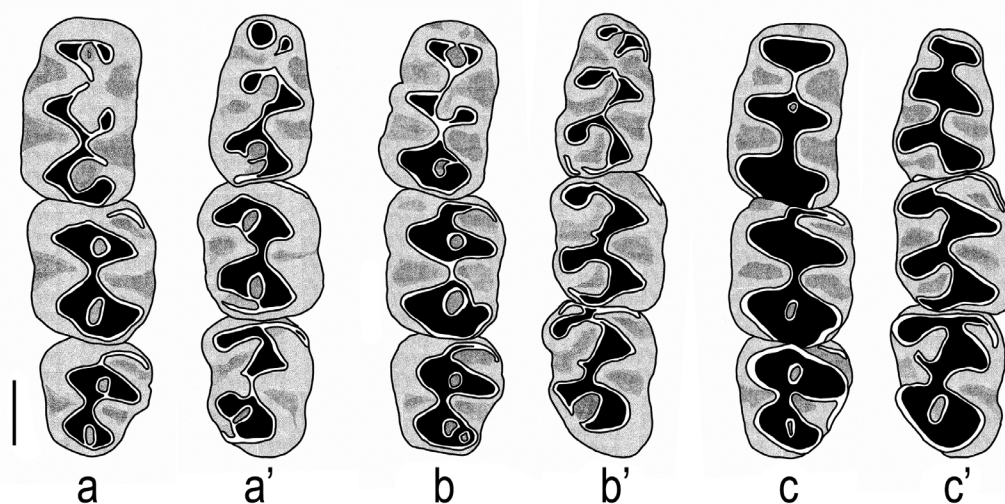

Figure 68: Grinding pattern of upper (a, b, c), and lower (a', b', c') molars in the Common hamster *Cricetus cricetus* from Vojvodina, northern Serbia. Scale bar = 1 mm.

streak is of variable shape, from short, broad and blunt to long, narrow and pointed. It is the longest to the west of the Rhine (Schröder et al. 2013) and short or absent to the east of the Urals (Kryštufek et al. 2016). Frequency of presence of the white chest spot is 67–100 % to the west of the Rhine, 0–8 % in central and Eastern Europe (Schröder et al. 2013) and 1.1% in Asia (Kryštufek et al. 2016). The spot is of smaller diameter and frequently diffused in the east. The white cuff is long and present at all times to the west of the Rhine, but is shorter and occasionally absent further east. The white thigh spot is omnipresent to the west of the Rhine, but was recorded in ~ 87% of hamsters from eastern Europe and Asia (Schröder et al. 2013, Kryštufek et al. 2016).

The most prominent feature of the individual and population variability in the common hamster is colour polymorphism, which was described as early as the 17th century (e.g. Topsel 1658, Falk 1786, Bechstein 1801, Gilibert 1805, Pallas 1811, Buhle 1821). List of variants includes black (atypical melanistic and melanistic proper), dark tricolour, bicolour, piebald, white, albino, yellow (flavistic), red, sand, ivory, and 'iron grey' coloured hamsters (Petzsch 1936a, 1941, Kayser & Stubbe 2000, Kryštufek et al. 2016). Since their

proportion within the population is usually low (frequency ≤ 0.01%; Kayser & Stubbe 2000), the main source of material was the fur market supplied by hundreds of thousands hamster pelts. *E. g.* Gershenson (1946) estimated proportions from a sample of over 2 million hamster skins collected in Ukraine and Russia during 1931–1940. The disadvantage of such huge samples was a lack of clear description of colour variants (Kayser & Stubbe 2000), which may distort the perception of reality. *E. g.*, Gershenson (1945) treated hamsters as being dimorphic (black *v.* tricolour), however, his black category possibly included a range of dark-coloured individuals (Kryštufek et al. 2016). Black colour is inherited as a simple autosomal dominant (Gershenson & Polevoy 1941), whereas albinotic and flavistic variants are recessive (Petzsch 1941, Petzsch & Petzsch 1956).

Black variant is regionally frequent and has been extensively studied. Black and tricolour hamsters mate freely (Gershenson & Polevoy 1941, Petzsch & Petzsch 1956) and have often been found in same litters (Lepekhin 1771, Pallas 1779, Novikov 1935). Black hamsters are typical of Thuringia (Germany) (Figure 64), parts of Ukraine and eastern European Russia. In Thuringia, they occupy a fertile area of 70 × 30 km.

Figure 69: Colour variation in common hamster *Cricetus cricetus* showing blurring of tricolour pattern (a) and darkening of pelage (b–f). a – A dull tricolour type which lost light thigh patch ("stavropolicus" variant; Vladikavkaz, Russian Federation); b – a bicolour type which lost all light patches (Kislovka, Tomsk District, western Siberia, Russian Federation); c – a black (atypical melanistic) variant from Novaya Chertoryja, Zhitomir oblast, Ukraine; d – a black variant with light patches from Belgrade, Serbia; e – a black variant with rusty shines on head and rump (Dresden, Germany); f – a black (melanistic) individual from Pişcolt, northern Romania. Photo B. Kryštufek.

Within this area, different populations contain diverse proportion of black individuals. During the 1960s, the proportion of black individuals was 0.5–18.0% per county (Zimmermann & Handtke 1968, Zimmermann 1969). In Ukraine in 1930s, black hamsters were tied exclusively to the forest steppe zone which received >500 mm of precipitation annually. Their proportion across 15 regions varied between 0.00–15.33% (annual total = 2.05–4.68%). Share of black hamsters was particularly high in 4 regions: Zhitomir (3.11%), Chernigov (3.40%), Kamenets-Podolsk (4.85%) and Poltava (8.20%) (Gershenson 1945, 1946). In European Russia, black hamsters are abundant in humid forest-steppe habitats of northern Bashkortostan and adjacent Tatarstan and Perm. During the 1930s, their frequency varied across 49 districts of Bashkortostan between 0.00–87.12% and was >50% in 15 districts (Gershenson 1945). The proportion of black variant positively correlated with humidity and population density (Gershenson 1945). During the 1930s, black hamsters expanded their ranges in Ukraine, both northward (in Chernigov) and southward (in Odessa region) and replaced the tricolour type (Gershenson 1946, Vorontsov 1982). Similarly, in Russia to the north of the Kama River, the black variant strongly predominated in the mid-19th century (Bogdanov 1871), but the tricolour type was widespread a century latter (Popov 1960). A similar turnover has been reported from the city of Gotha (Thuringia) in the late 18th and early 19th centuries (Weissenborn 1839, Zimmermann 1969). On the other hand, black hamsters are persistently present in Thuringia and the Volga-Kama region since the mid-18th century (Lepekhin 1771, Sulzer 1774, Georgy 1775, Erxleben 1777, Pallas 1779, Falk 1786); first reports for Ukraine date back to the mid-19th century at the latest (Kessler 1851). Single

Figure 70: Fur colouration in pale common hamsters *Cricetus cricetus* from Saxony-Anhalt, Germany (a–d) and Ukraine (e, f). Round skins (a–d) are shown in dorsal (top row) and ventral view (bottom row). Voucher (f) is flavistic with white belly and rusty fur between the snot and occipital region. Voucher (e) is light-grey above and blackish-grey below with abundant blackish hairs above; fur around the eyes and ears is light rusty. Note that vouchers (e) and (f) retained light patches on the cheek (I), neck (II), and in the axillary region (III) (*cf.* Figure 63). Photo B. Kryštufek (a–d) and Nedko Nedyalkov (e, f)

black hamsters were found here and there in other parts of the species' range to the west of the Urals. Adaptive significance of the black coat colour is not clear. Under experimental conditions, black hamsters prefer colder and moister conditions, while tricolour hamsters select warmer and drier microclimate (Samosh 1969).

Black hamsters are usually classified as melanistic, though they invariably show white feet, muzzle, chin and ear edge (Figures 64 & 69f); occasionally, they also have a white pectoral spot. Black hamsters, however, frequently show reddish shine and/or whitish patches (Figure 69c, e). Such hamsters, called 'atypical melanistics', are common in Thuringia (frequency = 60% of black hamsters; Zimmermann 1969) and were reported as single individuals from Rhein-Hesse (Thomas 1963), Poland, Ukraine, Ciscaucasia (Adygea), and Kazakhstan (Kryštufek et al. 2016). Also described as atypical melanistics are blackish hamsters which retain light patches (Figure 68d); they were reported as single individuals from a comparatively small area between eastern Austria (Bauer 1960), northern Serbia (Kryštufek et al. 2016) and Romania (Chişamera et al. 2023). In captivity, such a hamster from northern Serbia delivered normal tricolour offspring (Krsmanović et al. 1988). Dull tricolour hamsters (Figure 69a) were in the past classified as a subspecies in its own right (*stavropolicus*). This type is known primarily from steppes to the north of the Caucasus Mts. (Ciscaucasia), but was reported also from Thuringia (Zimmermann & Handike 1968). Light patches are exceptionally entirely lost, resulting in a bicolour variant, which is known only from Ciscauscasia and western Siberia (Kryštufek et al. 2016). To summarize: the black and the tricolour variants are connected through gradations of diverse atypical melanistics, of which not even two individuals are perfectly identical (Zimmermann & Handike 1968).

'White' hamsters were reported from Thuringia, the Urals (Bechstein 1801), and Bashkortostan (Popov 1960). Although such hamsters are rare everywhere, they were still the dominant colour variant (n = 50 individuals) in a large sample of skins (n = 73,567) from eastern Germany, accounting for ~ 80% of all colour aberrations (Kayser & Stubbe 2000). Similarly to black hamsters, the white also lack detailed description in the majority of cases. Nevertheless, at least some were albinos with red eyes (Bechstein 1801, Schlott 1924, Petzsch & Petzsch 1956). White museum skins

frequently have their fur interspersed with black hairs, which are denser along the spine (Figure 70a). Depending on their density, the fur assumes different shades of grey colour (Figures 70a, b, e & 71a).

White variants are linked to the standard tricolour type through a gradation of flavistic modifications with various intensity of yellowish or buff shades and with whitish or black belly (Figures 70c–f & 71c, d). Just like in black skins, not two light hamsters are identical in every detail. The pattern of light patches, which is typical of tricolour type, is either lost (Figure 70a–d) or retained (Figure 70e, f & 71 c, d), regardless of the overall colouration of an individual.

Common hamster was treated as a polytypic species. Number of subspecies varied widely among authors, ranging from 3 (Ellerman & Morrison-Scott 1951), 5 (Trouessart 1904), 6 (Truessart 1910), 7 (Berdyugin & Bolshakov 1998), 9 (Argyropulo 1933c), 10 (Petzsch 1936b, 1952) or 11 subspecies (Ellerman 1941). Truessart (1910) still classified black hamsters as subspecies *niger* Schreber, 1792, with its range in Germany and beyond. Novikov (1935), on the other hand, dismissed melanism as a taxonomic trait, treating it as a colour aberration. Subspecies were largely based on differences in colour shades, size and skull shape (cf. Novikov 1935, Surov & Feoktisova 2023). Craniometric analyses (Husson 1959, Grulich 1987a, Stefen 2013, Kryštufek et al. 2016) provided weak support for the subspecific taxonomy; these studies also showed that colour variants are more diverse (Husson 1959, Kryštufek et al. 2016) than craniodental size and shape. Novikov (1935) categorically claimed that subspecies lack diagnosability. When experts were asked to classify museum vouchers into subspecies, they failed as long as they did not know the collecting site. Husson (1959: 197) similarly concluded that "… one had better abstain from applying terms like subspecies or geographical race to this situation [in *C. cricetus*] which is so strikingly different from the usual situations in which these terms are applied." In a study on geographic variability of colour and size in *C. cricetus*, we came to similar conclusion: "division of the common hamster into a subspecies is not congruent with the pattern in morphological variability (or lack of it) and thus obscures reality" (Kryštufek et al. 2016:

Figure 71: Colour variants in common hamster *Cricetus cricetus* from Thuringia, Germany. Top row shows uniformly grey hamsters and bottom row shows yellow (flavistic) variants; individual (a) is light grey and (b) is dark grey (atypical melanistic). Note difference in blurring reddish-brown shade in flavistic individuals, which both retain a rusty head. Photo courtesy of Wolfgang Hock

153). Hence, no subspecies are recognized here (cf. also Kryštufek 2017e).

Phylogeographic analyses retrieved significant population structuring with 5 allopatric lineages, which diverged during the Last Glacial Maximum. These lineages are (1) Western (Benelux, Germany, western Poland), (2) Pannonian (Czech Republic, Slovakia, Hungary, Romania), (3) Central (Poland, Belarus, and most of Ukraine), (4) Eastern (eastern Ukraine and Crimea, European part of Russia, south-eastern foothills of the Ural Mts., and Western Kazakhstan), and (5) the Altay lineage (northern and eastern Kazakhstan, western Siberia and Altay) (Neumann et al. 2005, Feoktisova et al. 2017, 2018, 2022, 2023, Korbut et al. 2019). Noteworthy, the phylogeographic structuring does not match any subspecific division. *E. g.*, ssp. *canescens* with its putative range to the west of the River Rheine, is not supported by phylogeography, which was predicted already by Husson (1959).

Subtribe: Cansumyina – new subtribe

Taxonomy. Cansumyina new subtribe clearly differs in a set of external and craniodental traits from the remaining Cricetini, which we classify as a subtribe Cricetina. Cansumyina contains a single species *Cansumys canus*, hence we provide a detailed description in the species account below. In the multi-character cladistic analysis (Ross 1992) and mitochondrial (cyt*b*) phylogenetic reconstruction (Jiang et al. 2024), *Cansumys* emerged as a basal lineage in Cricetini; the divergence time was estimated as 10.37 Mya (CI = 7.81–13.06 Mya) (Pan et al. 2024).

Diagnosis and Comparisons. (1) The tail is long (~ 70% of head and body length) in Cansumyina and thickly clad with shaggy hairs which cover the annulation (Figure 73); in Cricetina, the tail is proportionally shorter (<65% of head and body length), sparsely haired and with exposed annulation. (2) The rostrum is parallel-sided in Cansumyina (Figure 75) but narrows anteriorly in Cricetina. (3) The interparietal of Cansumyina is broad and strap shaped (Figure 75), as opposed to triangular or diamond-shaped in the greater part of Cricetina. (4) The pterygoids are shorter than the maxillary tooth-row in Cansumyina (Figure 75), while they are longer in Cricetina. (5) The coronoid process of the mandible is short and blunt in Cansumyina, and does not extend beyond the level of sigmoid notch (Figure 75); in Cricetina, the coronoid process is normally long, slender, and extends beyond the level of the notch. (6) The upper incisors are thick and opisthodont in Cansumyina (Figure 75) but slender and orthodont in Cricetina. (7) In Cansumyina, the molars are robust (molar row is only slightly shorter than diastema) and surrounded by a bony ridge (Figure 75), but weaker (much shorter than diastema) and with no surrounding ridge in Cricetina. (8) The crowns of the molars are mesodont in Cansumyina (Figure 76b) and brachyodont in Cricetina (Figure 76a). (9) Mesoloph is present on M² in Cansumyina (Figure 77) but absent in Cricetina.

Type genus. *Cansumys* G. Allen, 1928.

Content. Contains a single monospecific genus *Cansumys,* which is restricted to a small area in central China.

Genus: *Cansumys* G. Allen, 1928 – Gansu Hamsters

Cansumys G. Allen, 1928: 244. Type species is *Cansumys canus* Allen.

A monotypic genus; see species account for further details.

Cansumys canus G. Allen, 1928 – Gansu Hamster

Cansumys canus G. Allen, 1928: 245. Type locality: "Choni [Jonê], southern Kansu [Gansu], China."

[Cricetulus Tscherskia triton] canus Argyropulo, 1933b: 248. Name combination.

Cricetulus triton canus Ellerman, 1941: 435. Name combination.

C[ricetulus] t[riton] camus: Chen & Min, 1982: 370. Incorrect subsequent spelling of *canus* Allen.

C[ricetulus] cansus: Chen & Min, 1982: 370. Incorrect subsequent spelling of *canus* Allen and new name combination.

Cricetuvs canus: Chen & Min, 1982: 371. Incorrect spelling of *Cricetulus* in combination with *canus.*

Cricetulus canus: Zhang, Jin, Quan, Li, Ye, Wang & Zhang, 1997: 216 (Chinese) & 217 (Eng.). Name combination.

Etymology. The name *Cansumys* is derived from 'Cansu' (*i. e.* Kansu, now Gansu) and 'mys' (Greek for mouse), *i. e.* a 'mouse from Gansu', a province in northwest China, where first specimens were captured.

The species name *canus* (Latin male adjective for 'hoary' or 'grey') is an allusion to the colour of dorsal pelage.

Taxonomy. The naming of the Gansu hamster in 1928 marked the last discovery of an obviously new type of hamster. The animal for long remained known only from the type series (type and paratype); it is housed in the Museum of Comparative Zoology at the Harvard University. Without seeing any of these vouchers, Argyropulo (1933b, c) downgraded the taxon to a junior synonym of *Tschersia triton*, a view that prevailed for the next half a century.

In a treatise on the mammals of China and Mongolia, Allen (1940) refrained from discussing Argyropulo's classification. He stressed that the relationship between *Cansumys canus* and *Cricetulus* (which in his book included also *Urocricetus* and *Tscherskia*) "is apparently not very close" (Allen 1940: 781). Despite this, Ellerman (1941) followed Argyropulo and retained *canus* as a subspecies of *Cricetulus triton*. It thus happened that *Cansumys canus* stayed in the synonymy of either *Cricetulus* or *Tscherskia* (Ellerman & Morrison-Scott 1951, Corbet 1978, Pavlinov & Rossolimo 1987), or was plainly ignored (Corbet & Hill 1980, 1986, Honacki et al. 1982, Vorontsov 1982).

Since the early 1980s, the Chinese authors turned their attention on the status of Allen's Gansu hamster. Chen & Min (1982) demonstrated the existence of two distinct morphological types among the long-tailed hamsters collected in Shangluo (Shaanxi) and named them *Cricetulus triton* and *C. canus*. Shortly afterwards, Ross (1988) re-examined the type series of *Cansumys canus* and confirmed its taxonomic distinction from *Tscherskia triton*. The latter view was promptly grasped (Corbet & Hill 1992, Musser & Carleton 1993, 2005, Pavlinov et al. 1995, Wang 2003, Peng & Zhong 2005, Smith & Hoffmann 2008, Jiang et al. 2015), though some authors continued to classify the Gansu hamster as a species of *Cricetulus* (Zhang et al. 1997). Starting with 2000, only the minority of authors ranked the Gansu hamster as a subspecies of *Tsherskia triton* (Luo et al. 2000, Liao et al. 2007) or even ignored it entirely (Jiang et al. 2015). Chinese authors provided a detailed comparison between *Cansumys* and *Tscherskia* exposing karyological (Yang et al. 2003) and morphological distinctness (Gu 2005) of the two. Despite all this, the taxonomic and geographic scope of *Cansumys canus* remained vague. Several authors (Lu & Wang 1996, Zhang et al. 1997, Wang 2003) included into *Cansumys* also *ningshaanensis* Song, 1985, as one of its subspecies. Following Musser & Carleton (2005) and Jiang et al. (2024), we classify *ningshaanensis* as a member of *Tscherskia* (see under that genus). The perception of the external appearance of *C. canus* continued to be perplexing and in published works the species is still portrayed either inaccurately (Peng & Zhong 2005) or plainly erroneously (Smith & Hoffmann 2008, Pardiñas et al. 2017).
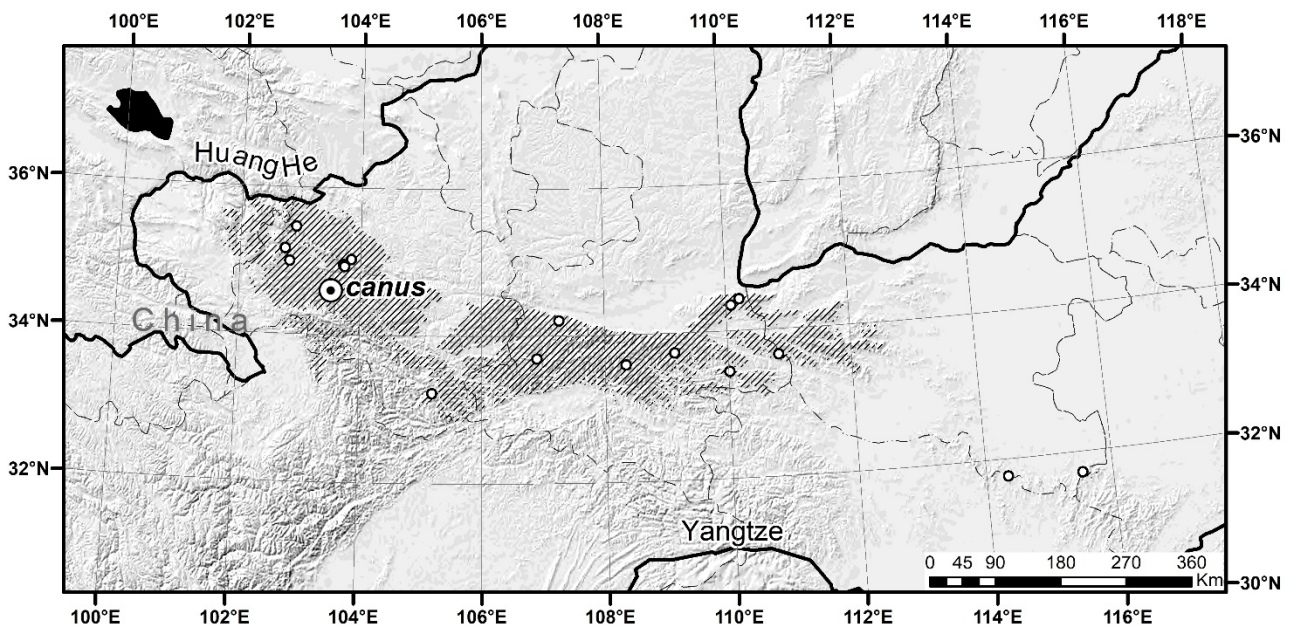

Figure 72: Distributional range of the Gansu hamster *Cansumys canus*.

Distribution (Figure 72). The range (estimated area = 92,870 km²) is situated in Central China between the middle flows of the Huang He and the Yangtze Rivers, and encompasses southern Gansu, southern Shaanxi, and south-eastern Henan. It stretches between the 103–106th meridians where tentatively embraced by the Ordos Plateau in the north and the Qinling Mts. and the Dabie Mts. in the south. Because the Gansu hamster was in the past not always securely delimited from *Tscherskia triton*, part of published distributional information remains puzzling. It is widely quoted for Nangxia (Zhang et al. 1997, Wang 2003, Smith & Hoffmann 2008), which is presumably based on a report of *Cricetulus triton canus* for the hilly South Ningxia Loess Plateau range (Zhang & Yu 1995). Peng & Zhong (2005) reported the Gansu hamster for the Ganzi Tibetan Autonomous Prefecture in north-west Sichuan. Neither Ningxia nor Ganzi are here accepted as a range of *C. canus* and are therefore not shown in Figure 72. The presence of *Cricetulus tscherskia canus* on the left bank of the Huang He River as plotted by Luo et al. (2000) is presumably also a misidentified *Tscherskia triton* proper.

The Gansu hamster inhabits deciduous and coniferous mountain forests and is presumably the only arboreal cricetine (Shenbrot 2017d). In a deciduous broadleaved forest in the Qinling Mts., the Gansu hamster is one of the most abundant rodents. Its range partly overlaps with that of *Tscherskia,* however, sympatry of these hamsters was only rarely reported (*e. g.* in Shenzhen; Gu 2005). Allopatry seems to prevail and was reported in the Qinling Mts. (Li & Wang 1996), the Gannan Plateau, and the Dubie Mts. (Huang et al. 2008). Altitudinal range of occurrence is 740–3,200 m (mean ≈ 2,000 m).

Characteristics. Moderately large hamster with proportionally long tail accounting for 77–82% of head and body length (Figure 73). External dimensions: body mass = 44–57 g, length of head and body = 129–140 mm, length of tail = 95–109 mm, length of hind foot = 17.9–20.4 mm, length of ear = 20.6–23.5 mm; means for cranial variables (n=20–21) are modified from Gu (2005): profile length of skull = 35.42 mm, zygomatic width = 18.28 mm, length of maxillary tooth-row = 6.17 mm. Ears are large (longer than the hind foot), rounded and protrude above the fur. They are densely clad with short hairs on both sides. Feet are small with proportionally long fore fingers. Hind foot is hairy around the heel; the nude soles have 6 pads of which the metatarsal pair is small; the central interdigital pair

Figure 73: Museum skin of the type specimen of Gansu hamster *Cansumy canus* in semidorsal (top), lateral (middle) and ventral (bottom) view (MCZ 23779). Note a white subaricular spot. Photo courtesy of Mark Omura

of pads is small, while the 2 outer interdigital pads are larger. The thumb of the hind foot is short, its claw short and slightly flattened, resembling a nail; claws are white. The tail is shaggy, thickly covered by 7–10 mm long fine hairs which hide the underlying annulation; hairs are longer at the base and the apical pencil is feeble. Dorsal fur is up to 15 mm long, hoary-grey and shaded brown, interspersed with all-black hairs; normally, the hair base is slate grey and the tip is whitish. Flanks are lighter and shaded cream; demarcation on the flanks is obscured. The belly is grey; hair bases are slate and tips are broadly whitish or cream. A narrow white streak extends from the chin to the sternum; its hairs are white to bases. There are 2 patches, both white to hair bases, on each side of the head: (1) a subauricular patch immediately below *porus acusticus*, and (2) a patch on the muzzle across the mystacial pad (Figure 74). The eyes are rimmed by a narrow dusky ring. Ears are dark-brown with a narrow white rim; the inner surface is more blackish. Paws are whitish-grey. The tail is brown-grey all-round, slightly lighter below. Juveniles are duller and have less shaggy tail.

The skull is somewhat long and narrow (zygomatic width accounts for ~ 51% of greatest skull length); rostrum is proportionally long, narrow and parallel sided (Figure 75). The nasals are comparatively narrow, the parietal bone is longer than wide, and the interparietal is broad and strap-shaped. The interorbital region is markedly more constricted (mean interorbital width = 3.52 mm) than in *Tscherskia triton* (= 5.39 mm; Gu 2005). Supraorbital ridges are prominent and extend backwards from the posterior tip of the frontal process of premaxilla, diverging evenly and following the lateral edge of the parietals; ridges are most prominent over the orbit, where they form a deep groove in-between. Incisive foramens are pretty short, the hard palate terminates beyond the posterior level of molars and pterygoids are remarkably short. The zygomasseteric complex is of pseudo-sciuromorphous type.
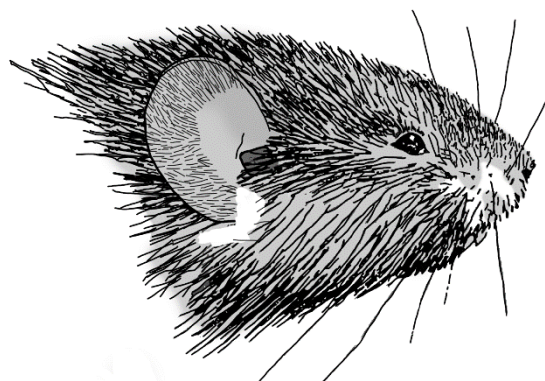

Figure 74: Head of the Gansu hamster *Cansumys canus*. Note white subauricular and mystacial patches. Modified from Gu et al. (2005)

Zygomatic plate is therefore narrow with emarginated anterior margin and the infraorbital foramen lacks the outer plate. Zygomatic keel and notch are both absent and infraorbital foramen is not seen from above; the anterior edge of zygoma transgresses into the rostrum as a smooth curve. A pair of grooves extends from the
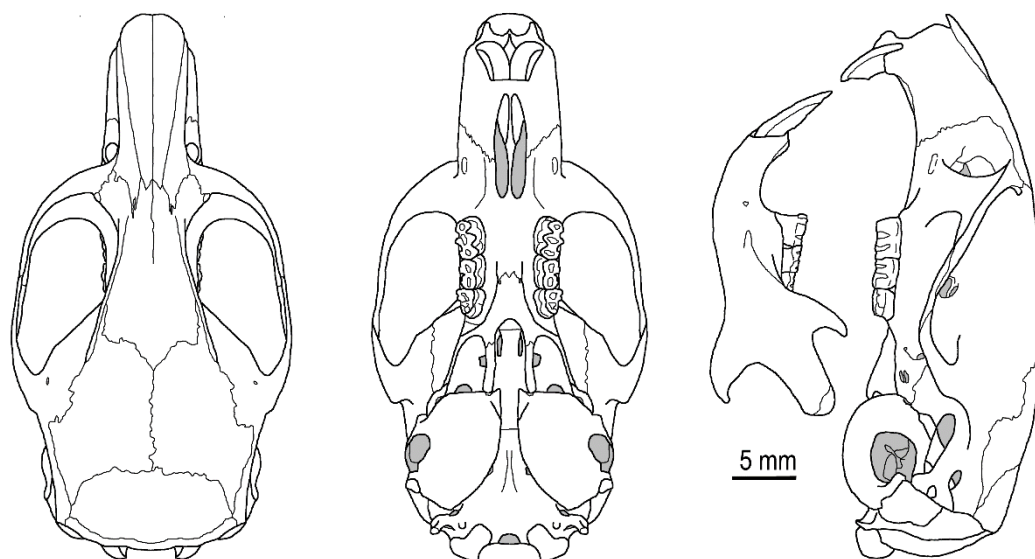

Figure 75: Skull and mandible in Gansu hamster *Cansumys canus*.

posterior edge of incisive foramens to the posterior edge of hard palate. Auditory bullae are large, rounded and closely approximated; their distance at the spheno-occipital synchondrosis is less than the width of interpterygoid fossa. The dorsal profile is evenly convex. Subsquamosal and postglenoid foramens are large. The mandible is slightly more robust that in *Tscherskia*, with blunter processes; the coronoid process is shorter and does not extend beyond the level of sigmoid notch (*incisura mandibulae*) (Allen 1928, Ross 1992).

The upper incisors are opisthodon and thicker than in other hamsters. Molars are robust and the molar-row is long (only slightly shorter than the diastema). Each row is enclosed by an elevated bony ridge. Molars are mesodont (hypsodont in terminology of Ross 1992) (Figure 76), their height from alveoli to crown amounting to 1.5–2.5 mm. Roots of the lower molars M_{2-3} overlap that of the incisor in lateral view and close in old adult age. The lower molars wear earlier than the upper ones. Well-worn molars display enclosed pits between each pair of major cusps (Figure 77). Mesoloph, a buccal projection of the endoloph (the enamel ridge connecting the protocone and hypocone) is present on M^2, which is presumably a plesiomorphic trait in hamsters (Ross 1992). Internal folds on M^{1-2} (particularly the internal fold *if*1 on M^1) remain confluent with primary folds even in worn molars. Anterior conuls of M^1 are large.

Karyotype: 2n = 24, consists of 16 pairs of metacentrics, 4 pairs of submetacentrics and 4 pairs of acrocentrics; the sex chromosomes have so far not been identified (Yang et al. 2003).
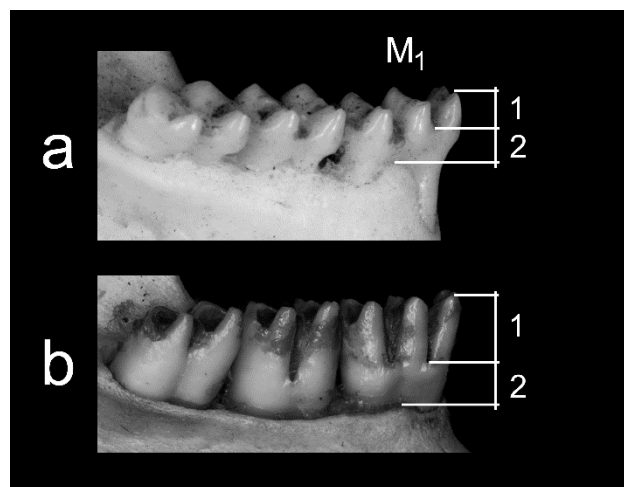

Figure 76: Lingual view of the lower molar row with slightly worn cusps in (a) *Cricetus cricetus* and (b) *Cansumys canus*. Note the difference in height of cusps (1) relative to crown height (2) in brachiodont (a) versus mesodont (b) molars. M_1 – 1st lower molar. Photo Mark Omura (b) and B. Kryštufek (a)

Variation and subspecies. Monotypic. Earlier reports on *C. canus* as a polytypic species (with *ningshaanensis* and the nominal subspecies) resulted from flawed delimitation between *Cansumys* and *Tscherskia*; *ningshaanensis* actually belongs to the latter (see the above account on Taxonomy).
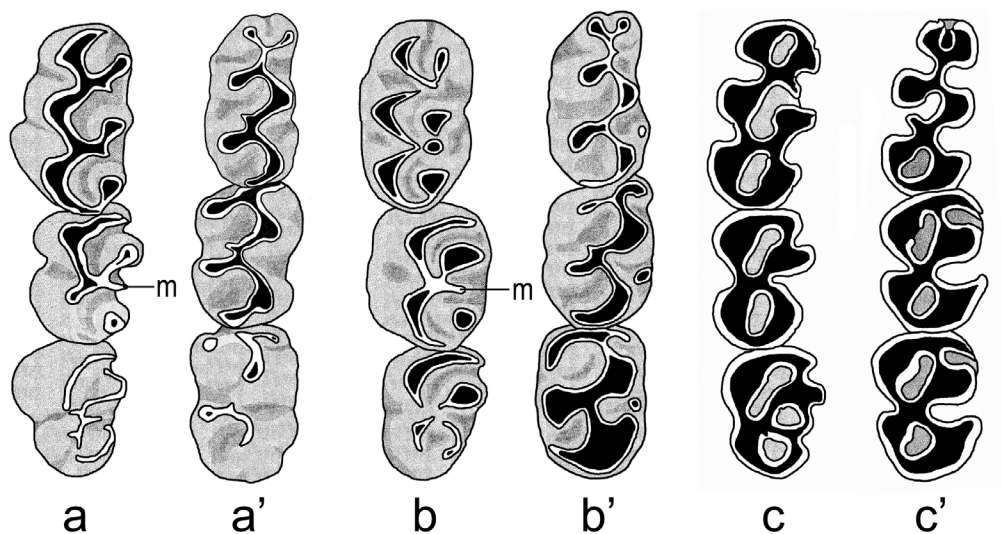

Figure 77: Grinding pattern of upper (a, b, c) and lower (a', b', c') molars in the Gansu hamster *Cansumys canus* from southern Gansu, China. m – mesoloph. Lingual is to the left; scale bar = 1 mm.

Tribe: Mesocricetini – New Tribe

Taxonomy. *Mesocricetus* was regarded as the most aberrant member of Cricetinae already by Miller (1912). Early cladistic analyses (Ross 1992, Potapova 2005), however, placed the genus deeply inside Cricetini and only subsequent attempts, based on chromosomal data (Romanenko et al. 2007) and nucleotide sequences (Neumann et al. 2006, Lebedev et al. 2018a) retrieved *Mesocricetus* as a sister group to tribe Cricetini (Figure 1). *Mesocricetus* lineage therefore deserves to be classified as a new tribe Mesocricetini.

Based on molecular clock, the divergence between Mesocricetini and Cricetini was estimated at 7.6 ±0.2–10.8 ±1.9 Mya, depending on the calibration point (Neumann et al. 2006). Lebedev et al. (2018a) arrived at a slightly older estimate of 11.65 Mya (CI = 9.69–13.96 Mya). Using chromosomal data, Romanenko et al. (2021) concluded that all major lineages of true hamsters, including *Mesocricetus*, diverged in a quick succession in the earliest Late Miocene which is a remarkable match with the estimates by Neumann et al. (2006) and Lebedev et al. (2018a). Contrary to this, Wang et al. (2024) estimated TMRCA, by using a complete genome and transcriptome, between *Mesocricetus* and *Cricicetulus griseus* (= *barabensis*) at 29.4 Mya. This estimate heavily predates the appearance of golden hamsters in fossil record. Specifically, *Mesocricetus* was present in the Eastern Mediterranean and the Caucasus regions since the Late Miocene (Vereshchagin 1959, Vasileiadou & Sylvestrou 2022) and throughout the Pliocene (Turnbull 1975, Peshev et al. 2004).

Type genus. *Mesocricetus*, Nehring, 1898.

Diagnosis and Comparisons. Mesocricetini new tribe belongs to Cricetinae as evident from its morphology (*e. g.* bicuspidate dentition and the presence of inner cheek pouches) and phylogenetic analyses based on nucleotide sequences (Steppan & Schenk 2017). On the other hand, Mesocricetini differ from the remaining tribes of Cricetinae, *i. e.* Cricetini and Urocricetini, in nucleotide sequences and in morphological and chromosomal data. In Mesocricetini, (1) the subauricular dark stripe is present (Figure 9), while it is absent in the remaining true hamsters; (2) the sternal patch is present (Figure 81) but absent in all other true hamsters except *Allocricetulus eversmanni*; (3) the soles are largely nude between the metatarsal pads and the heel (Figure 80) (soles are hairy at least posterior to pads in the remaining true hamsters); (4) *papillae foliatae* are arranged in 2 rows but in 1 row in the remaining true hamsters (Vorontsov 1958); (5) gallbladder is present, but is absent in the remaining true hamsters (Carleton & Musser 1984); (6) intestine is long (> 5.5-fold the head and body length); the remaining true hamsters, except *Cricetus*, have this quotient <5.0 (Vorontsov 1962, 1982); (7) mesolophid is present (Figures 86 & 95), but is absent in the majority of true hamsters (Ross 1992); (8) M_3 is larger than M_2 (M_3 is smaller than M_2 in the remaining true hamsters; Gromov et al. 1963, Ross 1992); (9) 2nd and 3rd molars, both upper and lower, are long and relatively narrow having width-to-length ratio < 0.75 (the ratio is 0.80–1.00 in the remaining hamsters; Lozan 1971); (10) rostrum is rectangular with parallel lateral margins (Figures 85 & 94); in the remaining true hamsters (except *Cansumys*), rostrum is the widest at nasolacrimal capsule; (11) subsquamosal foramen is absent and, as a consequence, hamular process is not separated from squamosal (Figures 85 & 94); subsquamosal foramen is present in the remaining true hamsters, dividing hamular from squamosal (the foramen is heavily squeezed and slit-like in *Tscherskia*); (12) entepicondylar foramen is absent in the distal end of humerus (Figure 78), but is present in the remaining true hamsters (Nehring 1898c); (13) number of mammae is high (> 10), while all the remaining true hamsters have 4 pairs of mammae (Figure 11) (Argyropulo 1933c, Ellerman 1941); (14) trident of the baculum is largely cartilaginous even in adults (Figure 17i), but is osseous in the remaining true hamsters (Argyropulo 1933c); (15) diploid number of chromosomes is high (2n = 38–44), but lower (2n =

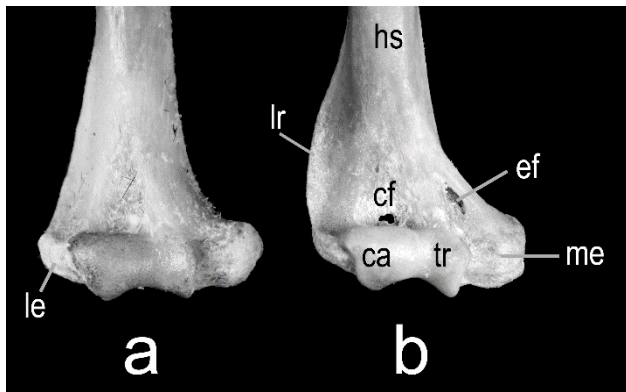20–34) in the remaining true hamsters (Romanenko et al. 2007).

Figure 78: Ventral view on the distal portion of right humerus demonstrating the absence (a – *Mesocricetus auratus*) and presence (b – *Cricetus cricetus*) of entepicondylar foramen (ef). Acronyms: ca – capitellum; cf – coronoid fossa; hs – humeral shaft; le – lateral epicondyle; lr – lateral epicondylar ridge; me- medial epicondyle; tr – trochlea.

Content. The new tribe contains the genus *Mesocricetus* Nehring, 1898, with 4 recent species (see below).

Genus: *Mesocricetus* Nehring, 1898 – Golden Hamsters

Mesocricetus Nehring, 1898c: 494. Type species by subsequent designation (Aharoni 1932: 172) is *Cricetus nigricans* Brandt (= *Mesocricetus raddei*).

Etymology. *Mesocricetus* is an amalgamated name consisting of the Greek 'μέδος' ('médos', i.e. 'medium') and *Cricetus* for hamsters (see the Etymology under *Cricetus*), therefore a hamster of medium size or "Mittelhamster" (Nehring (1898c: 494).

Nomenclature. In a footnote on p. 494, Nehring (1898c) discussed the (in)appropriateness of *Mesocricetus* as a combination of different languages, the Latin and Greek (*vox hybrida*). Nehring admitted that the new name combination could be all-Latin and quoted two possible solutions: 'Semicricetus' and 'Mediocricetus'. Nevertheless, he concluded that "The Greek language is much more suitable for forming compounds" (Die griechiche Sprache ist zur Bildung von Zusammensetzungen viel geeigneter) and chose *Mesocricetus* as this particular combination captures his intentions more accurately than any other. Neither

Semicricetus nor Mediocricetus have been proposed as taxonomic names.

Taxonomy. *Mesocricetus* was proposed as a subgenus of *Cricetus* (Nehring 1898c) and retained as such still in the 1970s (Trouessart 1904, Heptner 1926, Aharoni 1932, Argyropulo 1933b, c, Neuhäuser 1936, Vinogradov & Gromov 1956, Anderson & Sinha 1972, Ching-Mei & Anderson 1975, Kuznetsov 1975). On the other hand, only 2 years after the establishment of *Mesocricetus*, Satunin (1900) elevated its rank to a genus in its own right. Satunin's arrangement gradually prevailed (Dombrowski 1907, Miller 1912, Călinescu 1931b, Vinogradov 1933, Ellerman 1941, Vinogradov & Argyropulo 1941, Kuznetzov 1944, Ellerman 1948, Ellerman & Morrison-Scott 1951, Gromov et al. 1963, and subsequent authors) and was not challenged since the 1950s.

Nehring (1898c) defined *Mesocricetus* as an intermediate between the large *Cricetus* and small hamsters, which were in his time clumped under *Cricetulus*. Because of its colourful pelage and strongly ridged skull, many authors saw the nearest relative to *Mesocricetus* in *Cricetus* (*e. g.* Argyropulo 1933b, c), despite clear differences between them in zygomasseteric structure and baculum. Phylogenetic reconstructions based on chromosomal data (Romanenko et al. 2007) and molecular markers (Neumann et al. 2006, Lebedev et al. 2018a) showed that *Mesocricetus* is a sister genus to Cricetini (Figure 1).

With the exception of Ognev & Heptner (1927), who classified *Allocricetulus eversmanni* into *Mesocricetus*, the taxonomic scope of golden hamsters was not questioned ever since Nehring's (1898d) revision. Number of species was, however, for long contested and varied between a single polytypic species (*auratus*; Ellerman & Morrison-Scott 1951, Vereshchagin 1959, Harrison & Bates 1991), 2 species (a polytypic *auratus* and *raddei*; Vinogradov & Argyropulo 1941), 3 species (a polytypic *auratus, newtoni* and *raddei*; Ellerman 1941, Corbet 1978, Corbet & Hill 1980, 1986), 5 species (*auratus, brandti, koenigi, newtoni, raddei*; Trouessart 1904), or 6 species (*nigriculus* in addition to 5 species recognized by Trouessart *l. c.*; Dombrowski 1907). This number stabilized at current 4 species (*e. g.* Honacki et al. 1982), following revisions by Vorontsov (1960), Hamar & Schutowa (1966), and Lyman & O'Brien

(1977). Subsequent phylogenetic reconstructions confirmed the 4-species taxonomy of *Mesocricetus* (Neumann 2007, Neumann et al. 2006, Lebedev et al. 2018a).

Speculations on the phylogenetic relationships between species coincided with the progress in karyological analyses. Since the chromosomal number is much higher in *Mesocricetus* than in the remaining hamsters, the idea of polyploid evolution was launched in the 1950s. The hypothesis proposed a hybridogenic origin of *M. auratus* (2n = 44) from *Cricetulus griseus* (= *barabensis*) and *Cricetus*, each with 2n = 22 (Sachs 1952, Tobias 1953). It was therefore claimed that *M. auratus* was a tetraploid, while both parental species were putatively diploids. The hypothesis was seemingly concordant with other odd peculiarities of *M. auratus* and its congeners, specifically its high nipple counts (14–22 mammae; 8 mammae in putative parental species), a colourful pelage (similarly as in *Cricetus*) with only partially black underside (black throughout in *Cricetus* but light in *Cricetulus*), and small distributional range (ranges are large in *Cricetus* and majority of *Cricetulus*). It was further suggested that a putatively tetraploid *Mesocricetus* have arisen from diploids in the recent period (Sachs 1952). This hypothesis was refuted shortly afterwards (White 1959) and subsequent chromosomal banding analyses provided strong argument against polyploidy in golden hamsters (cf. Gamperl et al. 1978).

Another hypothesis on the evolution of golden hamsters presumed gradual reduction of diploid chromosomal number through successive centric fusions: 2n = 44 (*auratus*) → 42 (*brandti*) → 38 (*newtoni*) (Hamar & Schutowa 1966). Based on differential staining of chromosomes (G-banding), Popescu & DiPaolo (1980) agreed that *auratus* was the common ancestral species but suggested independent evolution for *brandti* and *newtoni*. Hamar & Schutowa (1966) further divided the genus into 2 major groups, separated by the Caucasus: the monospecific *raddei* group to the north of the Caucasus and the lineage with the remaining golden hamsters (*auratus, brandti, newtoni*) occurring to the south of the Caucasus Mountain chain. This idea was not a novel since several earlier authors distinguished between the larger black-bellied hamsters of Ciscaucasia from smaller hamsters with light bellies occupying Transcaucasia. These groups were classified either as distinct species (*auratus* and *raddei*; Vinogradov & Argyropulo 1941) or subspecies of *auratus* (Vereshchagin 1959), or as independent species groups (Hamar & Schutowa 1961).

Molecular phylogenies uniformly retrieved tandem groups of golden hamsters, the *auratus–raddei* tandem and the *brandti–newtoni* tandem (Neumann et al. 2006, Lebedev et al. 2018a, Steppan & Schenk 2017). TMRCA for recent species is estimated at 2.5–2.7 Mya (Neumann et al. 2006), hence suggesting speciation events during the Lower Pleistocene. Specifically, the divergence times between pairs of species were estimated at 1.81 Mya (CI = 1.04–2.61 Mya) for *auratus–brandti* (Lebedev et al. 2018a), 1.2–1.5 Mya for *auratus–raddei*, and 1.7-1.8 Mya for *brandti–newtoni* (Neumann et al. 2006).

Taxonomic status of species was tested in interspecific hybridization trials which included all species except *raddei*. Trials between *auratus* (2n = 44) and *brandti* (2n = 42) invariably failed (Matthey 1959, Todd et al. 1972, Lyman & O'Brien 1977). Early attempts to cross *newtoni* (2n = 38) and *auratus* (2n = 44) similarly failed (Marches 1964a, b), but subsequent efforts resulted in sterile offspring with intermediate chromosomal count (2n = 41; Raicu & Bratosin 1966, 1968, Todd et al. 1972). Tests between *newtoni* and *branti* produced hybrids with 2n = 40, but their sterility / fertility has not been assessed (Raicu et al. 1972, Todd et al. 1972).

As is the case with Cricetinae in general (Ross 1992), the fossil record contributed little towards clarification of the evolution of golden hamsters. Specifically, names of recent species were attributed to fossil material quite arbitrarily (Vereshchagin 1959). *Mesocricetus rathgeberi* Pieper, 1984, from the Southern Aegean Island of Armathia (near Kasos) and presumably of Holocene age is worth mentioning. This was a large golden hamster, of similar size as *M. raddei*, with strongly ridged skull and deep interorbital groove between the ridges (Pieper 1984). Pavlinov (2003) included *rathgeberi* on the list of recent mammals, albeit with a question mark.

Distribution. The extant species of golden hamsters have allopatric distributions in the north-eastern corner of the Mediterranean Sea and around the Black Sea,
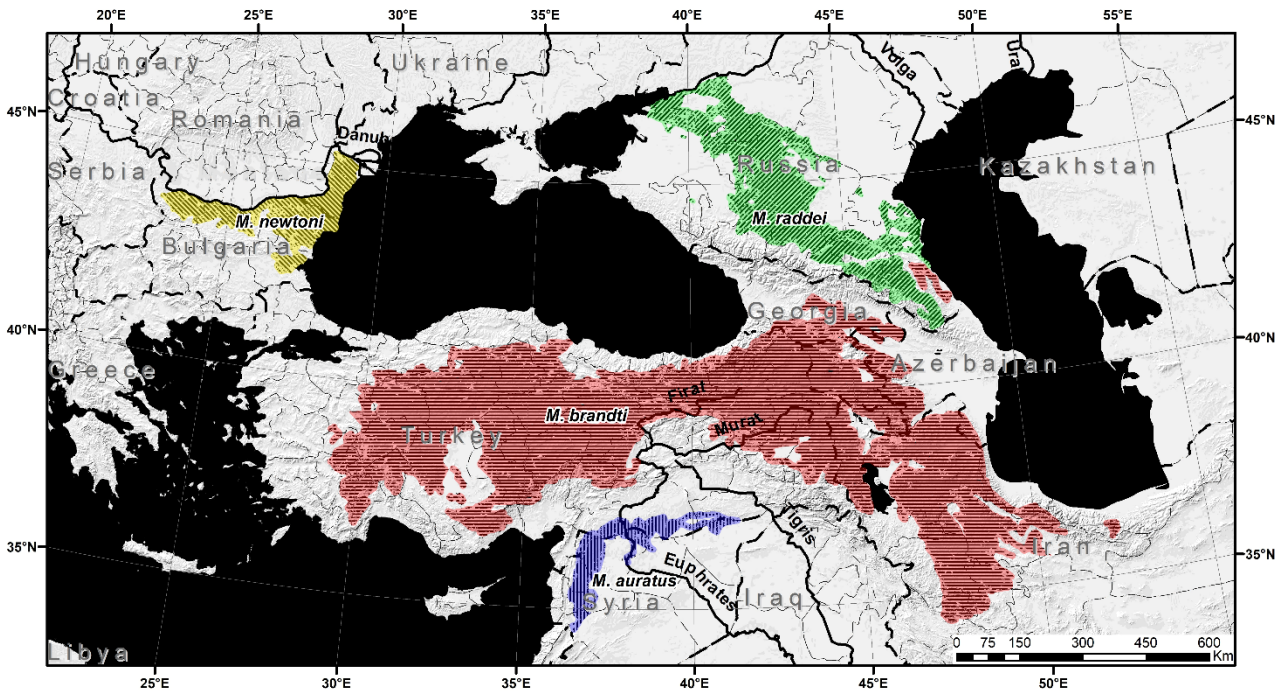
Figure 79: Distribution of the extant golden hamsters *Mesocricetus*. Note that species ranges are allopatric.

reaching the Caspian Sea in the east (Figure 79). Their total range is small (area ≈ 660,000 km²) and 2 species (*auratus* and *newtoni*) have the most restricted distributions of any hamsters (area < 40,000 km²). The Pleistocene ranges of at least 3 species (*auratus, raddei, newtoni*) exceeded the current ones (see species accounts for further details).

Characteristics. Form is robust and chunky; the eyes are fairly large (Figures 83, 88, 92 & 97). The ears are of moderate size, pigmented and clad with short fine hairs on both sides (Figure 8). Tail is short and stubby (Figure 97), concealed in fur; its surface shows no traces of scales or annulations, but is densely hairy, hairier below than above. Feet are comparatively short and broad with 4 and 5 fingers on front and hid feet, respectively; the front thumb is reduced. Soles and palms are nude, with 5 and 6 tubercles, respectively. All plantar pads are of similar size, however, the metacarpal pads are significantly larger than any of the 3 interdigital pads (Figure 80). Fur is moderately long (10–14 mm on the mid-back), dense and very soft; density of hair fibres is largest on the back, it declines gradually towards the flanks and is the least dense ventrally. Hairs at the tail base are noticeably longer from those on the rump; the terminal pencil is rather short (length = 1.5–4.5 mm). Mystacial vibrissae measure up to ~ 35 mm. Colouration is highly distinctive and although at glance similar to that of *Cricetus*, there are important

differences between the two genera (Figure 9). Characteristic of *Mesocricetus* is a dark subauricular (shoulder) stripe, which is followed by light neck (collar) patch (both are absent in *Cricetus*), and a transverse sternal stripe, which is nearly always darker than the rest of the underside (see also under *M. raddei*) (Figures 84, 90, 93 & 98).
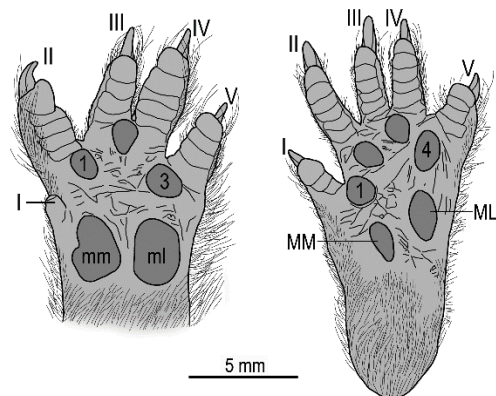

Figure 80: Left palm (left) and sole (right) in Syrian golden hamster *Mesocricetus auratus*. Digits are shown in Roman numerals (thumb = I) and interdigital pads are shown in Arabic numerals; pads: mm / MM – medial metacarpal / metatarsal pad, ml / ML – lateral metacarpal / metatarsal pad.

Females invariably have > 10 nipples (Figure 11b), but their number varies within species on the one hand and is poorly documented in the literature on the other hand. Ross (1992) gave range as 14–22; the maximum

Figure 81: Skins in dorsal (top row), ventral (middle row) and lateral view (bottom row) of golden hamsters: a – *Mesocricetus auratus* (Syria); b – *M. raddei* (Dagestan, Russian Federation); c – *M. brandti* (Sirbasan, Kars, Turkey); d – *M. newtoni* (Shabla, Bulgaria). Photo: C. Mlinar (c) and B. Kryštufek (a, b, d). Inset (c) is replicated from Kryštufek & Vohralik (2009: 55, Figure 26); reproduced with permission of the Science and Research Centre Koper.

is possibly from Kuznetzov (1944), who reported for *Mesocricetus* 7–11 pairs of nipples, but gave no further details. In *M. auratus*, which was studied in detail, the nipple count varies between 11 and 17 (median = 14); 44% of captive-born females (n = 168) deviated from the median value (Anderson & Sinha 1972, Ching-Mei & Anderson 1975). Nipples are continuous along the mammary line with 2 pairs of each, the pectoral, abdominal and inguinal mammae. Supernumerary nipples are located on the anterior or the posterior end of the mammary line.

Glans penis is the simplest of any true hamsters (Vorontsov 1982). The surface is densely covered by numerous spines, which are absent around the *meatus urinarius*. Three papillae stick from meatus, the central and 2 lateral papillae; the lateral papillae are expanded distally (Figure 16). The proximal stalk is short and strongly built with an expanded base; it is grooved ventrally. The three distal processes are long and widely expanded in their middle portion, but the lateral two converge distally with the central element into a pointed apex. Lateral processes are longer than the central one (Figure 17i). The baculum of *M. auratus* shows three or four ossification centres: 1 primary for the stalk, 1 secondary centre for each of the 2 lateral prongs, and sometimes the 4th centre for the medial distal process. Ossification of distal trident starts on lateral digits at the age of ~ 6 months; central digit remains cartilaginous, though some ossification may take place at the age of ~ 1 year (Callery 1951). In old males, processes ossify with the proximal stalk into a single bony element.

Skull is easily recognizable by a combination of prominent ridges, a long, heavy rectangular rostrum with parallel lateral margins, small and frequently triangular interparietal, short incisive foramina, which posteriorly do not reach molar line, and the pseudosciuromorphous zygomasseteric structure (Figures 85 & 94). The inferior maxillary root of zygoma lacks the forwardly extended plate that normally forms the external plate of the infraorbital foramen (Figure 19b2). Hence, when viewed from above, the anterior margin of the superior zygomatic root forms an unbroken curve to maxilla-premaxillary suture. The zygomatic notch and spine are also absent (Figure 19a2). In the absence of the outer plate, the infraorbital foramen assumes an oval outline which,

however, is frequently flattened from the inner or the outer side, or both (Figure 20b, h).

Cranial profile is slightly convex; brain-case is diamond shaped, short and deep. The occipital region is inclined towards condyles, which are shifted backward and clearly seen in dorsal view. Nasals are long with a pointed tip; posteriorly, they reach well behind the lacrimal bone. Parietals are squeezed by the expanded squamosals. Zygomatic arches are heavy and parallel; interorbital region is constricted and is much narrower than rostrum. Supraorbital ridges are present in adults and the lambdoid crest is strong. Palate extends behind the tooth row; pterygoid fossa is deep. Auditory bullae are relatively large and oval-shaped. Mandible shows no peculiarities, except for long and powerful coronoid process.

Incisors are robust but show no peculiarities. The two posterior molars are not much reduced in comparison to the 1st molar; besides, they are narrower than in other true hamsters. The anterior–to-posterior trend of size reduction, which is obvious in the maxillary row, is entirely absent in mandibular molars. The M_3 tends to be the largest and M_1 the smallest molar. The numbers of alveoli are 4, 4, 3 for M^1, M^2, and M^3, respectively, and 2 for each lower molar.

Key to species

Species of golden hamsters differ in fur coloration (*cf.* Figure 81) however, individual variation is significant and not all vouchers can be securely classified on this ground. For achieving reliable classification, we advise the readers to consult illustrations and text below.

1a) Dorsal pelage is bright golden-brown, the subauricular stripe is never black, the sternal patch is usually buff and never pure black, belly is whitish-creamy (Figure 81a); present in Syria and Turkish provinces of Hatay, Kilis, Gaziantep, and Şanlıurfa …………………...…………. *auratus*

1b) Dorsal pelage is grey or brown-grey, the subauricular stripe is black, the sternal patch is pure black, belly is grey or black (Figures 81b–d); present in south-eastern Europe, southern European Russia, Georgia, Armenia, Azerbaijan, Iran, and Turkey in Asia (absent in the provinces

of Hatay, Kilis, Gaziantep, and Şanlıurfa) …………………………………………………... 2

2a) Size is larger (head and body > 150 mm); underside usually dark-grey or black (Figures 81b & 90); occipital region is heavily inclined towards condyles; temporal ridges in full-grown individuals reach lambdoidal crest (Figure 85); mesopterygoid fossa (mean width = 3.28 mm) is on average conspicuously wider than incisive foramina (width = 2.34 mm); 4 autosomal pairs are acrocentric ……………………………………..…… *raddei*

2b) Size is smaller (head and body < 165 mm); underside usually light-grey (Figure 81c, d); occipital region is not particularly inclined towards condyles, or is nearly orthogonal (Figure 94); mesopterygoid fossa (mean width = 2.3 mm) is on average inconspicuously wider than incisive foramina (width = 2.2 mm); at most 2 autosomes are acrocentric ………….…………………….3

3a) Sternal patch is shorter (length < 35 mm), frequently surrounded by white patches and occasionally split medially (Figure 98); usually a single oblique black stripe (subauricular stripe) in front of light collar stripe (Figures 81c & 97); occipital stripe usually missing (Figure 81c); 2n = 42; present in south-western Asia and Dagestan ………………………………………….. *brandti*

3b) Sternal patch is longer (length > 50 mm), not surrounded by white patches and never split (Figure 93); usually 2 oblique black stripes (subauricular stripe and postero-lateral extension of sternal patch) anteriorly and posteriorly to light collar stripe (Figures 81d & 92); occipital stripe bold and long (Figure 81d); 2n = 38; present in south-eastern Europe ……….………..…*newtoni*

Species group *auratus*

The *auratus* group is characterized by nucleotide sequences (Neuman et al. 2006, Lebedev et al. 2018a) and higher diploid number of chromosomes (2n = 42–44). Gland penis is cylindrical and parallel sided. Temporal ridges are well developed and reach the lambdoidal crest in old individuals; they bent medially anterior to the fronto-parietal suture. In very old individuals, the ridges lie close together with medial groove in-between. The frontals are not much compressed posteriorly and the fronto-parietal suture is short (Figure 85). The *auratus* group contains 2 species (*auratus* and *raddei*) which presumably diverged 1.2–1.5 Mya (Neumann et al. 2006). In fossil record, they can be traced back to the Late Pleistocene (*auratus*; Tchernov 1975) and Middle Pleistocene (*raddei*; Argyropulo 1941b, Vereshchagin 1959, Baryshnikov & Baranova 1983).

These two golden hamsters are externally the most dissimilar in the genus *Mesocricetus* and their phylogenetic closeness was never assumed in the times of traditional morphology-based taxonomy. Hamar & Schutowa (1966) even proposed for *raddei* a basal position in the genus.

Mesocricetus auratus (Waterhouse, 1839) – Syrian Golden Hamster

Cricetus auratus Waterhouse, 1839a: 57. Type locality: "Aleppo", Syria.
Cricetus (Mesocricetus) auratus: Nehring, 1898d: 389. Name combination.
M[esocricetus] auratus: Satunin, 1900: 301. First use of the current name combination.
M[esocricetus] aureatus: Meulen & Kolfschoten, 1986: 206. Incorrect subsequent spelling of *auratus*.

Etymology. Species epithet *auratus* is a Latin adjective meaning 'ornamented with gold', in allusion to the fur colouration in the species. The adjective derives from the noun 'aurum' meaning 'gold'.

Taxonomy. Because *auratus* is the oldest name in *Mesocricetus,* it was occasionally used to incorporate all species group names of golden hamsters (e.g. Ellerman & Morrison-Scott 1951, Harrison & Bates 1991). This, however, was an extreme view and more frequently *auratus* was defined with the inclusion of *brandti* (Argyropulo 1933b, c, Ellerman 1941, 1948, Vinogradov & Gromov 1956) and also *newtoni* (Vinogradov & Argyropulo 1941). Current taxonomic scope of *auratus* was set by Hamar & Schutowa (1966). Syrian golden hamster is well defined by nucleotide sequences, diploid number of chromosomes, and external morphology. It is a sister species to *M. raddei* (Lebedev et al. 2018a).
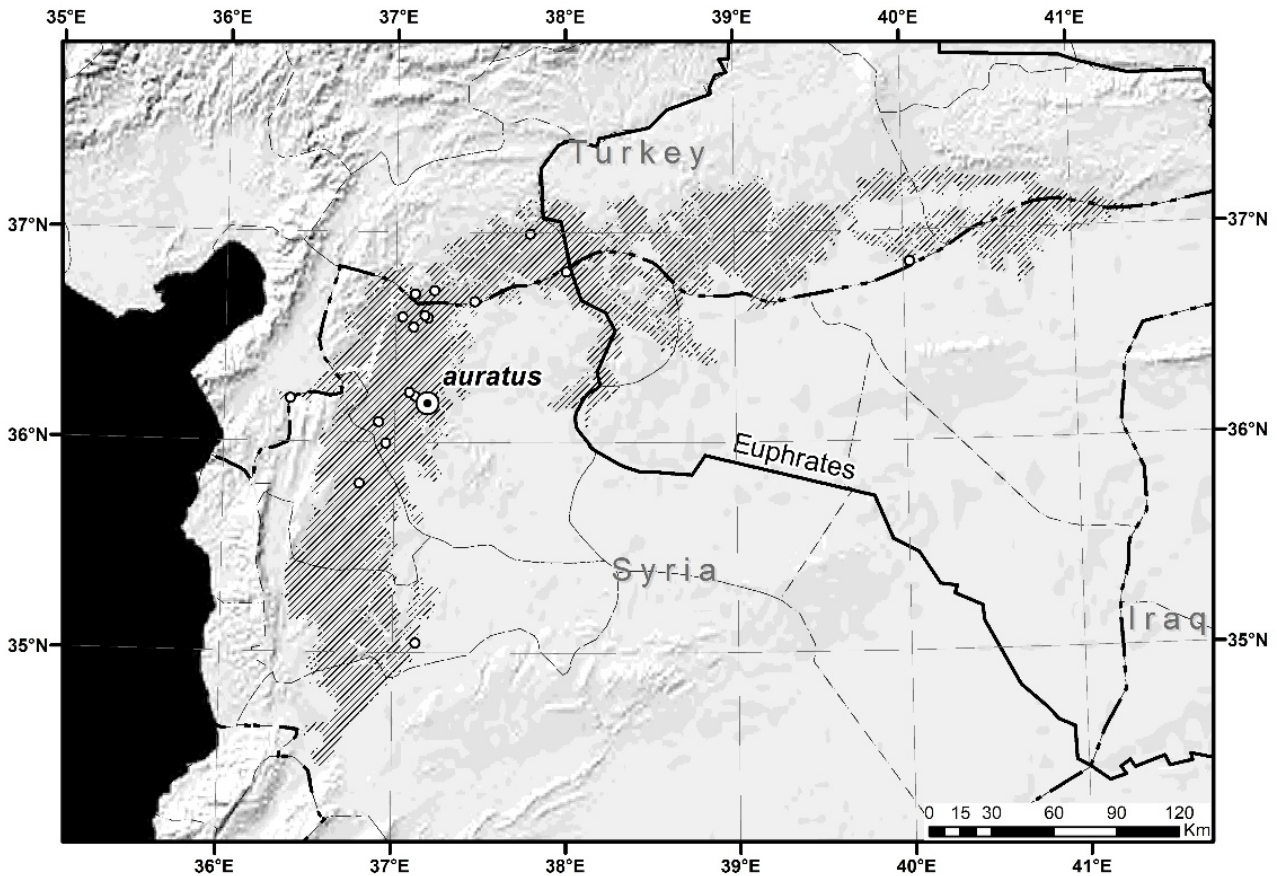
Figure 82: Distribution of the Syrian golden hamster *Mesocricetus auratus*.

Distribution. Syrian golden hamster occupies the smallest area (= 24,125 km²) of any true hamster. Range is spread in the bordering area between south-eastern Turkey and north-western Syria (Figure 82). The great majority of records come from the Halab Province (Syria); the species is known also from Idlib and Turkish provinces of Gaziantep and Kilis. There are 2 outliers, the eastern in Şanlıurfa (Yiğit et al. 2003) and the southern in Hama (Aidek & Amr 2021). In Syria, the species presumably reaches the southern Homs plains where it is prevented from further spreading by the north-western extension of the Syrian Desert and the Palmira Mountain range (Aidek & Amr 2021). A historical record from 1949 from Hatay (Eisentraut 1952) remains unconfirmed, and reports for Lebanon and Israel (Musser & Carleton 1993) are most likely erroneous (Shehab et al. 2004). Syrian golden hamster was, however, present in Israel during the Last Glacial Maximum but its range shrunk northwards since then (Kryštufek & Vohralík 2009). *Mesocricetus auratus* occupies steppes on sandy clay sediments overlying limestone (Gattermann et al. 2001, Kryštufek 2017a); such habitat is now largely transformed into rain-fed crop fields and rocky pastures.

Characteristics (Figure 83). External appearance is same as for the genus, the size, however, is on average slightly smaller than in *brandti* and *newtoni*. Lyman & O'Brien (1977) reported body mass in 2-year-old captive bread animals as 97–113 g (mean = 105 g) for *auratus* and 137–258 g (mean = 163 g) for *brandti*. Dimensions in free-living *M. auratus* are: body mass = 82–175 g, length of head and body = 128–165 mm, length of tail = 13–21 mm, length of hind foot = 19.0–22.0 mm, length of ear = 18.0–22.5 mm; condylobasal length of skull = 30.1–38.6 mm, zygomatic width = 17.2–19.8 mm, length of maxillary tooth-row = 5.0–6.6 mm. Dorsal fur is deep golden brown with rufescent hue over the body and particularly along the spine and on rump; the auricular region and the head are faintly yellow tinted. The sides of the muzzle, throat, and under parts of the body are white and frequently tinted creamy; hair bases are slate (Figures 81a & 83). The subauricular stripe is a mixture of brown and black hairs, and varies from deep brown to blackish brown; posterior to it is white collar stripe which connects to the underside. Dark-tipped hairs cluster on the crown, forming a blackish-brown patch of moderate size

Figure 83: Syrian golden hamster (*Mesocricetus auratus*). Photo courtesy of Christian Kern. Used with permission of the Science and Research Centre Koper.
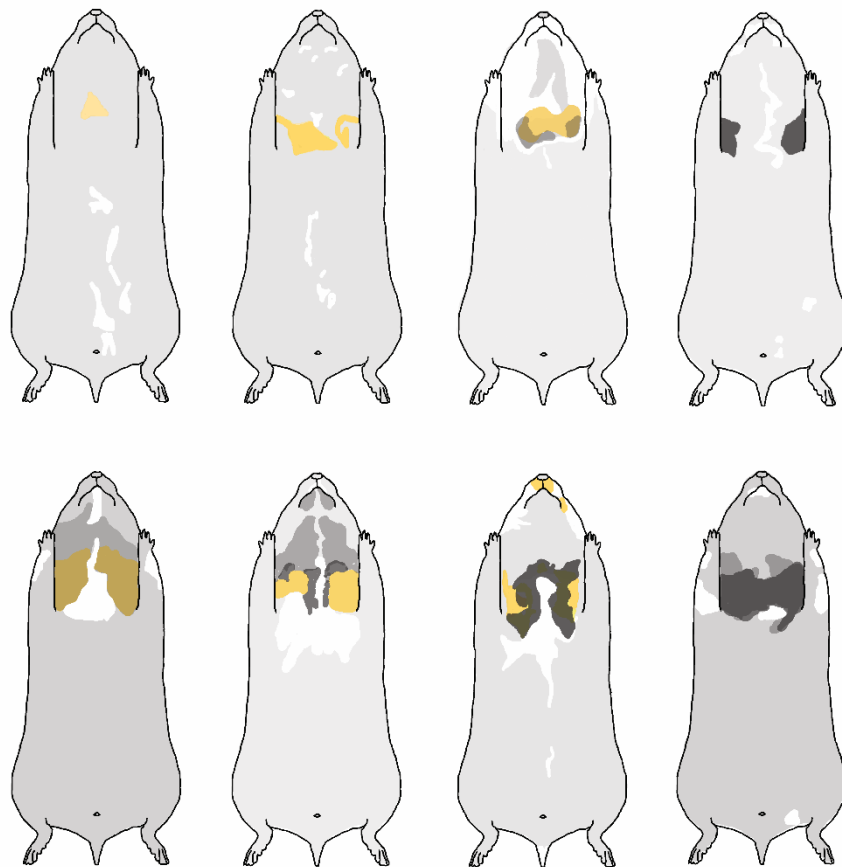

Figure 84: Ventral side of Syrian golden hamsters *Mesocricetus auratus* demonstrating variability of the sternal patch.

which, however, is frequently blurry. Sternal patch is of variable size, form and colour (Figure 84). It is exceptionally an isolated patch but more commonly a 21–32 mm long band which is frequently split by white medial stripe. The patch is usually golden brown and frequently with admixture of black-brown hairs, which may aggregate into a blackish area of variable size. Tail is of same colour as the back except for whitish terminal hairs. Feet are covered by white to light cream short hairs. The ears are pigmented grey and covered by creamy white fine hairs. Various colour variants were produced in captivity (Robinson 1968).

The usual number of nipples is 14, but this varies widely (range = 11–16). The glans penis is rather narrow but deep; length = 3.6 mm, width = 2.55 mm, depth = 2.9 mm. Lateral papillae are decidedly larger and longer than the central papilla; their distal ends are expanded (Figure 16). The entire baculum is ~ 4.3 mm long, and 1.3–1.4 mm wide at its triangular base (Kryštufek & Vohralík 2009).

The skull does not deviate appreciably from the appearance typical of the genus (Figure 85). Width across zygomatic arches accounts for 53.2–57.8% of

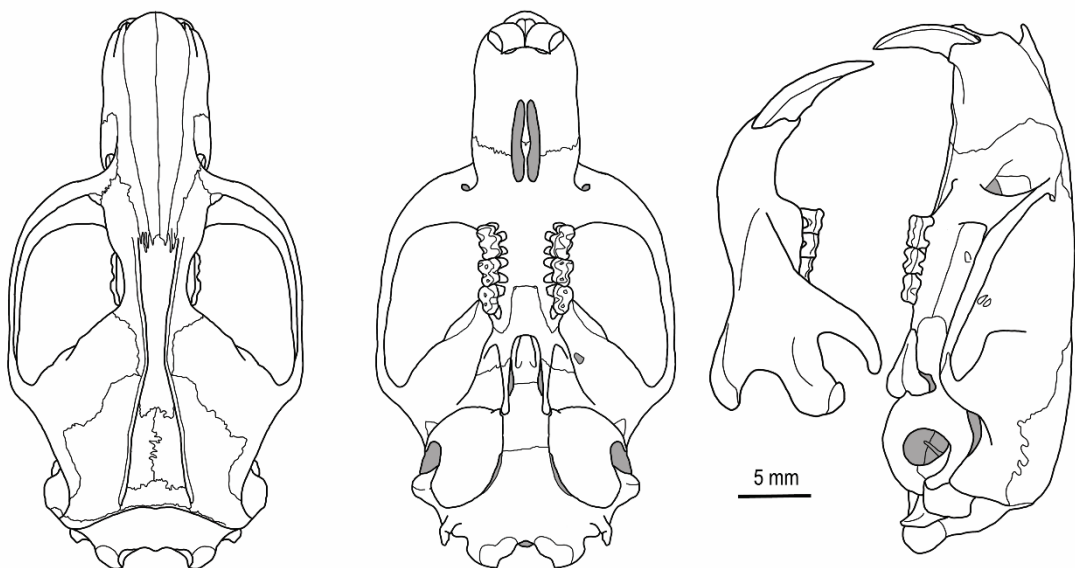*Mesocricetus auratus*

Mesocricetus raddei

5 mm
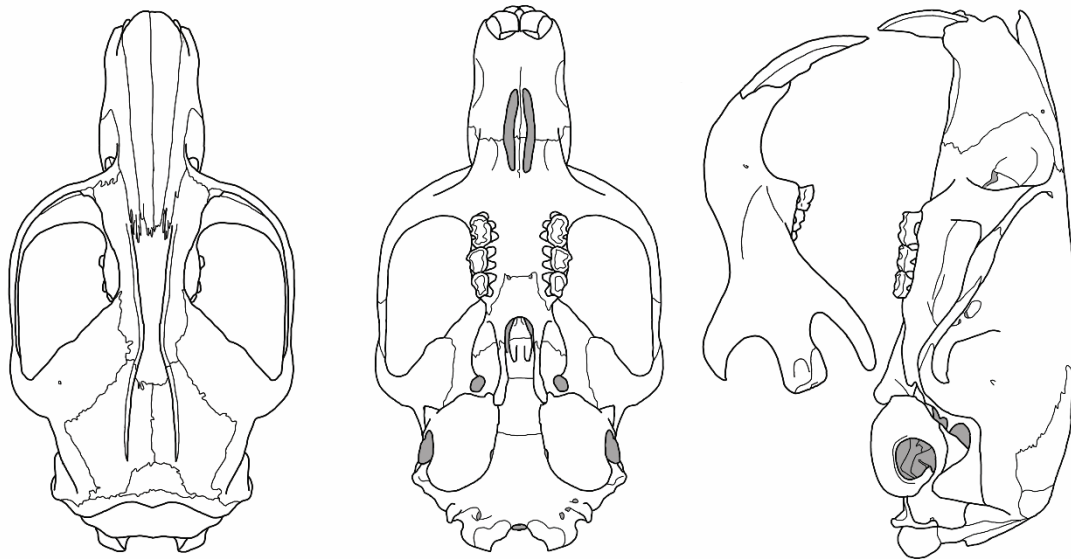
Figure 85: Skull in golden hamsters from the *auratus* species group (top to bottom): *Mesocricetus auratus* and *M. raddei nigriculus* (Rostov Oblast, Russian Federation).
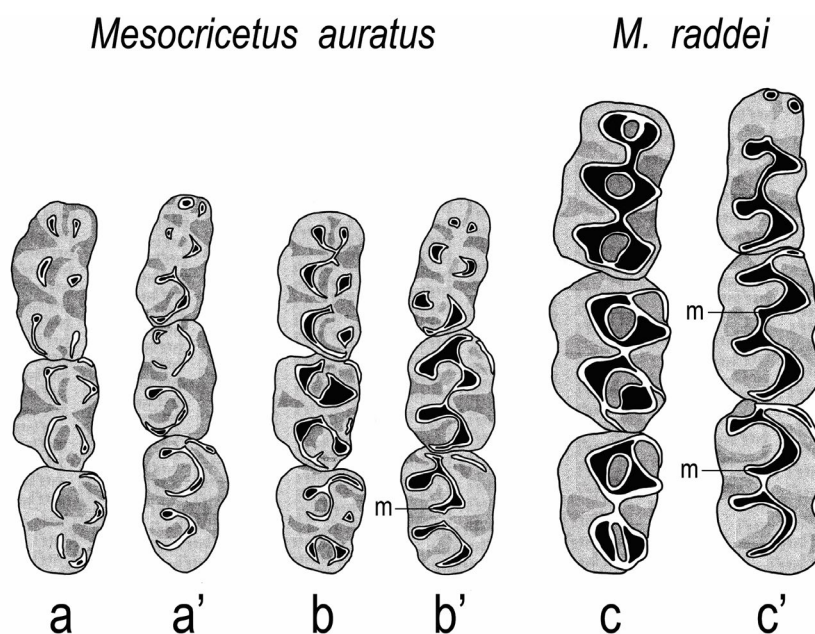
Mesocricetus auratus   *M. raddei*

Figure 86: Grinding pattern of upper (a, b, c) and lower (a', b', c') molars in the *auratus* species group of golden hamsters: a, b – *Mesocricetus auratus*, c – *M. raddei raddei*. m – mesolophid. Scale bar = 1 mm.

condylobasal length. The masseteric plate is short (~ 2.4 mm) and the infraorbital foramen is oval (Figure 20h).

Pterygoids normally converge anteriorly at the hard palate, hence the interpterygoid fossa is triangular in the greater part (= 71%) of the skulls; it is rectangular in 9% of individual and intermediate in the rest (Kryštufek & Vohralik 2009). Dentition shows no peculiarities (Figure 86a, b).

Karyotype: 2n = 44, NF = 82, NF_a = 78; 18 autosomal pairs are bi-armed, and further 3 pairs are acrocentric. Both sex chromosomes are large metacentrics; the X is the largest element in the set (reviewed in Arslan & Zima 2014). Note that old reports of 2n = 38 are erroneous (Robinson 1968).

Variation and subspecies. Monotypic (Kryštufek 2017a).

Mesocricetus raddei (Nehring, 1894) – Radde's Golden Hamster

Cricetus nigricans Brandt, 1832: 22 (in Ménétries 1832). Permanently invalid as secondary homonym of *Hamster nigricans* Lacépède, 1799 (= *Cricetus cricetus*) (Nehring, 1898c: 495) and replaced before 1961 but no longer considered congeneric (Article 59.3 of the Code); see also Pavlinov & Rossolimo (1987: 172–173) who referred to Article 59b of the 2nd edition of the Code (ICZN 1964). Replaced with *Cricetus nigriculus* Nehring, 1898.

Cricetus nigricans var. *Raddëi* Nehring, 1894b: 149. Type locality: "Ober Samur [upper valley of the Samur River]", with a footnote: "Der Samur ist ein Fluß in Dagestan [Samur is a river in Dagestan]", Russian Federation. The type is deposited in Berlin (NHMBe 45420) and not in ZIN St. Petersburg (Ross 1992: 322) (see also Pavlinov & Rossolimo 1987: 172, Baranova & Gromov 2003: 49).

Cricetus Raddei: Nehring, 1898a: 182. New rank for *raddei* Nehring.

Cricetus nigriculus Nehring, 1898c: 495. New replacement name (nomen novum) for *nigricans* Brandt. In accordance with Articles 67.8 and 72.7 of the Code (ICZN 1999), the replacement name has the same name-bearing type (and type locality) as Brandt's name, i.e. "montagnes du Caucase [mountains of the Caucasus]" (Ménétries 1832). Ellerman & Morrison-Scott (1951: 630) restricted the type locality to "River Malka, mountain of middle part of Northern Caucasus", Dagestan, Russian Federation.

Cricetus (Mesocricetus) nigriculus: Nehring, 1898d: 380. Name combination.

Cricetus (Mesocricetus) Raddëi: Nehring, 1898d: 381. Name combination.

M[esocricetus] Raddei: Satunin, 1900: 301. First use of the current name combination.

Mesocricetus nigriculus: Satunin, 1901: 40. New rank and name combination.

Mesocricetus raddei avaricus Ognev & Heptner, 1927: 142. Type locality: "Near the (village) aoul Khunsakh, Avarsky district. Province of Daghestan, 5530 feet [1,685 m] alt.", Russian Federation.

Cr[icetus] (Mesocricetus) raddei nigriculus: Argyropulo, 1933b: 244. Name combination.

Cr[icetus] (Mesocricetus) raddei avaricus: Argyropulo, 1933b: 244. Name combination.

M[esocricetus] r[addei] nigriculus: Kuznetzov, 1944: 323. First use of the current name combination.

M[esocricetus] r[addei] avaricus: Kuznetzov, 1944: 323. Name combination

Mesocricetus auratus raddei: Ellerman & Morrison-Scott, 1951: 630. Name combination.

Mesocricetus auratus nigriculus: Ellerman & Morrison-Scott, 1951: 630. Name combination.

Mesocricetus auratus avaricus: Ellerman & Morrison-Scott, 1951: 630. Name combination.

Etymology. Species epithet *raddei* is eponym for Gustav Ferdinand Richard Radde (1831–1903), a German naturalist who provided the type specimen now deposited in Berlin (NHMBe 45420). Radde is remembered for his explorations in the Caucasus and adjacent regions of the Russian Empire and has further eponyms in mammalogy, ornithology, herpetology, etc.

Taxonomy. Shortly after Brant's (1832) recognition of Radde's golden hamster as *Cricetus nigricans*, Gloger (1835) synonymized the name with *Cricetus cricetus*, being misled by the black belly, which is characteristic of both hamsters. Subsequent authors, starting with Giebel (1855), accepted Radde's hamster as a species in its own right (Trouessart 1904, Argyropulo 1933b, c, Ellerman 1941, Vinogradov & Argyropulo 1941, Kuznetzov 1944, Vinogradov & Gromov 1952, Flint et al. 1965). This hamster was only exceptionally synonymized with *auratus* (Ellerman & Morrison-Scott 1951, Vereshchagin 1959). Some authors, however, considered either *brandti* (Aharoni 1932, Vinogradov & Argyropulo 1941) or *newtoni* (Hamar & Schutowa 1961) as a race of *M. raddei*.

Distribution range of Radde's golden hamster (surface area = 103,520 km²) encompasses the northern and eastern slopes of the main Caucasian ridge, and the steppes of Ciscaucasia between the Sea of Azov and Black Sea in the west and the Caspian Sea in the east (Figure 87). The species is nearly endemic to Russian Federation with a single record being reported from the Mtskheta-Mtianeti region in north-eastern Georgia (Bukhnikashvili 2004). Inside Russia, Radde's hamsters occupy (north-west to south-east) Rostov Oblast, Krasnodarskiy Kray, Adygeya, extreme western Kalmykiya, Karachayevo-Cherkesiya, Stavropol'skiy Kray, Kabardino-Balkariya, Severnaya Osetiya, Ingushetiya, Chechniya, and Dagestan. Presence in Kalmikiya (Yashalta and Gorodovikovskiy) is said to be only temporary (Sandzhiev et al. 2013).

Prior to 1940, the north-western border tentatively followed the line River Malka–Manych–Sal'sk (Argyropulo 1941a), but Radde's golden hamsters subsequently spread westward for > 200 km and reached the line Delta of Don River–Bay of Taganrog; *cf.* Figure 1 in Yakovlev & Kolesnikov (1954) and Figure 11 in Bobrov et al. (2008). The expansion started in 1947, when the population density was very high (Luk'yanchenko 1954, Yakovlev & Kolesnikov 1954). Hamsters subsequently disappeared from the Don Delta (Minoransky et al. 1997), and currently the most exposed occurrence is in Maykop. During the Middle and Upper Pleistocene, Radde's hamsters occurred southward of their current presence in north-eastern Azerbaijan and northern Georgia (Vereshchagin 1959, Baryshnikov & Baranova 1983). The fossil material is taxonomically classified as *M. raddei planicola* Argyropulo, 1941 (Argyropulo 1941b).

During the 2nd half of the 20th century, Radde's golden hamsters benefited from deforestation and expansion of agriculture (Tembotov 1972). On the other hand, population decline and fragmentation have been reported since 2000 in Dagestan (Omarov & Yarovenko 2011, Chunkov 2018, 2020, Chunkov & Omarov 2020), Stavropol'skiy krai (Likhovid 2002, Vasilenko et al. 2021, Tsapko et al. 2022), and Kalmykia (Sandzhiev et al. 2013).
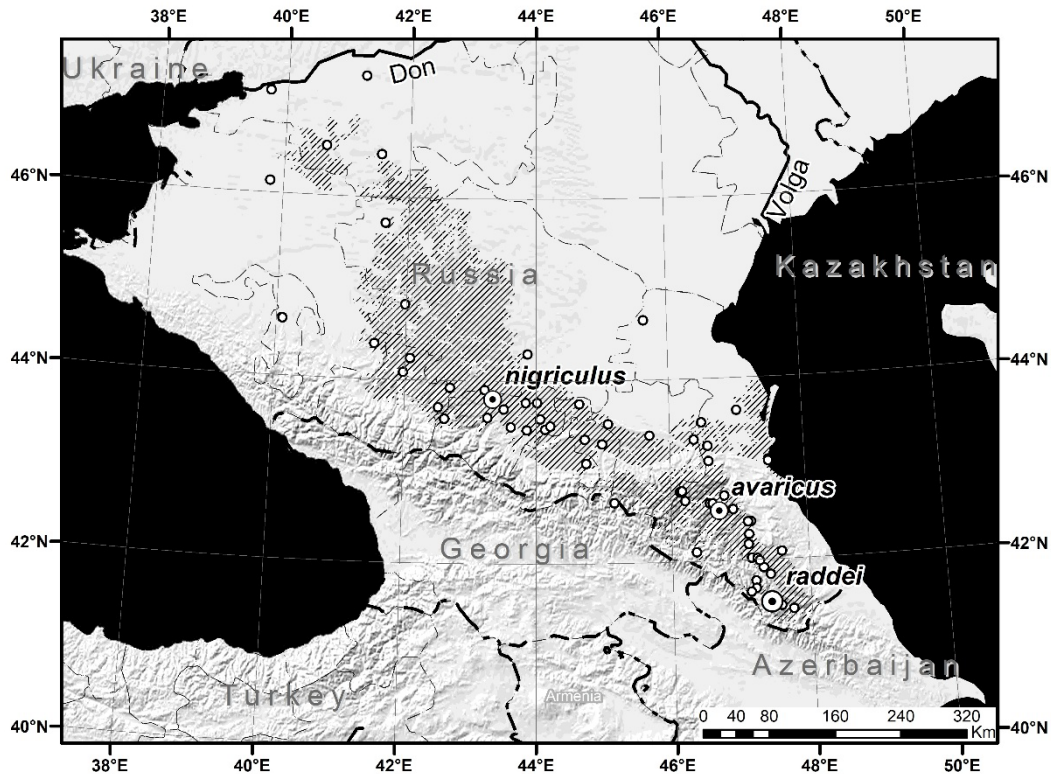
Figure 87: Distribution of Radde's golden hamster *Mesocricetus raddei*.

Radde's golden hamsters occupy pristine cereal and wormwood steppe in flat landscape, high-mountain xeric steppe, pastures and various types of cultivated land. Some authors (Minoransky et al. 1997, Sandzhiev et al. 2013) claim that uncultivated land is preferred and that this hamster avoids proximity to humans (Ognev 1924, Shidlovsky 1962). Tembotov (1972) report its presence for Dagestan in the sub-Alpine zone up to 2,400 m high. Elevational range is from –23 m in the Caspian Depression to 2,565 m (mean = 826 m).

Characteristics (Figure 81b & 88). A large hamster, second in size to *C. cricetus*. Dimensions: body mass = 200–350 g, length of head and body = 149–280 mm, length of tail = 12–34 mm, length of hind foot = 19.0–30.0 mm, length of ear = 14.2–31.0 mm; condylobasal length of skull = 31.9–60.0 mm, zygomatic width = 17.2–28.0 mm, length of maxillary tooth-row = 6.2–8.6 mm. Males are heavier than females; mean body mass in *M. r. raddei* before hibernation is 296±12 g in males and 248±9 g in females (Chunkov 2020). The fur is coarser and the overall colouration is darker than in the remaining golden hamsters due to denser all-black hairs. Colouration, however, varies individually and among populations. Dorsal fur is from plain grey to dull grey-brown; it is frequently heavily grizzled with black and

buffy or rusty hair tips. Muzzle and face are lighter and shaded buffy or rusty, though the crown is always grey or blackish. The cheek patch and the collar stripe are cream or greyish-white. The subauricular stripe is black and the postero-lateral extension of sternal patch is either absent or present (*cf.* Figures 81b, 88 & 89). The postauricular patch varies from being absent to an extensive buffy-reddish spot; the crown patch and the occipital stripe are usually bold though they are occasionally absent. The sternal patch is large and black; the rest of the underside is usually blackish grey or black, though lighter than the sternal patch (Figure 90).

The black area on the belly is occasionally narrowed to a wide stripe. The area between the belly and lateral line is never pure black, but grizzled with beige hairs. Rarely, the entire belly is light-grey (similarly to the cheek patch; Figure 90); in such cases, the demarcation on flanks is distinct, though not sharp. Chin is either black or whitish, and the inguinal region is frequently distinctly lighter than the belly. Exceptionally, a white spot is present also on the abdomen (M. M. Chunkov *in litt.*). Tail is grey and largely hidden by long hairs of the body; paws are white to light-grey. The ears are sparsely clad with fine greyish or brownish hairs.

Figure 88: Radde's golden hamsters from Dagestan (*Mesocricetus raddei raddei*). The bottom animal assumed aggressive defensive posture. Photo courtesy of A. V. Surov (top inset) and Yu. Yarovemko (bottom inset)

Nipple count is 16 (K. Z. Omarov *in litt.*) and 19 (M. M. Chunkov *in litt.*). Glans penis is cylindrical, parallel-sided, quite deep, and with ventral groove; lateral papillae are expanded distally and Γ-shaped (Vorontsov 1982). The baculum is short and robust, slightly wider basally than across the trident (Argyropulo 1933c).

The skull is large and massive with a heavy rostrum (Figure 85). Zygomatic width accounts for 54–60% of condylobasal length of the skull. Nasals are longer than in the remaining golden hamsters. In large individuals, the skull is heavily marked with ridges reaching the powerful lambdoidal crest; they bent medially anterior to the fronto-parietal suture. The occipital region is more inclined towards condyles than in congenerics;

the condyles are therefore shifted further back. Apart from its large size, dentition shows no peculiarities (Figure 86).

Two different diploid numbers have been reported for *M. raddei,* both from Chechen Republic: 2n = 42 from north-western (Vorontsov & Krjukova 1969c) and 2n = 44 from the southern parts of the country (Ivanov 1969a). Both cytotypes have identical fundamental number of chromosomal arms (NF = 76, NF_a = 72).

Figure 89: Flat skin of Radde's golden hamster *Mesocricetus raddei raddei* from Kuli, Dagestan (SZM 23874).

The number of metacentrics is identical in both (5 elements); the 44 cytotype has 10 submetacentric and 6 acrocentric elements, while the 42 cytotype contains 11 submetacentric and 4 acrocentric chromosomes (cf. Table 1 in Vorontsov & Krjukova 1969c). Both sex chromosomes are metacentric; the X is the largest element in the karyotype and the Y is next in size to X (Graphodatsky 2006b).

Variation and Subspecies. Nehring (1898c, d) classified *raddei* and *nigriculus* as independent species, which was accepted in first decades of the 20th century
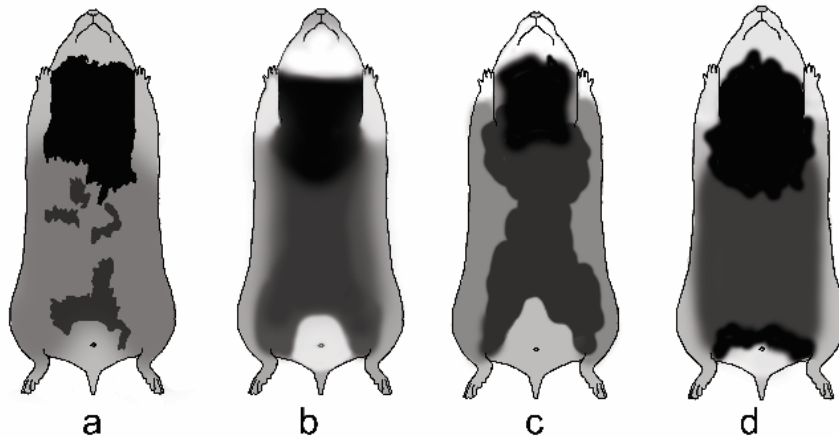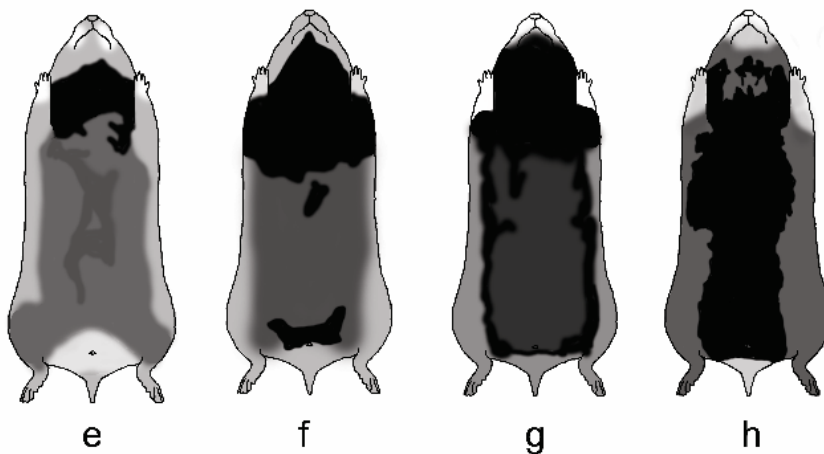
Mesocricetus raddei raddei

a   b   c   d

Mesocricetus raddei nigriculus

e   f   g   h

Figure 90: Ventral side in Radde's golden hamsters *Mesocricetus raddei* demonstrating variability in colouration. *Mesocricetus raddei raddei* (a–d) is from Dagestan and *M. r. nigriculus* (e–h) is from Rostov Oblast.

(Satunin 1900, 1901, Dombrowski 1907, Heptner 1926, Ognev & Heptner 1927) and is exceptionally still recognised (Hamar & Schutowa 1966, Gromov & Baranova 1981, Yiğit et al. 2006a). Argyropulo (1933b) defined *M. raddei* as polytypic species with 3 subspecies (*nigriculus* and *avaricus* in addition to the nominotypical *raddei*), which received wide support (Sviridenko 1936, 1940, Heptner & Formozov 1941, Kuznetzov 1944, Vinogradov & Gromov 1952, Shidlovskiy 1962, Gromov et al. 1963, Hamar & Schutowa 1966, Gromov & Baranova 1981). A prevailing view was of 2 subspecies, the larger *raddei* and the smaller *nigriculus* (Heptner 1926, Ellerman 1941, Vinogradov 1933, Vinogradov & Argyropulo 1941, Vereshchagin 1959, Kuznetsov 1965, Ross 1992, Lebedev 2012, Kryštufek 2017b). These subspecies supposedly differ in diploid number of chromosomes (2n = 44 in the nominotypical *raddei* and 2n = 42 in *nigriculus*; Vorontsov & Krjukova 1969c, Ross 1992); geographic ranges of the two cytotypes are actually little known. Two subspecies are

accepted here; they split 0.4–0.5 Mya (Neumann et al. 2006). Fossil golden hamsters from Ciscaucasus are usually classified as an extinct subspecies *M. r. planicola* Argyropulo, 1941 (Argyropulo, 1941b), which was of intermediate size (Vereshchagin 1959, Gromov & Baranova 1981).

Mesocricetus raddei raddei (Nehring, 1894)

Synonym: *Mesocricetus raddei avaricus* Ognev & Heptner, 1927.

Distribution. South-western and southern Dagestan and central Chechnya (south of Grozny – Makhachkala Road), in the basins of rivers Samur, Argun, Andi Koysu and Sulak, and on the plateaus of Khunzakh and Gunib (Heptner & Formozov 1941, Vereshchagin 1959, Chunkov 2020).

Characteristics. Karyotype: 2n = 44. A large subspecies: length of head and body = 185–280 mm, length of tail = 22–34 mm, length of hind foot = 24.2–30.0 mm, length of ear = 20.0–31.0 mm; condylobasal length of skull = 39.1–50.0 mm, zygomatic width = 19.6–28.0 mm, length of maxillary tooth-row = 7.8–8.6 mm. The underside, which is either light-grey or blackish-grey, is always lighter than the sternal patch (Figures 81b, 89 & 90a–d). The skull is more robust and more heavily ridged; the rostrum is heavier and broader. Incisive foramina are frequently the widest in their anterior part; the upper incisors are heavier.

Mesocricetus raddei nigriculus (Nehring, 1898)

Etymology. The epithet *nigriculus* is diminutive from 'nigri' (Latin adjective, inflection of 'niger' for black) in allusion to black underside of this hamster.

Distribution. Lowlands (< 1,000 m of elevation) in Ciscaucasia, including northern Dagestan (Khasan-Yurt; Sviridenko 1936, 1940). Throughout most of its range, *nigriculus* is sympatric with *C. cricetus*.

Characteristics. Karyotype: 2n = 42. A small subspecies: length of head and body = 149–186 mm, length of tail = 12–20 mm, length of hind foot = 19.0–26.0 mm, length of ear = 14.2–24.0 mm; condylobasal length of skull = 31.9–42.3 mm, zygomatic width = 17.2–23.5 mm, length of maxillary tooth-row = 6.2–7.3 mm. Underside tends to be darker and in some individuals both the sternal patch and the rest of the underside are black (Figure 90e–h). The skull is more gracile and the ridges weaker or entirely absent; the rostrum is weaker and narrower. Incisive foramina are wider in their posterior part; the upper incisors are weaker.

Species group *newtoni*

The group is characterized by nucleotide sequences (Neuman et al. 2006, Lebedev et al 2018a) and lower diploid number of chromosomes (2n = 38–42). Glans penis is conical, narrowing from base towards the apex. Temporal ridges are weak and parallel, not reaching beyond the fronto-parietal suture. The frontals are not much compressed posteriorly and the fronto-parietal

suture is long (Figure 94). The *newtoni* group contains 2 species (*newtoni* and *brandti*), which presumably diverged at 1.7–1.8 Mya (Neumann et al. 2006). Fossil record allows tracing their history into the Middle Pleistocene; for *newtoni* see Santel & Koenigswald (1998) and for *brandti* see Storch (1975) and Erdal et al. (2018). These two golden hamsters are externally and cranially quite similar and Hamar & Schutowa (1961) proposed for them to be conspecific.

Mesocricetus newtoni (Nehring, 1898) – Romanian Golden Hamster

Cricetus Newtoni Nehring, 1898b: 329. Type locality: "bei Schumla in Ostbulgarien [near Shumen in Eastern Bulgaria]". Between 1950–1965, Shumen was renamed to Kolarovgrad (cf. Musser & Carleton 2005: 1045).

Cricetus (Mesocricetus) Newtoni: Nehring, 1898d: 386. Name combination.

Mesocricetus Newtoni: Nehring, 1899a: 1. First use of the current name combination.

Cricetus auratus newtoni: Vinogradov & Argyropulo, 1941: 167. Name combination.

Mesocricetus auratus newtoni: Ellerman & Morrison-Scott, 1951: 630. Name combination.

Etymology. The species epithet is eponym for English zoologist Alfred Newton (1829–1907) who published (Newton 1870) the first record of Romanian hamster in Europe under the name *Cricetus nigricans* Brandt (now *Mesocricetus raddei*). The voucher, which is portrayed as colour plate XXVI in Newton's paper, is deposited in the Zoological Museum of the Cambridge University (no. E 2373), where Newton was Professor of Comparative Anatomy (1866–1907). Newton has eponyms in ornithology, which was his primary interest.

Taxonomy. The first Romanian golden hamster ever collected was classified as *Cricetus nigricans* Brandt (Newton 1870), but later on recognized as species in its own right under the name *newtoni* (Nehring 1898b). Shortly afterwards, *newtoni* was shifted to the genus *Mesocricetus* (Nehring 1899a), with this name combination remaining in use throughout the first half of the 20th century (Trouessart 1904, Dombrowski 1907, Miller 1912, Călinescu 1931a, b, Argyropulo 1933b, c, Ellerman 1941). Vinogradov & Argyropulo

(1941) and Ellerman & Morrison-Scott (1951) relegated *newtoni* to a subspecies of *auratus,* which remained the prevailing view in the 1950s and 1960s (Petrov 1954, Popov 1955, Markov 1960, Ausländer & Hellwing 1957, Hamar 1958, Atanassov & Peschev 1963). At about the same time, Hamar & Schutowa (1961) synonymized *newtoni* with *brandti* of Asia Minor, a step which did not receive support. Species status for *newtoni* was reinstated by Raicu & Bratosin (1966) on the basis of its unique karyotype (2n = 38).

Distribution. The range covers an area of 37,710 km² in south-eastern Romania and Bulgaria (Figure 91). It stretches along the Black Sea Coast (from Dobrogea as far south as northern Burgas) and along the right bank of the Danube River as far west as the districts of Montana and Vratsa (Bulgaria). All the records are to the south of Danube (Hamar & Schutowa 1966, Murariu & Stanciu 2009). Contrary to some earlier reports (e.g. Ross 1992), this species does not occur in Ukraine. During the Late Pleistocene, the range encompassed parts of Serbia and Greece and the species also occupied high elevations, where it is not present any longer (summarized in Peshev et al. 2004). Nedyalkov et al. (2015) reported on 2 translocations in Bulgaria (Sofia and Kazanlak) outside the current range.

Romanian hamsters occupy xerophilic grasslands and fallow fields with perennial cereals, herbs and cruciferes (Gavril et al. 2023). In the 1950s and 1960s, they were relatively abundant, particularly in uncultivated land (Petrov 1954, Zlatanov 1961). This is a lowland species, occupying elevations from close to sea level (minimum = 4 m a. s. l.) up to 467 m in the Măcin Mts. (Tulcea County, Romania; Hamar & Schutowa 1966); mean elevation is 135 m.

Characteristics (Figures 81d & 92). Size is approximately as in *auratus* and *brandti.* Dimensions: body mass = 60–130 g, length of head and body = 135–160 mm, length of tail = 18–26 mm, length of hind foot = 15–22 mm, length of ear = 14–20 mm; condylobasal length of skull = 32.0–38.2 mm, zygomatic width = 18.0–21.2 mm, length of maxillary tooth-row = 6.0–8.8 mm. Romanian hamsters are characterized by colouration and a rat-like head with more pointed snout than in other golden hamsters (Lyman & O'Brien 1977). Dorsal fur varies from light drab-brown to blackish-grey and is usually inconspicuously speckled with blackish hairs. Underparts are light greyish with cream, buffy or blackish shades (Figure 93). In the extreme the underside is as dark as in *M. raddei.* The sternal patch is blackish-brown or pure black and more extensive than in other golden hamsters; its length is
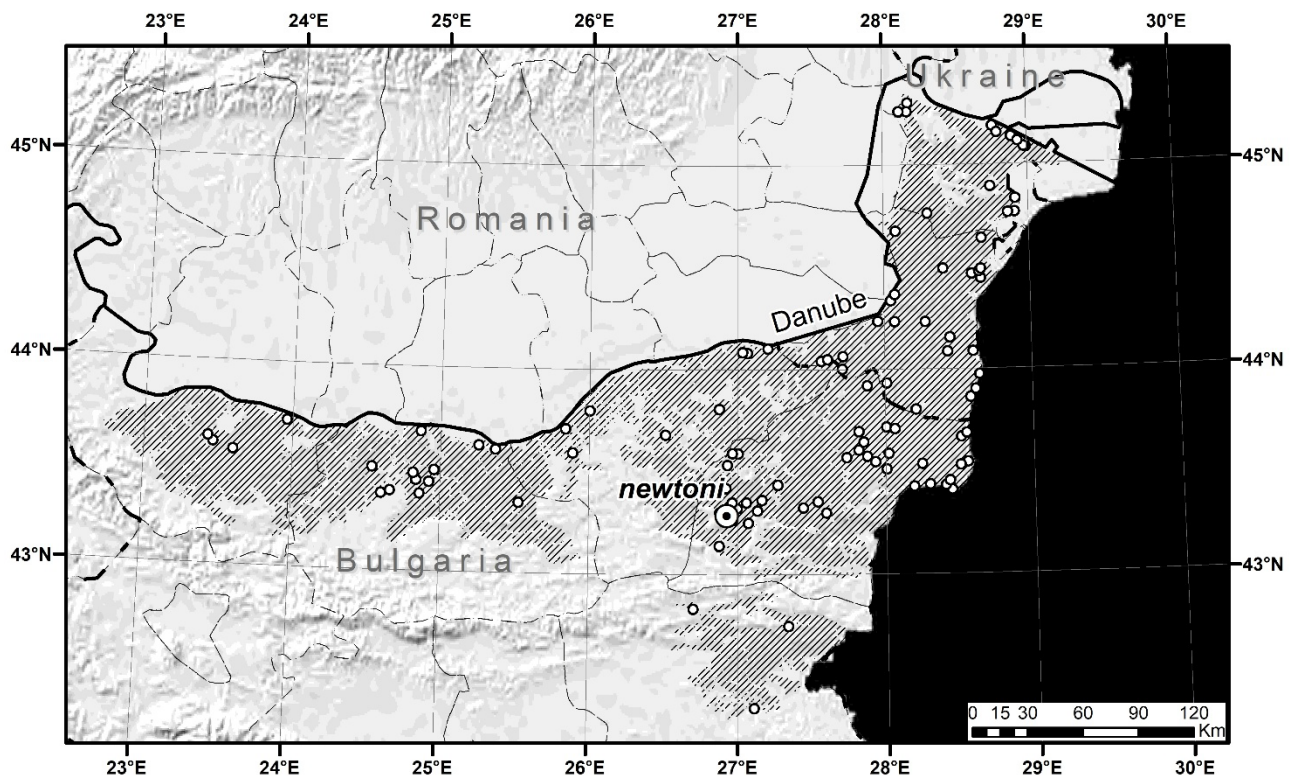

Figure 91: Distribution of Romanian golden hamster *Mesocricetus newtoni.*

Figure 92: Romanian golden hamster (*Mesocricetus newtoni*) from Dobrogea, Romania. Photo courtesy of Gabriel Chişamera.
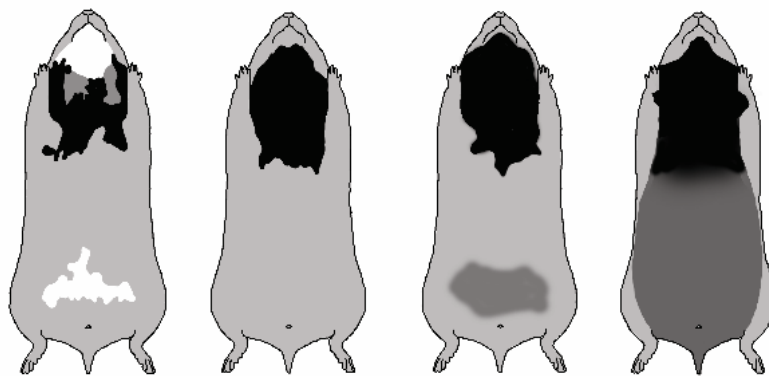

Figure 93: Ventral side of Romanian golden hamsters *Mesocricetus newtoni* demonstrating variability in sternal patch.

~50 mm. Approximately ½ of skins we saw showed an additional blackish patch in the inguinal region. White patches, either in the chin or the inguinal part, or both, are rarely present (Figure 93). A blackish crown patch is well marked and larger than in other golden hamsters.

Usually, the crown continues posteriorly as a stripe which reaches the scapular region or extend even beyond (Figures 81d & 92). The face and the postauricular patch are beige-brown or bright buffy-

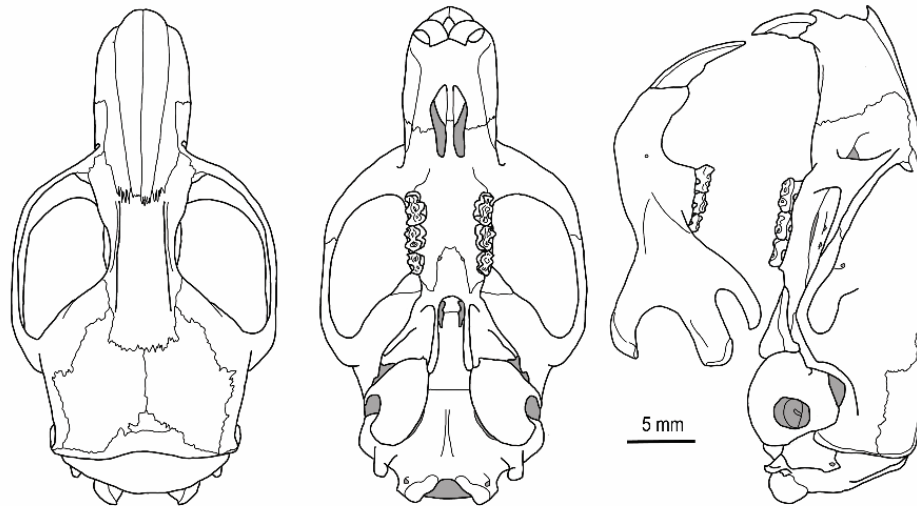## *Mesocricetus newtoni*
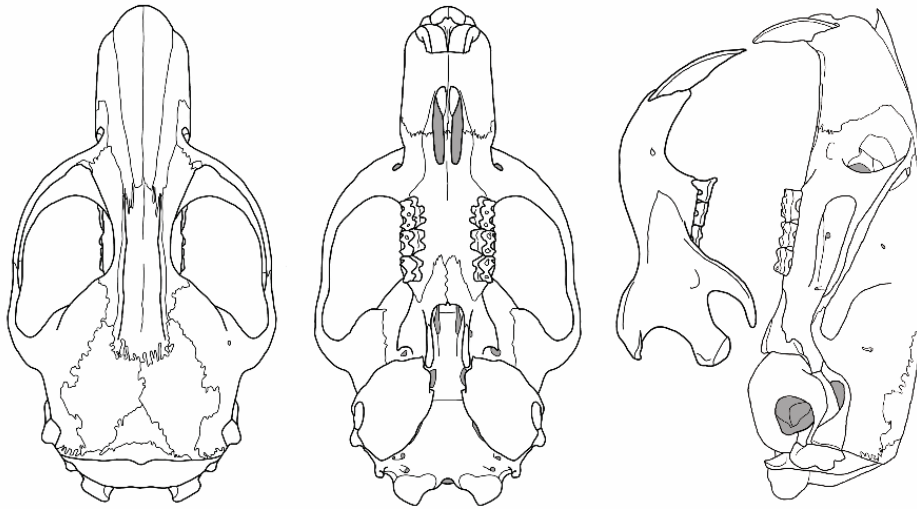
Mesocricetus brandti

Figure 94: Skull in golden hamsters from the *newtoni* species species group (top to bottom): *Mesocricetus newtoni* and *M. brandti* (Kırşehir, Central Anatolia). Scale bar = 5 mm.
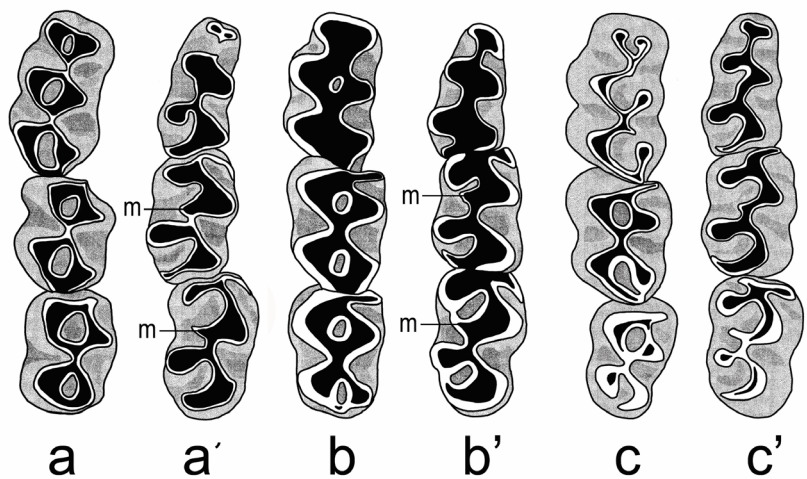

Figure 95: Grinding pattern of upper (a, b, c) and lower (a', b', c') molars in the *newtoni* species group of golden hamsters: a, b – *Mesocricetus newtoni*, c – *M. brandti*. m – mesolophid. Scale bar = 1 mm.

brown; the cheek patch and the collar stripe are cream. The subauricular stripe is bold and black; the light collar stipe is posteriorly frequently margined by a black postero-lateral expansion of the sternal patch. The tail and paws are whitish and the ears are grey. Females have 13–16 nipples (Miller 1912, Niethammer 1982). Gland penis and baculum were not studied. The skull is comparatively weekly ridged (Figure 94). Zygomatic width accounts for 53–59% of condylobasal length; in dorsal view, the zygomatic ridges converge anteriorly. Dentition shows no peculiarities (Figure 95a, b).

Karyotype: 2n = 38, NF = 76; all the chromosomes are bi-armed. Sex chromosomes are bi-armed and large; the X is one of the largest elements (Popescu & DiPaolo 1980).

Variation and subspecies. Monotypic (Kryštufek 2017d).

Mesocricetus brandti (Nehring, 1898) – Brandt's Golden Hamster

Cricetus Brandti Nehring, 1898b: 331. Based on "transcaucasischen Exemplare". Of the 3 syntypes cited in a subsequent paper (Nehring 1898d: 384), only 1 has known locality ("Marienfeld, östlich von Tiflis"), which Ellerman (1941: 444) accepted as a restricted type locality ("Gouv. Tiflis, Transcaucasia"), *i. e.* Tbilisi, Georgia.

Cricetus (Mesocricetus) Brandti: Nehring, 1898d: 383. Name combination.

M[esocricetus] brandti: Satunin, 1900: 301. First use of the current name combination.

Mesocricetus Koenigi Satunin, 1900: 301. Type locality: "Kasikoporan (Gouvt. Eriwan)", now Göle, Villayet Ardahan, Turkey. Ellerman (1941: 464) mistakenly stated Nehring as the taxonomic authority for *koenigi*, which is followed in the mainstream literature (e.g. Ellerman & Morrison-Scott 1951, Corbet 1978, Pavlinov & Rossolimo 1987, Musser & Carleton 1993, 2005).

[Cricetus (Mesocricetus)] koenigi: Trouessart, 1904: 394. Name combination.

Cricetus (Mesocricetus) raddei brandti: Aharoni, 1932: 172. Name combination.

Cr[icetus] (Mesocricetus) auratus brandti: Argyropulo, 1933b: 244. Name combination.

Cricetus auratus brandti: Vinogradov & Argyropulo, 1941: 167. Name combination.

M[esocricetus] auratus brandti: Kuznetzov, 1944: 323. Name combination.

M[esocricetus] a[uratus] koenigi: Kuznetzov, 1944: 323. Name combination.

Mesocricetus brandt: Vorontsov, 1958: 334. Incorrect subsequent spelling of *brandti* Nehring.

Etymology. The species epithet is eponym for Russian naturalist of German ethnicity Johann Friedrich von Brandt; in Russian Fedor Fedorovich Brandt (Фёдор Фёдорович Брандт or Иоганн Фридрих фон
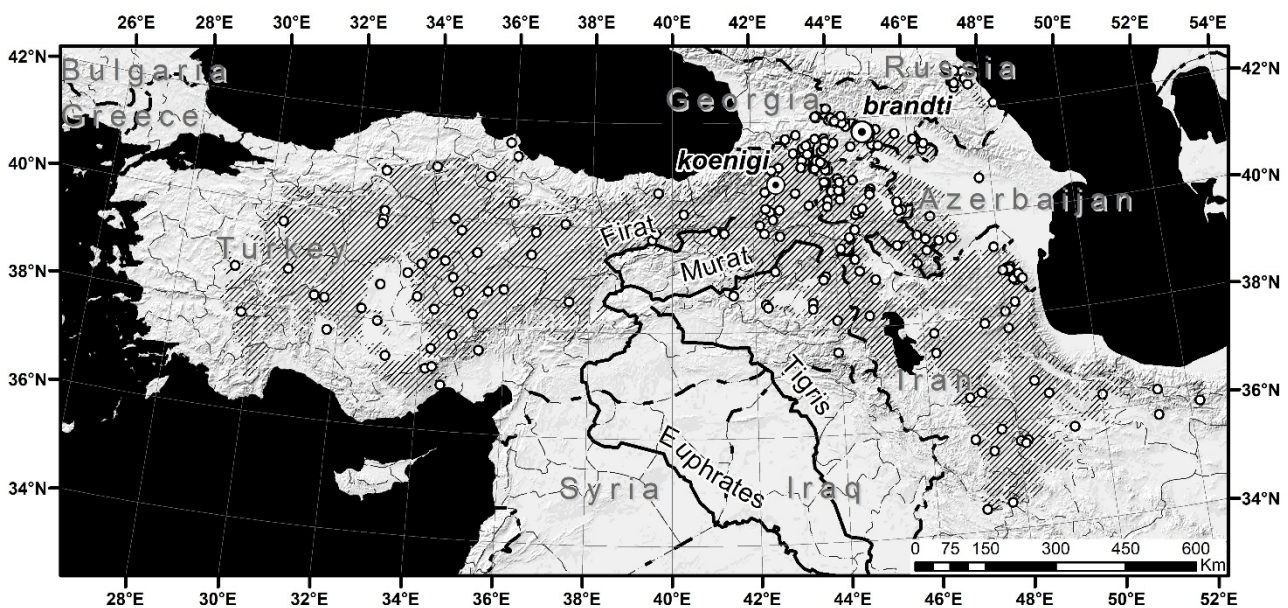

Figure 96: Distribution of Brandt's golden hamster *Mesocricetus brandti*.

Брандт) (1802–1879), the first director of the Zoological Museum of St. Petersburg Academy of Sciences. Brandt has eponyms also in other branches of natural history.

Taxonomy. Brandt's golden hamster was originally reported for 'Assyria' as *Cricetus vulgaris* (Ainsworth 1838: 39) and for Mersin, Turkey, as a species "identical with our European species" (Kotschy 1858: 234; interpreted as *Cricetus frumentarius* in Danford & Alston 1877: 280). Subsequent reports were as *Cricetus nigricans* (now *Mesocricetus raddei*) for Iran (Filippi 1865) and Asia Minor (Danford & Alston 1877, 1880). The opinion that Brandt's golden hamster is a subspecies of *M. raddei* was still advocated by Aharoni (1932). After being separated from the scope of *raddei* as a species in its own right (Nehring 1898b), *brandti* was rarely treated as an independent species (Trouessart 1904, Satunin 1906, Dombrowski 1907, Vinogradov 1933), being usually ranked as a subspecies of *auratus* (Argyropulo 1933b, c, Neuhäuser 1936, Ellerman 1941, 1948, Ellerman & Morrison-Scott, 1951, Vinogradov & Gromov 1952, Dal' 1954). Although karyotypes for both, *auratus* and *brandti,* were known already in the early 1950s (Matthey 1952) and hybridization tests demonstrated their reproductive incompatibility (Matthey 1959), many authors continued pooling these taxa well into the 1990s (Osborn 1965, Lay 1967, Sickenberg 1971, Atallah 1977, Corbet 1978, Harrison & Bates 1991, Qumsiyeh 1996). On the other hand, the evidence quoted above, followed by generic revision by Hamar & Schutowa (1966) convinced many to accept species status for *brandti* (Missone 1959, Tembotov 1965, 1972, Lehmann 1969, Zil'fyan et al. 1969, Shidlovskiy 1962, Kumerloeve 1975, Storch 1975, Lyman & O'Brien 1977, Kittel 1984, and all subsequent authors). In the past, *brandti* was exceptionally synonymized with *newtoni* (Hamar & Schutowa 1966, Kurashvili et al. 1981).

Mesocricetus koenigi was recognized in the 1900s as a species distinct from *M. brandti* on the basis of fur colouration. Its validity was accepted only occasionally (Trouessart 1904, Dombrowski 1907, Vereshchagin 1959) and the name was soon synonymized with *brandti* by the majority of authors.

Distribution. The range of Brandt's hamster is by far the most extensive in the genus and covers an area of 494,197 km² in south-western Asia (Figure 96). It is split by the main ridge of the Caucasus Mts. into two fragments, the southern (Turkey, Iran, Armenia, Azerbaijan, Georgia) and the northern in Dagestan (Russian Federation). Earlier reports for northern Iraq, Syria, Lebanon, and northern Israel (Musser & Carleton, 2005) are erroneous (Shehab et al. 2004, Kryštufek & Vohralík 2009). In Turkey, *M. brandti* occupies central and eastern Anatolia, to the east of the Çardak (Denizli) – Uşak line, and the eastern Black Sea Mts. It is marginally present in the Taurus Mts. (Kryštufek & Vohralík 2009). In Iran, the range is restricted to the north-western part of the country, with the border crossing the following provinces (north-west to south-east): Mazanderan, Tehran, Qazvin, Hamadan, Kordestan, and Kermanshah (Missone 1959, Yusefi et al. 2019). The rest of the Transcaucasian range tentatively coincides with the Lesser Caucasus (east of Arskiansk and Suramsk ridges), and Talysh (Vereschchagin 1959, Shidlovskiy 1962, Omarov & Chunkov 2020). Within this frame, the Brandt's hamster is widespread in Armenia (Dal' 1954), and occupies western Azerbaijan and south-central Georgia, as far north as the Caucasian main ridge, and as far west as the coastal lowlands in Imereti, Guria, and Samegrelo-Zemo Svaneti (Bukhnikashvili 2004). The isolate in Dagestan is bordered by the Sulak and Gimrinskiy ridges in the north and west, respectively (Shidlovskiy 1962), and encompasses the Levashinskiy Plateau in the territory of 5 Rayons: Buynakskiy, Levashinskiy, Akushinskiy, Sergokalinskiy, and Karabudahkentskiy (Omarov & Yarovenko 2011, Omarov & Chunkov 2020). Brandt's hamsters are rarely present on the seashore (*e. g.* along the Black Sea coast of Turkey) and do not occupy islands.

The range was seemingly more extensive in the Upper Pleistocene when *Mesocricetus cf. brandti* was present also in northeastern Iraq (Palegawra Cave, 14,400 ±760 years old and identified as *M.* cf. *armatus*) (Turnbull 1975) and Lorestan (Iran; Rey-Rodríguez et al. 2020).

Its main habitat consists of dry *Artemisia* and *Festuca* steppe with abundance of cereal grasses; Brandt's hamsters are regularly present in the fields of cereals and multi-annual crops. Woodland, thickets, damp and desertified places are avoided. The range is contiguous in subalpine meadows but patchy in places of

Figure 97: Brandt's golden hamster (*Mesocricetus brandti*) from Turkey. Photo courtesy of Christian Kern. Used with permission of the Science and Research Centre Koper.

pronounced aridity where hamsters aggregate in mesic sites and in river valleys. Elevational range is 37–3,365 m (mean = 1,382 m) with the majority of records between 1,100 and 2,200 m a. s. l. (Kryštufek & Vohralík 2009).

Characteristics (Figures 81c & 97). Size is similar as in *M. auratus* and *M. newtoni*. Dimensions: body mass = 81–271 g, length of head and body = 135–166 mm, length of tail = 10–27 mm, length of hind foot = 17.5–22.0 mm, length of ear = 17.5–24.0 mm; condylobasal length of skull = 31.1–38.2 mm, zygomatic width = 17.6–21.4 mm, length of maxillary tooth-row = 5.9–7.0 mm. Dorsal pelage is sand-brown to tawny-olive; on average, it is less grey than in *newtoni* and *raddei* and never as richly reddish as in *auratus* (Figure 81). In some individuals, the shoulders are more blackish and the rump rustier. Flanks are yellowish and demarcation line is indistinct. Belly is grey-white to white, invariably washed with slate grey undercolour. Chin and throat are frequently white and some animals have white patches or / and white medial line on the belly (Figure 98a). The sternal patch (length = 29–34 mm) is larger and more

prominent than in *auratus* but smaller than in *newtoni*. The patch is blackish-brown or black; it is frequently surrounded by white patches and split medially. The oblique black subauricular stripe extends from cheeks to shoulders and is usually bold blackish-brown or black; in rare cases, the stripe is narrow and ill-defined. The postero-lateral extension of sternal patch is absent or ill-defined; it is never as bold as in *newtoni*. Light patches on chin, neck and cheeks (the cheek and postauricular patches and the collar stripe) are cream or yellowish. Head is normally buffier than the back, and some individuals show a dark line across masseters. A dark crown patch is usually present but never as bold and prominent as in *newtoni*; the occipital stripe is absent. Fore feet are yellowish; hind feet are grey and covered by short buff hair. Ears are grey, covered by buff hair. Tail is whitish or yellowish at the tip.

Females have 8 pairs of nipples. Glans penis resumes shape of a broad truncated cone; it is wider than deep. The ventral groove is restricted to the proximal part of the glans (Vorontsov 1982). Baculum is essentially like in *M. auratus*, except being larger and less expanded in
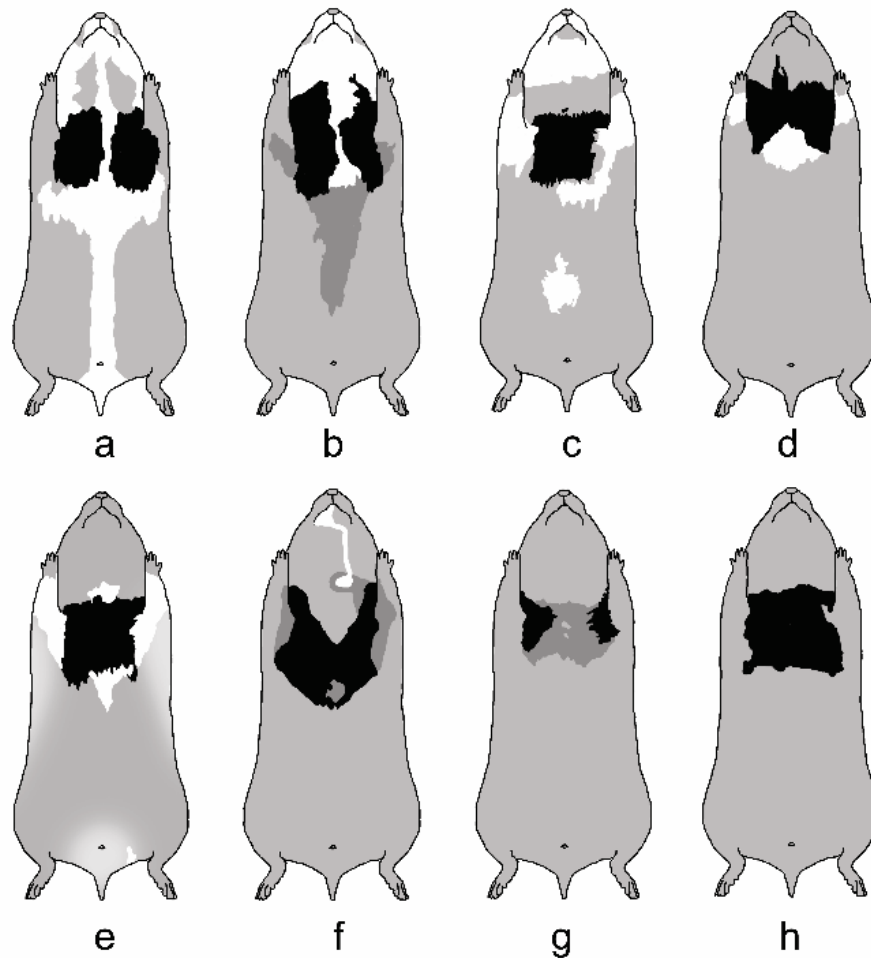
Figure 98: Ventral side of Brandt's golden hamsters *Mesocricetus brandti* demonstrating variability in sternal patch: a–c, h – Anatolia; d – Iran; f, g – Azerbaijan.

its medial part; its distal portion is longer relative to proximal stalk (Yiğit et al. 2000). The entire baculum is about 5.5 mm long, 2 mm wide across its basal shaft and 1.6 mm across distal processes (Kryštufek & Vohralík 2009).

The skull is essentially as in *M. newtoni* (Figure 94). Zygomatic width accounts for 52.4–58.2% of condylobasal length of the skull. Pterygoids tend to be parallel and join orthogonally the posterior margin of the hard palate. Interpterygoid fossa is thus mainly rectangular, though some individuals show triangular fossa. Masseteric plate is slightly longer (length = ~ 3 mm) than in *M. auratus* (~ 2.0 mm), and infraorbital foramen is laterally compressed (Figure 20b), while it is oval in *auratus*. Dentition shows no peculiarities (Figure 95c).

Karyotype: $2n = 42$, $NF_a = 80$, $NF = 84$; sex chromosomes are bi-armed, X is medium-sized or large and Y is of medium size or small. Karyotype was studied throughout the range, specifically in Turkey, Iran, Armenia, Georgia and Dagestan (Ivanov 1969a, Zil'fyan et al. 1969, Todd et al. 1972, Lyman & O'Brien 1977, Popescu & Di Paolo 1980, Doğramacı et al. 1994, Yiğit et al. 2006b, Aşan 2012, Arslan & Zima 2014, Çam et al. 2015). The individual descriptions may differ in evaluation of the centromere position in two smaller pairs of autosomes (acrocentric or biarmed), which resulted in different fundamental numbers ($NF_a = 76$, 78, 80, $NF = 80$, 82, 84). Hamsters with different NF_a hybridized in captivity and hybrids have intermediate NF (Çam et al. 2015). Additionally, Popescu & Di Paolo (1980) reported $2n = 44$ ($NF_a = 80$) in hamsters from Ankara, presumably a result of Robertsonian rearrangement (Arslan & Zima 2014); this observation remains unconfirmed. Romanenko et al. (2007) retrieved 1 heteromorphic autosomal pair (chromosome 18), consisting of 1 metacentric and 1 acrocentric chromosome, which gave odd number of chromosomal arms $NF_a = 77$.

Variation and subspecies. Various authors reported interpopulation variation in size and fur colour; chromosomal variation is seemingly irrelevant for subspecific taxonomy. Brandt's hamsters are smaller in the western part of their range (central and eastern Anatolia), large in Iran and of intermediate size in north-eastern Anatolia, where they are also the darkest. Pale fur is characteristic for populations occupying the extreme eastern Anatolia (Van) and Iran (Lyman & O'Brien 1977, Yiğit et al. 2000, 2006b, Kryštufek & Vohralík 2009). Vereschagin (1959) classified Brandt's hamsters from the Greater Caucasus as *koenigi* and those from the Lesser Caucasus as *brandti*. The remaining authors made no attempt to use trinomials for categorizing geographic variation. Subsprecific taxonomy in Brandt's golden hamster remains a task for the future (Kryštufek 2017c).

TRIBE: Urocricetini – New Tribe

Taxonomy. In the past, *Urocricetus* and *Phodopus s. lato* were never classified into the same family-group taxon below the level of Cricetinae. Some authors (Ellerman 1941, Ellerman & Morrison-Scott 1951) stressed, however, small and flattened bullae shared by these genera that separate them from all other true hamsters. Cladistic analysis of Cricetinae conducted by Ross (1992) further showed that *Urocricetus* and *Phodopus s. lato* were sister taxa, occupying basal position in the subfamily. This was subsequently confirmed in morphological study based on the structure of auditory bullae (Potapova 2005) and in phylogenetic studies using chromosomal data (Romanenko et al. 2007) and molecular markers (Lebedev et al. 2018a) (Figure 1). Time of evolutionary divergence of Urocricetini *v.* Cricetini + Mesocricetini was estimated at 12.25 Mya (95% CI = 10.24–14.54 Mya) (Lebedev et al. 2018a). Urocricetini new tribe is well diagnosed by a set of morphological, chromosomal and molecular data.

Type genus. *Urocricetus* Satunin, 1902.

Diagnosis and Comparisons. Urocricetini new tribe belong to Cricetinae, as evident from their morphology (*e. g.* bicuspidate dentition and the presence of inner cheek pouches) and phylogenetic analyses based on nucleotide sequences (Steppan & Schenk 2017, Lebedev et al. 2018a). On the other hand, Urocricetini differ from remaining tribes of Cricetinae, *i. e.* Cricetini and Mesocricetini, in nucleotide sequences and in a set of morphological and chromosomal data. In Urocricetini, (1) the plantar surface is partly (Figure 101) or completely furry (Figure 109), while hairs are present only posterior to metatarsal pads in the remaining Cricetinae (Figures 33 & 80). (2) Bony eustachian tube is elongated (Figure 99a), but is short in other true hamsters (Figure 99b). (3) Corneous epithelium of the stomach extends along border of isthmus and may occupy most of the glandular region while it is mainly restricted to the forestomach in the remaining Cricetinae (Figure 15). (4) There is 1 ampulla

coli in *Urocricetus* and *Cricetiscus*, which is subdivided into 3 segments in *Phodopus* (Vorontsov 1967). (5) The central digit of the trident is short and rounded (known only in Phodopina new subtribe), while it is usually long and narrow in the rest of true hamsters (Figure 17). (6) Diploid number of chromosomes (2n = 28–34) is intermediate between Cricetini (2n = 20–28) and Mesocricetini (2n = 38–44).

Content. The new tribe contains 3 genera (*Urocricetus* Satunin, 1902, *Phodopus* Miller, 1910, *Cricetiscus* Thomas, 1917) with 5 recent species. These genera are classified in 2 subtribes: Urocricetina and Phodopina new subtribe which split at approximately 9.2–10.1 Mya, *i. e.* during the early Late Miocene (Romanenko et al. 2021).

Distribution. Southern Siberia in Russia, north-eastern and eastern Kazakhstan, Mongolia, northern China, Tsaidam Depression and the plateaus of Ordos and Tibet in China, northern Nepal and north-western India. The two subtribes, Urocricetina and Phodopina, are largely allopatric, although their ranges are locally in contacts along the northern border of Tibet (Figure 100).
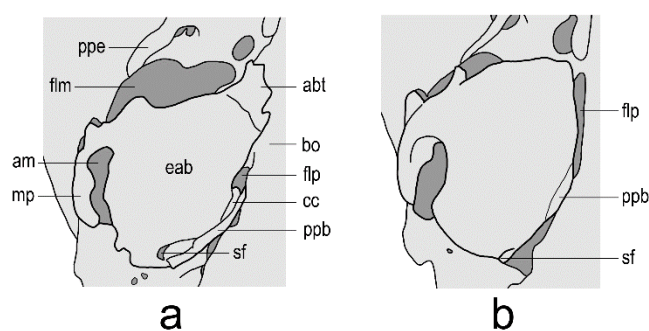

Figure 99: Right bulla in ventral view in *Urocricetus lama alticola* (a) and *Nothocricetulus migratorius* (b). Mesial is to the right, anterior is at the top. Not to scale. Abbreviations: abt – auditory bullar tube (bony eustachian tube); am – auditory meatus; bo – basioccipital bone; cc – carotid canal; eab – ectotympanic part of auditory bulla; flp – *foramen lacerum posterior*; flm – *foramen lacerum medius (fissura petrotympanica)*; mp – mastoid process; ppb – petrosal part of bulla; ppe – *processus pterygoideus externus*; sf – stapedial foramen.
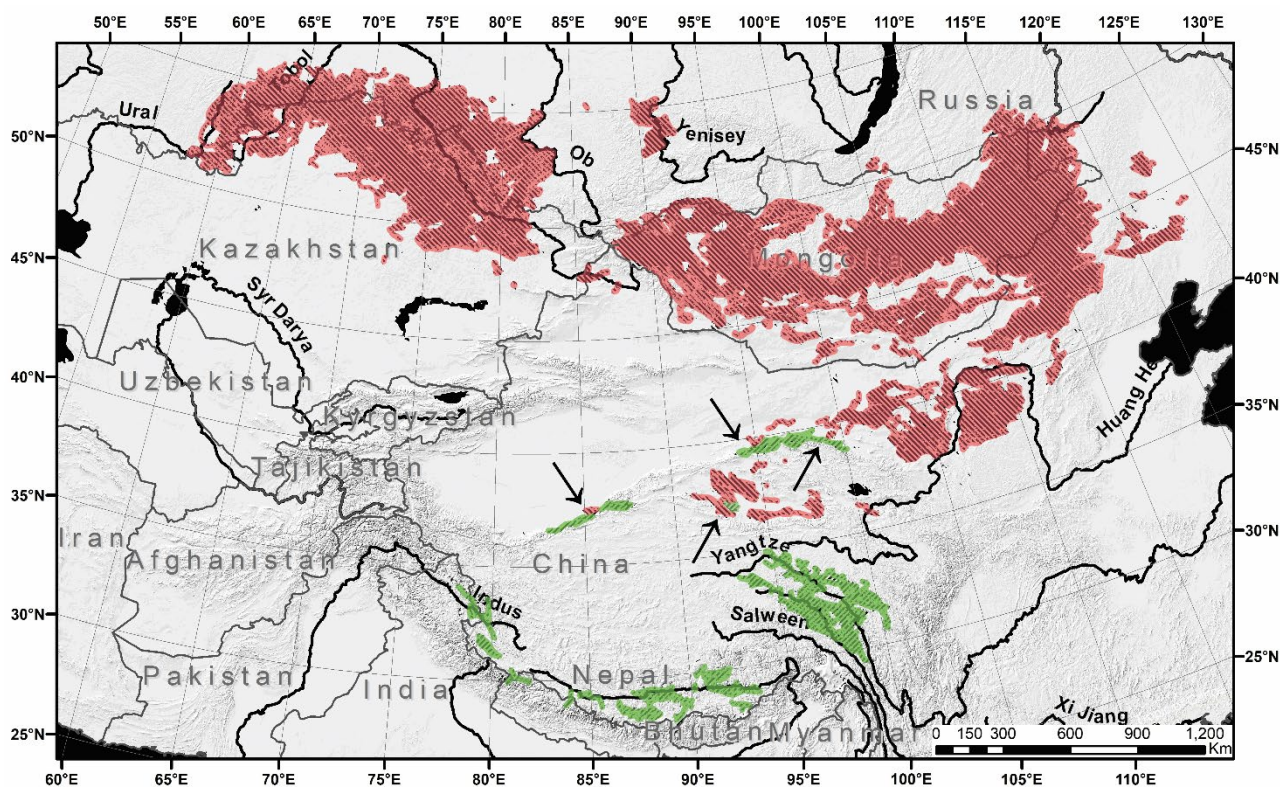
Figure 100: Distributional ranges of the Urocricetini subtribes, Urocricetina (green) and Phodopina (red). Zones of contact between these subtribes are pointed by arrows.

SUBTRIBE: Urocricetina – New Rank

Type genus. *Urocricetus* Satunin, 1902.

Diagnosis and Comparisons. Urocricetina differ from Phodopina new subtribe in nucleotide sequences (Lebedev et al. 2018a, Romanenko et al. 2021) and in a set of morphological and chromosomal data. In Urocricetina, (1) the plantar surface is only partly hairy between the pads (Figure 101), but completely furry in Phodopina (Figure 109); (2) there are 6 plantar pads (1 or 3 pads in Phodopina); (3) the tail is long (> 30% of head and body length), while it is vestigial in Phodopina (shorter than 20% of head and body length); (4) the corneous epithelium of the stomach extends along the border of isthmus, but does not occupy most glandular region as is the case in Phodopina; (5) the sphenofrontal foramen is present (absent in Phodopina) (the foramen is situated on the fronto-sphenoidal suture and can be seen on the ventral side of the skull).

Content. Urocricetina contain a single genus *Urocricetus* with 2 recent species.
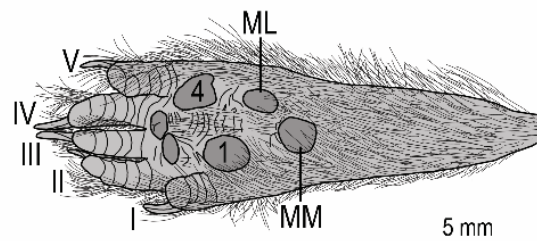

Figure 101: Left palm in *Urocricetus lama*. Digits are indicated by Roman numerals (I = thumb); medial and lateral interdigital pads are indicated by Arabic numerals (1 and 4, respectively); ML – lateral metatarsal pad, MM – medial metatarsal pad.

Genus: *Urocricetus* Satunin, 1902 – Tibetan hamsters

Urocricetus Satunin, 1902: 573. Not 1903 (e.g. Ellerman & Morrison-Scott 1951: 624; *cf.* Trouessart 1904: 395). Type species: *Urocricetus kamensis* Satunin (by monotypy).

Etymology. The name is a composite of 'ouros' meaning '-tailed' (from Greek 'oura', *i. e.* 'tail') and *Cricetus* for a hamster (see the Etymology under *Cricetus*), therefore 'a (long)tailed hamster'. Satunin (1902) coined the name for a group of small hamsters, classified in

Cricetulus, which had proportionally long tails: *Urocricetus kamensis, Cricetulus longicaudatus* and *Tscherskia triton*.

Taxonomy. Satunin (1902) established *Urocricetus* as a subgenus of *Cricetulus* (thought used it as a full generic name) for the sole long-tailed small grey hamster in Kozlov's collection from China (*U. kamensis*). In Satunin's (*l. c.*) view, the new subgenus encompassed further 2 long-tailed members of *Cricetulus s. lato*, specifically *Cricetulus longicaudatus* and *Tscherskia triton*. Trouessart (1904) still acknowledged *Urocricetus* as a valid subgenus of *Cricetus*, however, Argyropulo (1933b, c) synonymized it with the subgenus *Cricetulus*. By then, all species-group taxa of the current *Urocricetus* have already been named (*lama, alticola,* and *tibetanus*) and they were all classified as *Cricetulus*. True identities of these taxa and their interrelationships remained controversial. Ellerman (1941) classified these taxa into different groups within *Cricetulus*; taxa represented in London (*lama, alticola,* and *tibetanus*) were in the *lama* group, while *kamensis* was in the *longicaudatus* group. Wang & Cheng (1973) showed close taxonomic links between *kamensis, lama* and *tibetanus*, though still keeping them in *Cricetulus*. The current scope of *Urocricetus* was finally set by Ross (1992); her results, however, were overlooked and *Urocricetus* remained for the next three decades in a synonymy of *Cricetulus* (Huang et al. 2008, Musser & Carleton 1993, 2005, Zhang et al. 1997, Smith & Hoffmann 2008, Hu et al. 2014, Kang et al. 2016, Jiang et al. 2015, Ding et al. 2016b, Pardiñas et al. 2017, Ding & Liao 2019). Generic status of *Urocricetus* was at last restored by Lebedev et al. (2018a).

Corbet (1978) proposed a 2-species solution for *Urocricetus* with a polytypic *kamensis* and monotypic *alticola*. This arrangement remained largely unaltered for the next 4 decades. Scope of the polytypic *kamensis* was defined already by Wang & Cheng (1973), and included *lama* and *tibetanus*. Phylogenetic analysis by Ding & Liao (2019) showed, however, that *lama* and *tibetanus* align with *alticola,* which necessities nomenclatural and taxonomic changes. We therefore recognize a monotypic *kamensis* and polytypic *lama* (with *alticola* and *tibetanus*). The 2 species presumably diverged in the Early Pleistocene at about 1.73 Mya (95% CI = 1.46–2.03 Mya; Ding & Liao 2019) or 0.94 Mya (95% CI = 0.02−1.89 Mya; Lebedev et al. 2018a). In the estimate by Pan et al. (2024), the evolutionary split is significantly

older (*c.* 3.93 Mya) being triggered by the formation of the Mekong-Salween Divide in the early Pliocene.

Distribution. The range is encircling the Tibetan Plateau in China (southern Xinjiang, southern Gansu, south-eastern Qinghai and adjacent Sichuan, and southern Xizang), northern Nepal and north-western India (Uttaranchal, and Jammu and Kashmir). The 2 species of Tibetan hamsters are allopatric, while the genus is parapatric with respect to Phodopina (Figure 100).

Figure 102: Carded skin of *Urocricetus lama alticola* (from Menshi, Xizang, China) in dorsal view. Note a dorsad expansion of white ventral fur posterior to the rib cage and at the inguinal region, which is due to undulating lateral line.

Characteristics. Small and long-tailed hamsters (Figures 102, 106 & 108), which are externally most similar to *Nothocricetulus migratorius* and *Cricetulus longicaudatus*, yet they are of smaller size. Some authors stressed the external similarity between Tibetan hamsters and mountain voles (*Alticola argentatus* and *A. staliczkanus*) (*e. g.* Thomas 1917, Lim & Ross 1992). Fur is soft, dense and moderately long (length = 9.5–11 mm) with longer sparse hairs protruding by 2.5–3 mm. Mystacial vibrissae measure 33–37 mm. Ears are large (as long as hind foot), rounded and sparsely clad with short hairs. Tail is moderately long, thick, and densely covered by hair, which usually conceals the underlying annulation; the terminal pencil is long (length = 4–7 mm). Feet have 5 plantar and 6 palmar pads; interdigital plantar pads 2 and 3 are distinctly small, while the remaining pads (pads 1 and 4) are large and of same size. Plantar surface is largely nude, though there are some hairs between the pads (Figure 101); palms are nude. Claws are less robust than in the remaining hamsters; they are whitish or cream. The front thumb is rudimentary but with distinct claw. Dorsal fur varies between pale fulvous-grey and dull-brown; it is grizzled by black hairs which are more numerous on the crown
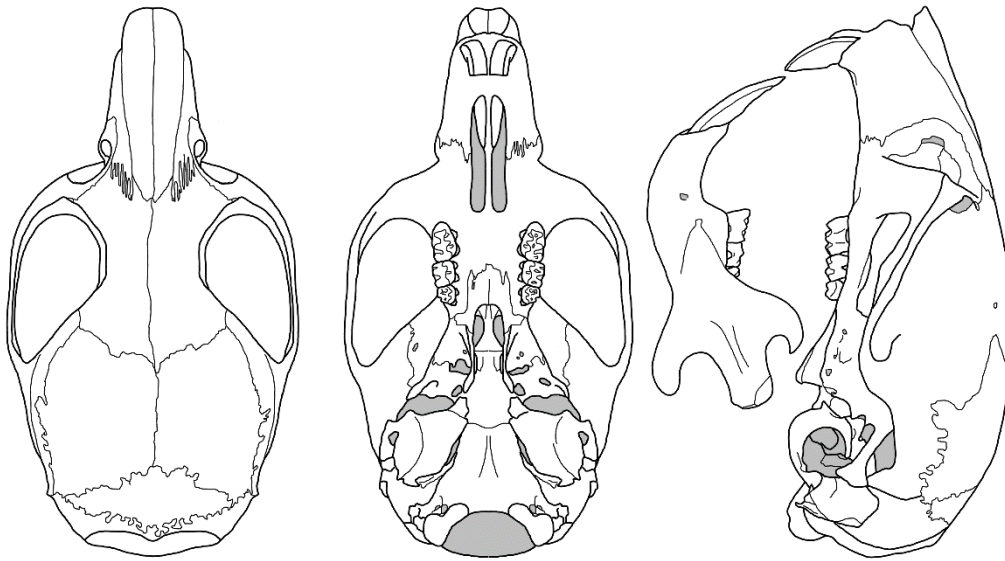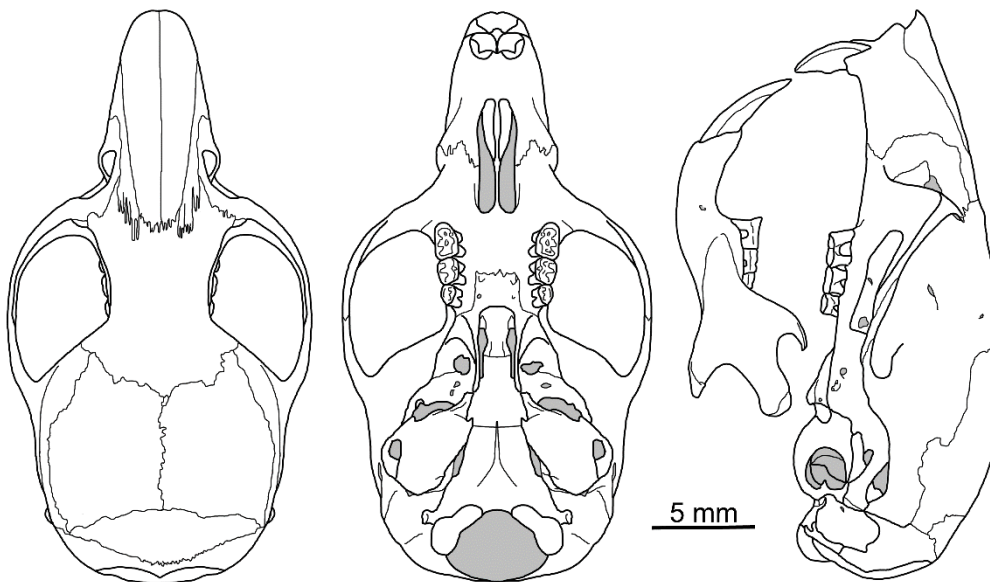
Urocricetus lama

Urocricetus kamensis

Figure 103: Skulls in Tibetan hamsters; top – *Urocricetus lama* (Dzakar Chu, Xizang, China); bottom – *U. kamensis* (Qinghai, north-eastern Tibet, China).

of the head and on the posterior back. Hairs on the belly have slate bases and white tips; demarcation line is clear and wavy. White underside makes a deep salient posterior to the rib cage (Figure 102); there are further 2 shallower salient angles on the cheeks and in the inguinal region. Ears are grey and frequently white margined; feet are white. Females have 4 pairs of nipples (2 pectoral and 2 inguinal pairs). Glans penis and baculum have not been studied yet.

Skull (Figure 103) closely resembles condition in *Cricetulus* and *Nothocricetulus* in size and proportions. It is comparatively narrow; zygomatic width accounts for 53.9–58.8% of condylobasal length. Occipital condyles are not visible in dorsal view. Rostrum is moderately long and braincase is large; nasals are long and the nasal process of the premaxillary does not reach far beyond the naso-maxillary suture. Frontals, parietals and occipitals are not ridged. Interorbital constriction is wide; interparietal bone is not restrained but expands across the entire roof of the skull. The masseteric plate is relatively small with the anterior margin inclined backward; viewed in dorsal profile, the zygomatic spine is weak and the notch is shallow. Incisive foramens are

long and wide; posteriorly, they nearly reach the M^1 level. The palate terminates at the posterior margin of M^3. The bullae are small (length = 3.9–5.0 mm) and flat, with large bony eustachian tube at their anteromedial portion. Mandible is shallow; the coronoid process is short and blunt. The upper incisors tend towards the opisthodont condition; molars are decidedly shorter than the incisive foramina. The 1st and 2nd internal folds (*if1* and *if2*) are contiguous with the 1st and 2nd primary folds (*pf1* and *pf2*) on M^1 (Figure 104). Diploid number of chromosomes is 30 (known only in *U. kamensis*).

Key to species

1a) Tail longer (> 50% of length of head and body), sharply bicolour, blackish above; present in Qinghui and Sichuan, and along the northern and eastern edges of the Tibetan Plateau …………………….………......……… kamensis

1b) Tail shorter (< 50% of length of head and body), indistinctly bi-colour or entirely white; present along the southern and western edges of Tibetan Plateau ………………………......………. *lama*

Urocricetus kamensis Satunin, 1902 – Satunin's Tibetan hamster

Urocricetus kamensis Satunin, 1902: 574. Type locality: "Fluss Mok-tschjun im Gebiete des Mekong", "im Lande Kam (die locale Benennung N.-O. -Tibets)". Ellerman (1941: 433) spelled the type locality as "River Mok-tschjun [Moktschjun in Ellerman & Morrison-Scott 1951: 625], district of Mekong, North-Eastern Tibet". In current transcription, the locality is the Mokchu River, a tributary of the Yuchu in the Mekong Basin; Province of Qinghai, north-eastern Tibet, China.

[Cricetus (Urocricetulus)] kamensis: Trouessart, 1904: 395. Name combination.

Cr[cetulus] (Cricetulus) kamensis: Argyropulo, 1933b: 246. Name combination.

U[rocricetus] camensis: Werth, 1934: 212. Incorrect subsequent spelling of *kamensis* Satunin.

[Cricetulus longicaudatus] kamensis: Flint, 1966b: 14. Name combination.

Etymology. The species epithet is derived from 'Kham' with the addition of adjectival suffix '-ensis'.

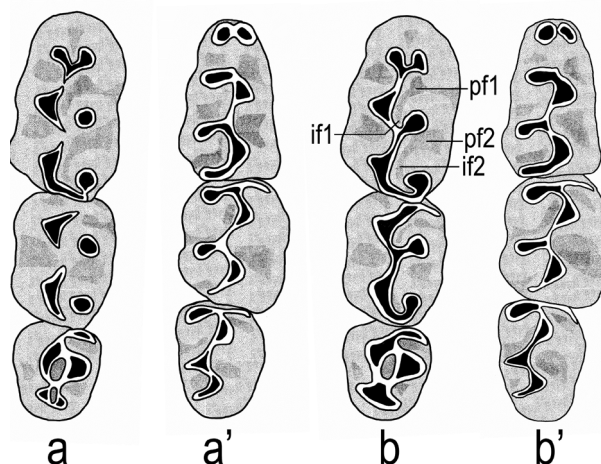Kham is one of 3 traditional Tibetan regions in which the type specimen has been collected.

Figure 104: Grinding pattern of upper (a, b) and lower (a', b') molars in (a) *Urocricetus lama lama* (Tingri, Xizang, China) and (b) *U. l. alticola* (Ladak, Jammu and Kashmir, India). Abbreviations: *if1, if2* – internal folds 1 and 2, respectively; *pf1, pf2* – primary folds 1 and 2, respectively. Scale bar = 1 mm.

Taxonomy. Although Satunin's Tibetan hamster was nearly uniformly classified as a species in its own right, its taxonomic status was uncertain (Corbet 1978); Ellerman & Morrison-Scott (1951) commented on *kamensis* as being *nomen dubium*. In a revision of Chinese Tibetan hamsters (Wang & Cheng 1973), *C. kamensis* was defined as a polytypic species with 4 subspecies (the nominotypical, *lama, tibetanus* and *kozlovi*); note that *kozlovi* is currently in the synonymy of *Nothocricetulus migratorius*. Wang & Cheng (*l. c.*) extracted *kamensis* from the scope of *Cricetulus longicaudatus,* where allocated by Flint (1966b) and retained until very recently (Honacki et al. 1982, Musser & Carleton 1993, 2005, Zhang et al. 1997, Luo et al. 2000, Wang 2003, Huang et al. 2008, Smith & Hoffmann 2008, Hu et al. 2014, Jiang et al. 2015, Pardiñas et al. 2017, Burgin et al. 2020, Romanenko et al. 2021). Evidence for a monotypic scope of *kamensis* and a shift of *lama* and *tibetanus* into synonymy of *alticola* was provided by Romanenko et al. (2021).

Distribution. The range outspreads across an estimated 103,775 km² of mountainous landscape in central and south-central China and centres in the Hengduan Mts. in the Three Rivers Source Region (Sanjiangyuan) (Figure 105). The majority of records are
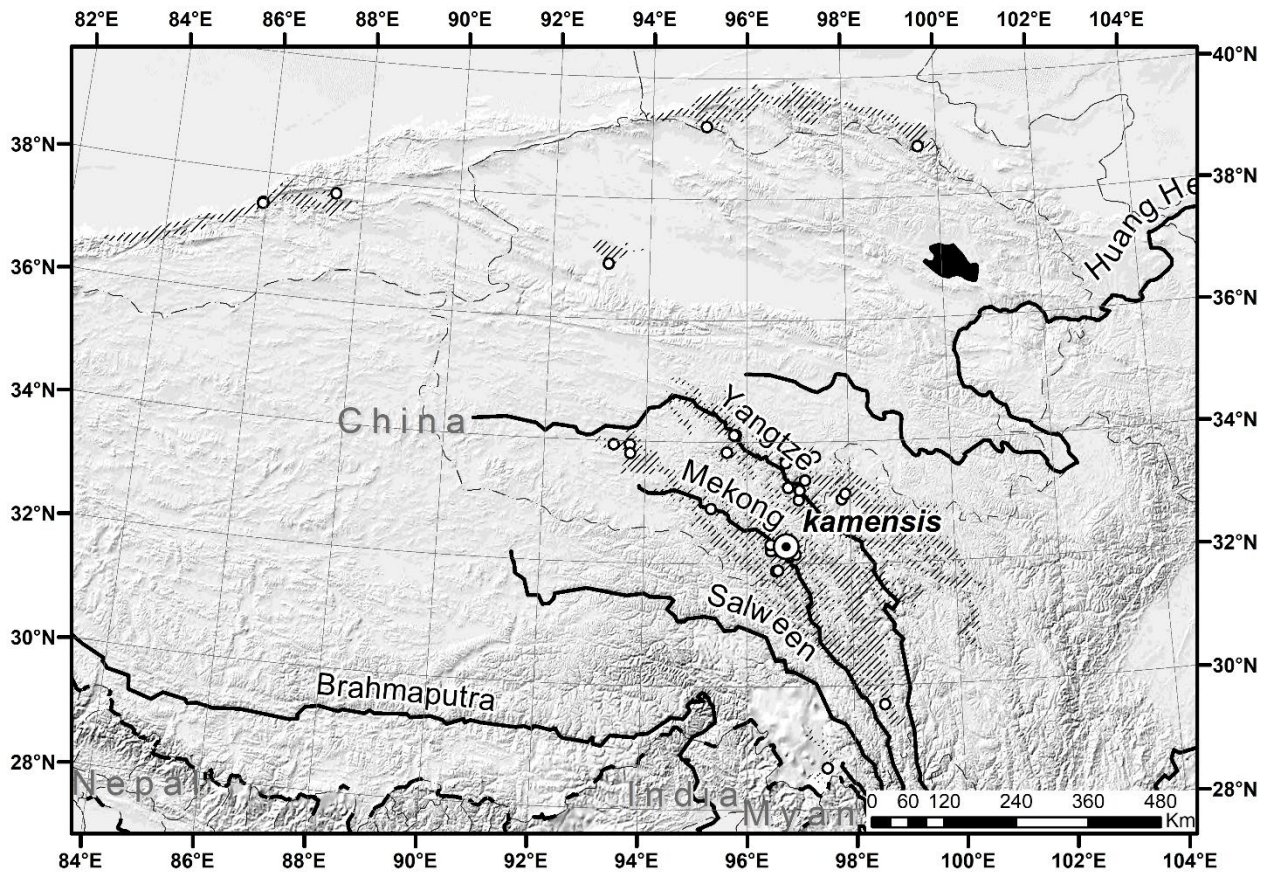
Figure 105: Distributional range of Satunin's Tibetan hamster *Urocricetus kamensis.*

from the upper Yangtze and Mekong Rivers in southern Qinghai; the range stretches further south into north-western Sichuan and encompasses the extreme south-eastern Xizang. There are at least 3 isolates to the north of the Yangtze River in the Qaidam Basin (eastern Qinghai), the Qilian Mts. (southern Gansu), and in the Altun Shan Mts. (south-eastern Xinjiang).

Satunin's Tibetan hamster occupies thickets, grasslands and cultivations, but prefers valleys with goosefoot and legumes; readily enters human dwellings (Zheng 1986,

Figure 106: Satunin's Tibetan hamster *Urocricetus kamensis* from Xizang, China. Photo courtesy of A. V. Surov.

Luo et al. 2000). Elevational range is 2,485–4,630 m (mean = 3,925 m); Zheng (1986) reports it as high as 5,150 m.

Characteristics. A long-tailed species (Figure 106); length of tail accounts for 50–75% of length of head and body. Dimensions: body mass = 21–42 g, length of head and body = 80–112 mm, length of tail = 48–64 mm, length of hind foot = 17–20 mm, length of ear = 16–18 mm; condylobasal length of skull = 23.5–26.3 mm, zygomatic width = 13.2–14.8 mm, length of maxillary tooth-row = 3.9–4.2 mm. Dorsal colour is greyish buff to greyish brown with no decided yellowish or russet tinge, noticeably clouded with an admixture of blackish hair tips that may form a fuzzy spinal stripe. The head and ears are grey. Ventral side is white and clouded by slate hair bases; chin is white to hair bases. Demarcation line is sharp. The tail is sharply bicolour, dark brown or blackish above and creamy below; terminal pencil is pure white (Figure 106). Skull and dentition as for the genus (Figures 103).

Karyotype: $2n = 30$, $NF_a = 50$; the autosomal set contains 11 pairs of biarmed chromosomes and 3 pairs of acrocentrics; both sex chromosomes are acrocentric; the X chromosome is of medium size and the Y chromosome is the smallest element. The karyotype has 38 autosomal conserved segments, which is more than in any other representative of Cricetinae (Romanenko et al. 2021).

Variation and subspecies. Monotypic.

Urocricetus lama (Bonhote, 1905) – Ladak Tibetan Hamster

Cricetulus lama Bonhote, 1905a: 14. The emended description and the type locality ("Lhasa, Tibet") were reported subsequently (Bonhote 1905b: 304–305).

Cricetulus alticola Thomas, 1917: 455. Type locality: "Shushal [Shushul; Ellerman 1941: 433], 13.500' [4,115 m]", Ladak, Jammu and Kashmir, India.

Cricetulus alticola tibetanus Thomas & Hinton, 1922: 180. Type locality: "Tingri, Tibet 14,000' [4,267 m]", Xizang, China.

Cr[icetulus] (Cricetulus) lama: Argyropulo, 1933b: 247. Name combination.

Cr[icetulus] (Cricetulus) lama lama: Argyropulo, 1933b: 247. Name combination.

Cr[icetulus] (Cricetulus) lama alticola: Argyropulo, 1933b: 247. Name combination.

Cr[icetulus] (Cricetulus) tibetanus: Argyropulo, 1933b: 247. Name combination.

Cricetulus alticola alticola: Ellerman, 1947: 361. Name combination.

C[ricetulus] kamensis lama: Wang & Cheng, 1973: 64. Name combination.

Cricetulus kamensis alticola: Zheng, 1986: 374. New rank and name combination.

Urocricetus k[amensis] lama: Ross, 1992: 197. Name combination.

Urocricetus alticola: Ross, 1992: 197. Name combination.

U[rocricetus] a[lticola] alticola: Romanenko, Lebedev, Bannikova, Pavlova, Serdyukova, Feoktistova, Qu, Sun, Surov & Graphodatsky, 2021: not paginated. Name combination.

U[rocricetus] a[lticola] lama: Romanenko, Lebedev, Bannikova, Pavlova, Serdyukova, Feoktistova, Qu, Sun, Surov & Graphodatsky, 2021: not paginated. Name combination.

U[rocricetus] a[lticola] tibetanus: Romanenko, Lebedev, Bannikova, Pavlova, Serdyukova, Feoktistova, Qu, Sun, Surov & Graphodatsky, 2021: not paginated. Name combination.

U[rocricetus] lama: Pan, Wang, Liu, Li, Liao, Chen, Peng, Zhu, Li & Liu, 2024: not paginated. First use of the current name combination.

U[rocricetus] a[lticola] tibetanus: Pan, Wang, Liu, Li, Liao, Chen, Peng, Zhu, Li & Liu, 2024: not paginated. Name combination

Etymology. Bonhote (1905a, b) did not explain the etymology of the species epithet *lama* which, in any case, was common practice in his time. The name is probably in allusion to Dalai Lama, the title of the foremost spiritual leader of one of the leading schools of Tibetan Buddhism. Until 1951, the Dalai Lamas headed the Tibetan Government in Lhasa, which is also the type locality of Bonhote's *Cricetulus lama*. 'Lama' (bla-ma) is Tibetan for 'master, guru'. Bonhote (1905b: 304) believed that *U. lama* was identical to "the little white mouse" reported by Walton (1905: 423) for the Jo-kang Shrine in Lhasa. Although Walton (*l. c.*) remarked that these rodents "belong to the species of the ordinary house-mouse of Tibet", Bonhot was seemingly

impressed by the presence of a "surprisingly tame" mouse inside the shrine, which was possibly an additional inspiration for the new name. Perhaps even more relevant is the fact that in Bonhote's time, *lama* was used as species epithet for several taxa from Tibet, *e.g. Lanius lama* Dresser, 1905 (now *Lanius tephronotus*), and *Microtus (Alticola) lama* Barrett-Hamilton, 1900 (now *Alticola stoliczkanus lama*); *Ovis dalai-lama* Przewalski, 1888 (now *Ovis ammon dalailamae*) is particularly eloquent in this context. Similar inspirations in naming exotic taxa were not exceptional at the turn of the 19th into 20th century, *e. g. Evotomys mikado* Thomas, 1905, from Japan (now *Clethrionomys rutilus*), *Tigris mikado* Satunin, 1915, from Korea (now *Panthera tigris altaica*), *Micromys geisha* Thomas, 1905, from Japan (now *Apodemus argenteus*), and *Arvicola mandarinus* A. Milne Edwards, 1871, from China (now *Lasiopodomys mandarinus*). Species epithets were derived from 'Mikado' (a Japanese word meaning 'emperor'), 'geisha' (a female Japanese performing artist and entertainer), and 'mandarin' (a high official in the Chinese empire).

Taxonomy. Wang & Cheng (1973) classified all forms of Ladak Tibetan hamsters as subspecies (or synonyms) of *kamensis*. Corbet (1978) accepted this view, though he simultaneously admitted *alticola* as a species in its own right. It therefore happened that taxa which are now inside *lama* were split between 2 species, *kamensis* (with *lama* and *tibetanus*) and *alticola* (Corbet & Hill 1980,

1986, Honacki et al. 1982, Musser & Carleton 1993, 2005, Zhang et al. 1997, Huang et al. 2008, Hu et al. 2014, Jiang et al. 2015, Haslauer 2017c, f, Burgin et al. 2020). Ross (1992) was uncertain over taxonomic status of the Ladakh hamster and although provisionally synonymized *lama, alticola* and *tibetanus* with *kamensis* (p. 191), also concluded that "*alticola* […] is a species distinct from *U. kamensis*" (p. 198). In a revision of Chinese mammals, Smith & Hoffmann (2008) elevated *lama* to a species rank, but did not comment on *alticola*, which was in any case a geographical outlier. Romanenko et al. (2021) finally classified *lama, alticola*, and *tibetanus* as subspecies of *alticola*; here we treat them in similar way, although under *lama*, which is the oldest name in the group (*cf.* Peng et al. 2024). The scope of *lama* was defined by Ding & Liao (2019) who, however, still classified it as a subspecies of *kamensis*. Prior to the revision by Wang & Cheng (1973), Argyropulo (1933b, c) recognized *lama* as a species in its own right with the inclusion of *alticola* and *tibetanus*. Ellerman (1961) and Ellerman & Morrison-Scott (1951) treated *lama* and *alticola* as independent species inside the *lama* group of *Cricetulus*.

Distribution. Range (area = 51,625 km²) covers the southern and south-western border of the Tibetan Plateau in southern Xizang (China), northern Nepal (Pashchimanchal and Sudur Pashchimanchal), northern Uttaranchal and western Jammu and Kashmir in India,
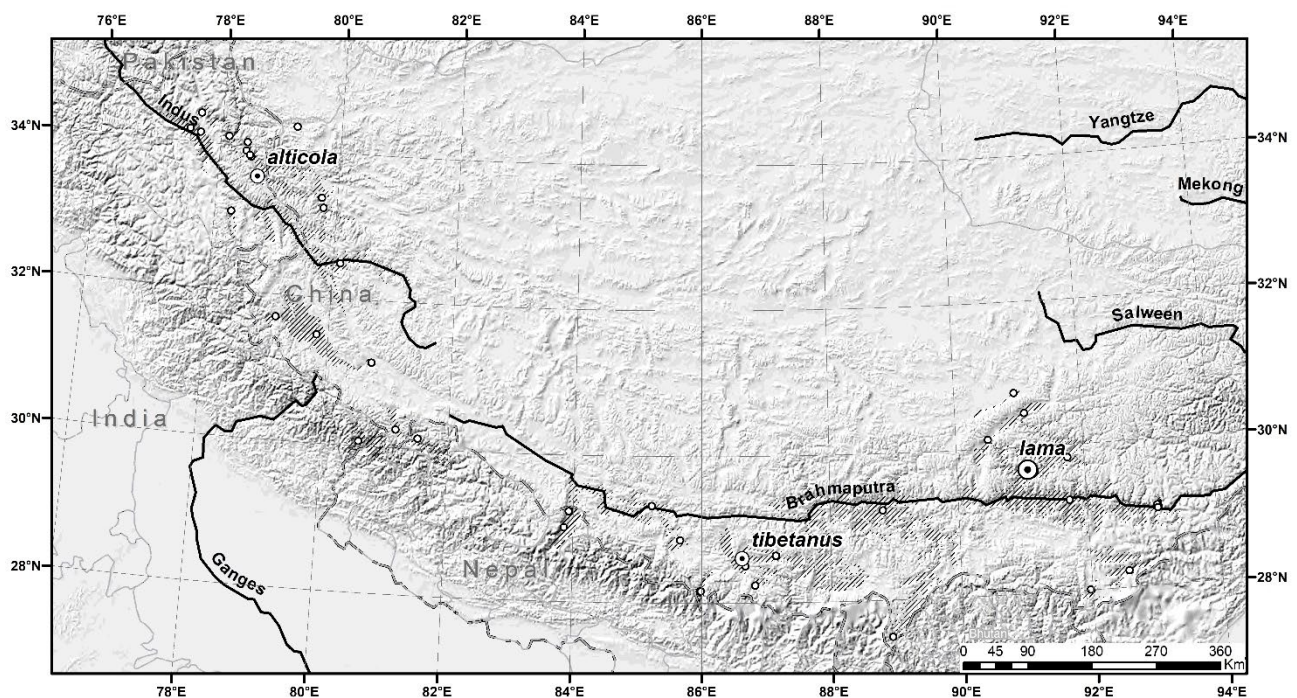

Figure107: Distributional range of Ladak Tibetan hamster *Urocricetus lama.*

and the Kongkashan Pass in extreme southern Xinjiang (China) (Figure 107). This hamster occupies wide range of habitats: mountainous coniferous and catawba forests, thickets, swampy meadows, alpine grassland, farmland and human dwellings (Zheng 1986). Elevational range is 2,175–5,200 m (mean = 4,065 m), and Hu et al. (2014) stressed that *U. lama* ascends higher in the Mt. Qomolangma National Nature Reserve than any other muroid rodent.

Characteristics. Dimensions: body mass = 22–48 g, length of head and body = 84–103 mm, length of tail = 27–44 mm, length of hind foot = 15–18 mm, length of ear = 14–17 mm, condylobasal length of skull = 22.6–25.6 mm, zygomatic width = 12.5–14.7 mm, length of maxillary tooth-row = 3.7–4.2 mm. Relative length of tail varies depending on the subspecies, and accounts for 31–50% of the length of head and body. Dorsal pelage is on average lighter than in *kamensis*, pale fulvous grey, beige-brown or greyish-brown (Figures 102 and 108); the chin and upper part of throat are white to hair bases. The tail is wholly white or with a narrow median dusky streak along its upper surface; it is never blackish dorsally as in *kamensis*. Skull and dentition as for the genus (Figures 103 and 104).
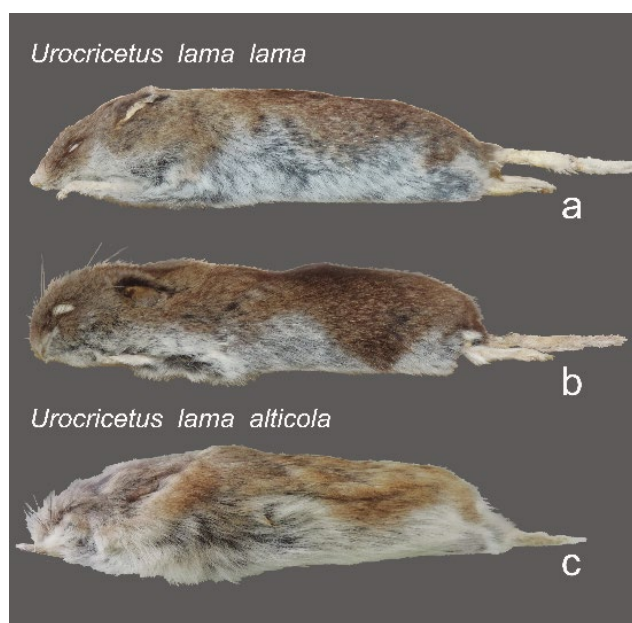

Figure 108: Skins of Ladak Tibetan hamsters *Urocricetus lama* in lateral view: a, b – *U. l. lama* from Lhasa, Xizang, China (a), and Loro Chu, Xizang, China (b); c – *U. l. alticola* from Ladak, Jammu and Kashmir, India.

Variation and subspecies. Early authors recognized 3 subspecies (*lama, alticola, tibetanus*) (Argyropulo 1933b, c,

Ellerman 1941), but subsequent students synonymized *tibetanus* with *lama* (Ellerman & Morrison-Scott 1951, Zheng 1986, Zhang et al. 1997, Luo et al. 2000, Wang 2003). Romanenko et al. (2021) reinstalled *tibetanus*, largely following the results by Ding & Liao (2019) who retrieved 3 genetic lineages of *U. lama*; 2 of these lineages are allopatric, while the third one overlaps with both of them. Because of this overlap, we accepted 2 subspecies admitted also by earlier authors.

Urocricetus lama lama (Bonhote, 1905)

Synonym. *Cricetulus alticola tibetanus* Thomas & Hinton, 1922.

Distribution. The eastern portion of the species' range, to the east of ~ 86th meridian (Zheng 1986, Ding & Liao 2019).

Characteristics. Dimensions: body mass = 24–42 g, length of head and body = 84–103 mm, length of tail = 34–44 mm, length of hind foot = 15–18 mm, length of ear = 15–17 mm, condylobasal length of skull = 22.6–25.6 mm, zygomatic width = 12.7–14.7 mm, length of maxillary tooth-row = 3.9–4.2 mm. Tail longer, accounting for 42–50% of length of head and body. Dorsal pelage darker, greyish-brown, tail with a narrow median dusky streak along its upper surface instead being wholly white (Figure 108a, b).

Urocricetus lama alticola Thomas, 1917

Etymology. The epithet *alticola* is composed of Latin 'altus' for 'high' and '-cola' for 'dweller' (from 'colere' meaning 'to dwell'), *i. e.* a dweller of high elevations in allusion to its habitat.

Distribution. The western portion of the species' range, to the west of ~ 86th meridian (Zheng 1986, Ding & Liao 2019).

Characteristics. Dimensions: body mass = 22–48 g, length of head and body = 85–103 mm, length of tail = 27–37 mm, length of hind foot = 16–18 mm, length of ear = 14–16 mm, condylobasal length of skull = 22.6–24.6 mm, zygomatic width = 12.5–14.2 mm, length of maxillary tooth-row = 3.7–4.2 mm. Tail shorter, accounting for 31–40% of length of head and body.

Dorsal pelage on average lighter than in *lama*, pale fulvous grey; tail entirely white or with slight brown shade dorsally (Figures 102 & 108c).

SUBTRIBE: Phodopina – New Subtribe

Type genus. *Phodopus* Miller, 1910

Diagnosis and Comparisons. Phodopina new subtribe differs from Urocricetina in nucleotide sequences (Lebedev et al. 2018a, Romanenko et al. 2021) and in a set of morphological and chromosomal particularities. In Phodopina, (1) the plantar surface is completely furry (Figure 109), while there is bare skin present between the pads in Urocricetina (Figure 101); (2) the number of plantar pads is reduced to 3 or less, while there are 6 plantar pads in Urocricetina; (3) the tail is vestigial (< 20% of head and body length), but normally developed in Urocricetina (longer than 20% of head and body length); (4) the phallanges are relatively shorter than in Urocricetina and the remaining hamsters, hence the species of Phodopina run at slow speed and frequently move by hopping (Wynne-Edwards et al. 1992); (5) distal trident remains cartilaginous and is less than ½ of the length of proximal stalk[1] (Figure 17a, b); in the remaining hamsters, the distal trident is usually ossified and long (Figure 17c, d, f–h); if distal trident remains cartilaginous, it is then distinctly longer than ½ of length of proximal stalk (*Mesocricetus*; Figure 17i); (6) the corneous epithelium of the stomach occupies most of the glandular region (Figure 15b), but extends only along the border of isthmus in Urocricetina; (7) the stapedial artery is lost, which is reflected in the loss of spheno-frontal foramen and squamoso-alisphenoid groove (these structures are present in all the remaining Cricetinae) (Ross 1992).

Content. Phodopina contains 2 genera (*Phodopus* and *Cricetiscus*) with 3 recent species. The genera separated before the end of Miocene at an estimated 4.9–6.9 Mya (Neumann et al. 2006) or 5.69 Mya (95% CI = 4.38–7.04 Mya; Lebedev et al. 2018a), depending on the marker and calibration point used. Alhajeri (2021) suggested a much older divergence of 10.9 Mya.

Distribution. The northern portion of the range of Urocricetini in southern Siberia (the upper reaches of the Ural, Tobol, Black Irtysh, Ob, and Yenisey), northern and eastern Kazakhstan, Mongolia and northern China, to the north of the Huang He and the plateaus of Ordos and Tibet. Along the Tibetan Plateau, the range of Phodopina marginally overlaps that of Urocricetina (Figure 100).
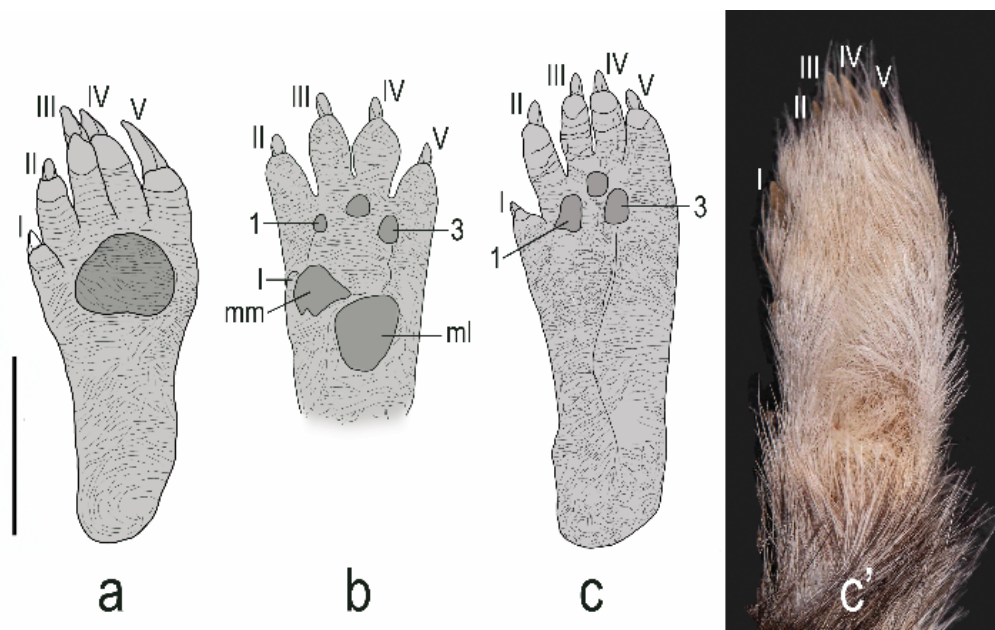

Figure 109: Left palm in *Phodopus roborovskii* (a) and *Cricetiscus sungorus* (b, c, c'). Hairs are removed in insets a–c to expose pads (shaded dark grey). Digits are indicated by Roman numerals (I = thumb); scale bar = 5 mm.

[1] In *Nothocricetulus*, the distal baculum is shorter than ½ of the proximal baculum, but is osseous (Figure 17e).

GENUS: *Phodopus* Miller, 1910 – Desert Hamsters

Phodopus Miller, 1910: 498. Type species: *Cricetulus bedfordiae* Thomas (= *Phodopus roborovskii* Satunin).

Etymology. The generic name is a composite of 'phodos' (the genitive case of the Greek 'phos' for a 'burn' or 'blister') and 'pous' meaning 'foot' in Greek, hence a 'foot with a blister' in allusion to the only plantar pad present, which resumes shape of a large blister or bubble (Figure 109a) (Ross 1994).

Taxonomy. *Phodopus* traditionally encompasses all 3 species of Phodopina. *Cricetiscus*, although described as a genus in its own right (Thomas 1917), was only exceptionally used that way (Howell 1929, Allen 1940), but was mainly synonymized with *Phodopus*. Within *Phodopus*, some authors recognized 2 species groups (the *sungorus* group and the *roborovskii* group), which match the current genera *Cricetiscus* and *Phodopus*, respectively (Ellerman 1941, Pavlinov & Rossolimo 1987, Pavlinov et al. 1995); Lebedev (2012) ranked *Cricetiscus* as a subgenus of *Phodopus*. Phylogenetic reconstructions based on molecular markers retrieved deep divergence between *roborovskii* on the one hand and *sungorus* + *campbelli* on another hand. Based on this evidence, Neumann et al. (2006) proposed a restoration of *Cricetiscus* as an independent genus, but their suggestion gained no support (Feoktisova 2008, Smith & Hoffmann 2008, Pardiñas et al. 2017, Burgin et al. 2020). We agree with Neumann et al. (2006) and classify *Phodopus* and *Cricetiscus* as distinct genera. These genera diverged at an estimated 4.9±0.3–6.9±1.3 Mya (Neumann et al. 2006) or, according to a more recent estimation (Lebedev et al. 2018a), 5.69 Mya (96% CI = 4.38–7.04 Mya). In the course of independent evolution, they accumulated ample morphological synapomorphies (see below), which further support the proposed taxonomy. Besides, *Phodopus* clearly differs from *Crictiscus* in various behavioural and physiological characteristics, *e. g.* slower rates of growth and behavioural development (Ross & Cameron 1989), faster response to changes in photoperiod and lower seasonal variation in body mass and testes size (Müller et al. 2015).

Phodopus roborovskii (Satunin, 1902) – Desert Hamster

Cricetulus roborovskii Satunin, 1902: 571. Syntypes are from "Oberlauf des Scharogol-dschin (Nan-schan)" and "Syrtyn". Type locality subsequently restricted to "the upper course of the Shara Gol in extreme western Nan Shan, China" (Allen 1940: 776). A lectotype (ZIN 5829) was collected from "верховья р. Шароголджин в Нань-Шане [upper reaches of the River Sharogoldzhin in Nan'-Shan']" (Gromov & Baranova 1981: 159), *i. e.* "верх. р. Шарогол-Джин (р. Шара-Гол), Нань-Шань, (Китай)" [upper reaches of the River Sharogol-Dzhin (River Shara-Gol), Nan'-Shan' (China)] in Baranova & Gromov (2003: 45). Currently, the type locality is spelled 'the upper [part of] Scharogol-Dzhin [River valley], Qinghai, China'.

[*Cricetus (Cricetulus)] roborovskii:* Trouessart, 1904: 395. Name combination.

Cricetulus bedfordiae Thomas, 1908a: 45. Type locality: "Yu-lin-fu, Shen-si", "4000' [1,220 m] [added in Thomas 1908d: 975]", amended to "Yulinfu, North Shensi, China" (Ellerman & Morrison-Scott 1951: 628), currently Yulin, Shaanxi, China.

Phodopus bedfordiae: G. Allen, 1925: 7. Name combination.

Phodopus praedilectus Mori, 1930: 418. Type locality: "Cheng-chia-tun, Central Manchuria", China.

Phodopus roborovskii: Formozov, 1929: 54. First use of the current species name combination.

Phodopus roborovskii: Argyropulo, 1933b: 244. Incorrect subsequent spelling of *roborovskii* Satunin.

Cricetulus roborovski: Chaworth-Musters, 1934: 591. Incorrect subsequent spelling of *roborovskii* Satunin.

Phodopus roborovskii bedfordiae: Ellerman, 1941: 437. Name combination.

Phodopus roborovskii praedilectus: Ellerman & Morrison-Scott, 1951: 628. Name combination.

Phodopus przhewalskii Vorontsov & Krjukova, 1969b: 102. Type locality: "пески востока Зайсанской котловины между Юлькен-Араталом [now Улькен-Каратал] и Акжоном на левом берегу Черного Иртыша [sands of eastern Zaysan Depression between Ul'ken-Karatal and Akzhon

on the left bank of the Black Irtysh]”, East Kazakhstan Region, Kazakhstan.

[Phodopus] przewalskii: Gromov & Baranova, 1981: 159. Incorrect subsequent spelling of *przhewalskii* Vorontsov & Krjukova, 1969.

Ph[odopus] roborovskii przhewalskii: Vorontsov, 1982: 356. Name combination and new rank.

Cricetulus betfordiae: Feoktisova, 2008: 14. Incorrect subsequent spelling of *bedfordiae* Thomas.

Etymology. The species epithet is eponym for Vsevolod Ivanovich Roborovsky (Всеволод Иванович Роборовский, 1856–1910), a Russian army officer and participant of Przewalski's expeditions to Central Asia. He served as a natural history collector and scientific illustrator, and secured syntypes of *P. roborovskii*. Roborovsky has eponyms also in herpetology, ornithology and botany.

Taxonomy. We regard *Phodopus* as a monospecific genus which, however, has not always been the case. Shortly after Satunin's description of *roborovskii*, Thomas (1908a, d) named a new species *bedfordiae*, presumably on the basis of smaller size. Subsequent authors used *bedfordiae* and neglected *roborovskii* (Allen 1925, 1940, Howell 1929, Mori 1930); these 2 names were synonymized around 1930 (Formozov 1929, Argyropulo 1933a, b, Chaworth-Musters 1934).

Vorontsov & Krjukova (1969b) described a new species of desert hamster *Phodopus przhewalskii* from the Zaysan Depression in eastern Kazakhstan. The diagnosis was based exclusively on karyology, *i. e.* 2n = 34 in the new species, while 2n = 28 was taken from Matthey (1960) as the correct count in *roborovskii*. The latter report is an evident error, and most likely refers to *Cricetiscus campbelli*. Corbet (1978) synonymized *przhewalskii* with *roborovskii*; Sludskiy (1977b) maintained it as a species in its own right, while Vorontsov (1982) and Shenbrot (2017a) rank it as a subspecies of *roborovskii*.

Distribution. Geographic range is wide but highly fragmented (area = 433,274 km²) due to narrow habitat preferences of the species. The range covers north-western and southern Mongolia and northern China, reaching the margins of Kazakhstan, Russia and India (Figure 110). Mongolian range encompasses the Great Lake Depression, Valley of Lakes and the Gobi Desert to the south of the 44th parallel; desert hamsters are absent from the Altai Mountain range, the Eastern Sayan and the Khangay Range (*cf.* Sokolov & Orlov 1980). The north-western extension of Mongolian range in the Uvs Province marginally captures Tuva (Tyva) Province in Russian Federation (Flint 1960). In China, the bulk of range overlaps with the Gobi Desert and the Ordos Plateau in the Provinces of central Nei Mongol, Gansu, north-eastern Qinghai, Ningxia, northern Shaanxi, and northern Hebei. Further east, a
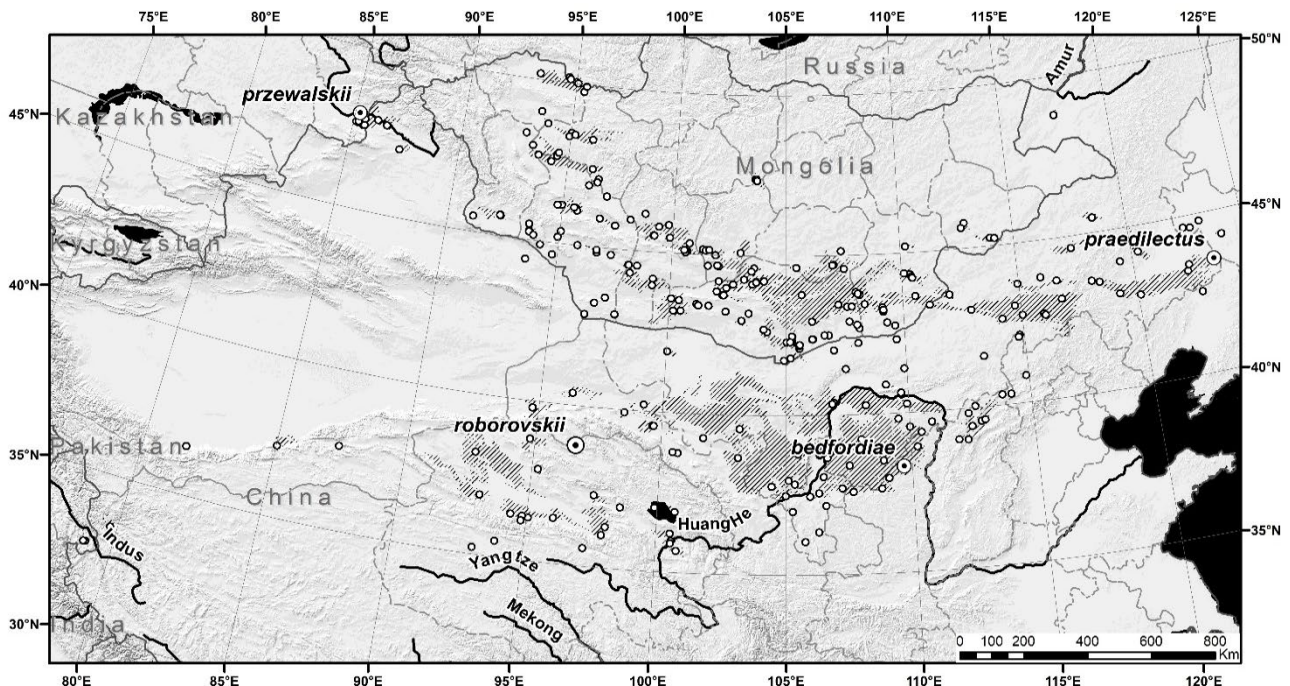

Figure 110: Distributional range of the desert hamster *Phodopus roborovskii*.

large fragment of geographic range is isolated by the Great Khingan mountain ridge; the fragment encompasses eastern Inner Mongolia, western Jilin and western Liaoning (Zhang et al. 1997, Luo et al. 2000, Wang 2003). The following population fragments are scattered at the periphery of northern and western range borders (south-west to north-east): (1) Changthang Plateau (part of Tibet Plateau) in eastern Ladakh, India (Ramachandran et al. 2020) and Rutog County in Xizang, China (Liu et al. 2020); (2) Altun Shan Mts. in southern Xinjiang (Zhang et al. 1997); (3) Zaysan Basin in eastern Kazakhstan and adjacent Xinjiang (China) northward and mainly eastward of the upper Black Irtysh (Sludskiy 1977b, Zhang et al. 1997); (4) Uvs-Nuur depression (north-western Mongolia) and Tuva (southern Siberia); (5) Mongolyn-Els in Bulgan Province, Mongolia (vouchers in ZMMU); and (6) Xin Barag You Qi in north- eastern Inner Mongolia (Xu 2016).

Desert hamsters inhabit sandy and sandy-gravel plains and the periphery of sand dunes and semi-fixed sands, but avoid inner parts of large sand massifs. They prefer sparse vegetation cover and avoid steppes and saline habitats (Flint 1960, Sludskiy 1977b). In Mongolia, their northern and north-eastern range border coincides pretty close with the spring vegetation cover of <20% (*cf*. Figures 7 & 12 in Judger et al. 2018). Elevational range is 115–4,637 m (mean = 1,382 m).

Characteristics. The smallest living hamster with a short and broad torso (Figures 111c & 112). Dimensions: body mass = 10.5–19 g, length of head and body = 66–86 mm, length of tail = 7–11 mm, length of hind foot = 10.5–12.0 mm, length of ear = 9–14 mm, condylobasal length of skull = 19.2–21.7 mm, zygomatic width = 11.3–12.8 mm, length of maxillary tooth-row = 3.1–3.5 mm. Ears are moderately long, eyes fairly large; whiskers white and black, very dense and long (up to 25–30 mm). Tail is vestigial and stumpy (Figure 113a), equalling 8–15% (usually ≈ 10%) of length of head and body; it is densely furry and the terminal pencil is long (≈ 5 mm). Feet are unusually short and broad, densely hairy throughout; plantar and palmar tubercles are confluent into a single blister-like mass (Miller 1910; Figure 109a). Fur is soft and fine, hairs on the mid-back measure 6–10.5 mm; sparse all-black hairs protrude by up to 4 mm and are denser on the posterior rump. General dorsal colour is drab-grey and clouded by grey hair bases; flanks are pinkish buff. Young hamsters tend to be darker. Undersurface from just below the eyes, the limbs and the tail are pure
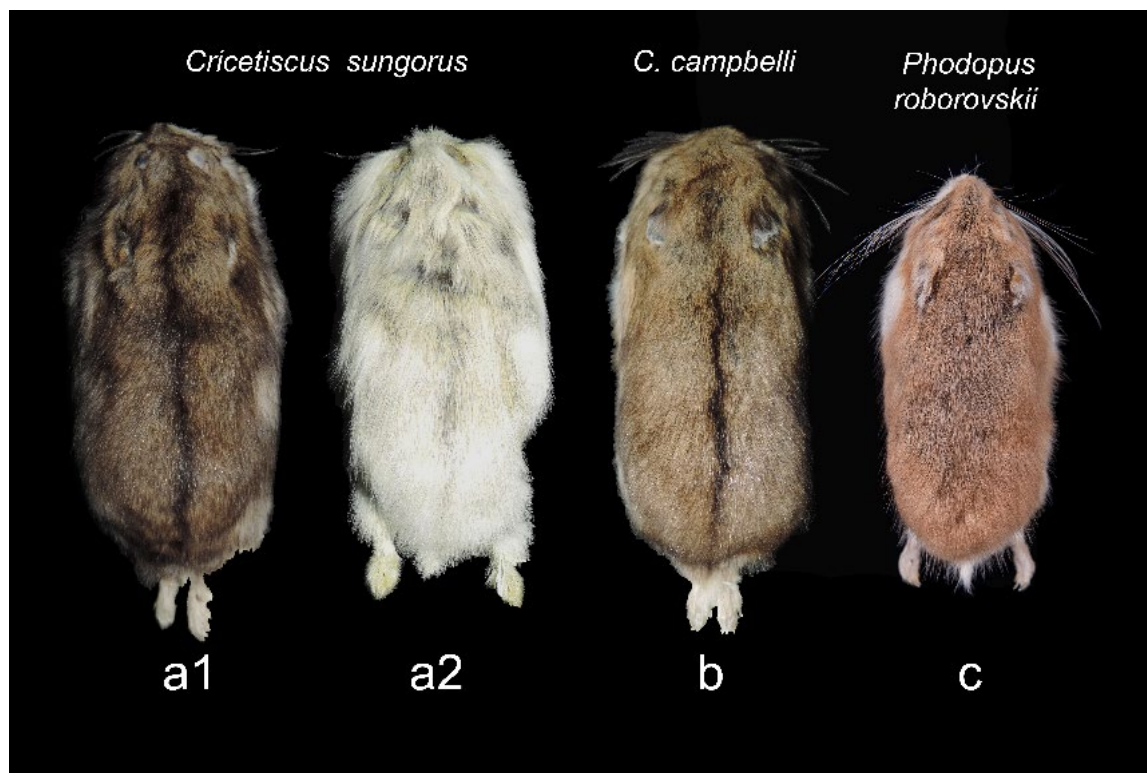

Figure 111: Museum skins in dorsal view of *Cricetiscus sungorus* in summer (a1) and white winter (a2) pelage; *C. campbelli* (b) and *Phodopus roborovskii* (c). Museum vouchers originate from Karasukskiy Rayon (a1), Novosibirsk Oblast (a2), south-eastern Altay Republic (b), and Mongolia (c). Photo by B. Kryštufek (a1, a2 & b) and David Kunc (c)

snowy-white and the white of the lower side extends to dorsal side of the tail base (Figure 113a). The basal ⅘ of dorsal hairs are slate, while ventral hairs are white to base. Line of demarcation is well defined and serpentine with a distinct upward salient between the cheeks and shoulder and another one though less prominent, on hips. There are 2 white patches on the head, one over the eye and another below the ear; the latter is more prominent in adults. Ears are greyish brown. Females have 4 pairs of nipples.
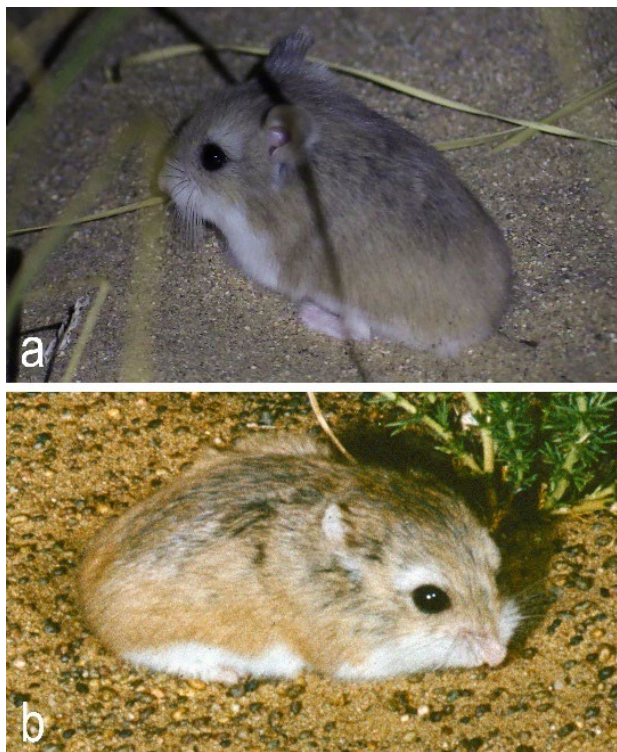
Figure 112: Desert hamster *Phodopus roborovskii*. Photo by Konstantin A. Rogovin (a) and Georgy Shenbrot (b)
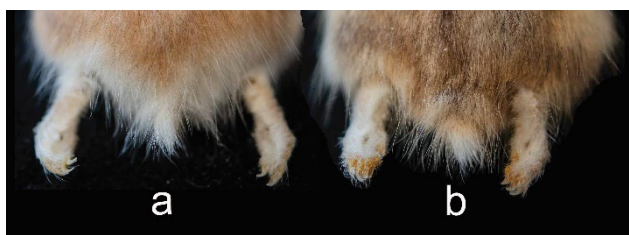
Figure 113: Museum skins of *Phodopus roborovskii* (a) and *Cricetiscus campbelli* (b) in semi-caudal view. Dorsal side of the tail base is white like the underside in *Phodopus* (a), and brown like the rest of back in *Cricetiscus* (b). Photo by David Kunc

The glans penis is club-shaped with expanded distal portion. There are no dorsal or ventral papillae, while the lingual papilla shows forked tip. Baculum (Figure 17b) has moderately expanded lancelike base and its

width accounts for ~ 37% of length of the proximal baculum. Distal trident is short and cartilaginous; its length approximates 23% of length of the proximal stalk; the central distal digit is longer than the lateral ones (Tokuda 1941, Vorontsov 1982).

The skull is small and delicate, with widely expanded zygomatic arches (Figure 114); zygomatic width accounts for 56.7–63.8% of condylobasal length (mean = 59.6%). The nasals are truncate at the top and comparatively short, not reaching behind the level of lacrimals. The anterior edge of the superior maxillary root of zygoma forms right angle at its junction with the rostrum; zygomatic arches run parallel to sagittal plane.

Zygomatic plate lacks the masseteric expansion and is therefore narrow; despite this, the infraorbital foramen is of myomorphous type (Figure 20f); zygomatic keel and notch are both absent. Interorbital region is flat and broad, nearly as wide as rostrum. There is no trace of supraorbital ridges. Braincase is rounded and broad, as wide as long; parietals extend across much of cranial roof, but the interparietal is rather small. The profile is evenly bowed and the skull is comparatively deep. Incisive foramens are wide and quite short, only slightly exceeding the length of maxillary tooth-row; posteriorly, they do not reach the level of M^1. Hard palate and pterygoid fossa are wide. Bullae are small and flattened, with characteristic tube-shaped anterior portion; basioccipital bone is wide. Mandible shows no peculiarities except for a short coronoid process. Upper incisors are opisthodont. The occlusal surface of molar cusps is simplified and M^3 is reduced. The major cusps directly oppose each other forming transverse lophs; there are no internal fields (Figure 115).

Corneous epithelium occupies most of glandular region of the inner stomach in *Phodopus* (Figure 15b), but extends only along the border of isthmus in *Cricetiscus*. Besides, *Phodopus roborovski* is the only true hamster without pyloric glands in the glandular portion of the stomach (Vorontsov 1967, 1982, Ross 1992).

Karyotype: 2n = 34, NF = 59; 12 autosomal pairs are biarmed and 4 pairs are acrocentric. Sex chromosomes are of medium size; the X chromosome is submetacentric and the Y chromosome is acrocentric (Spyropoulos et al. 1982, Schmid et al. 1986).
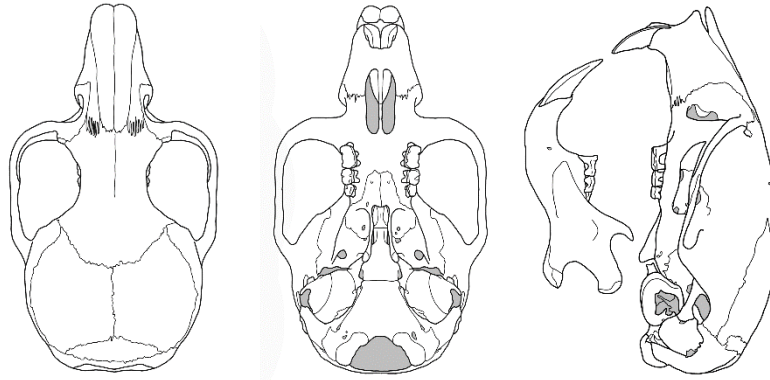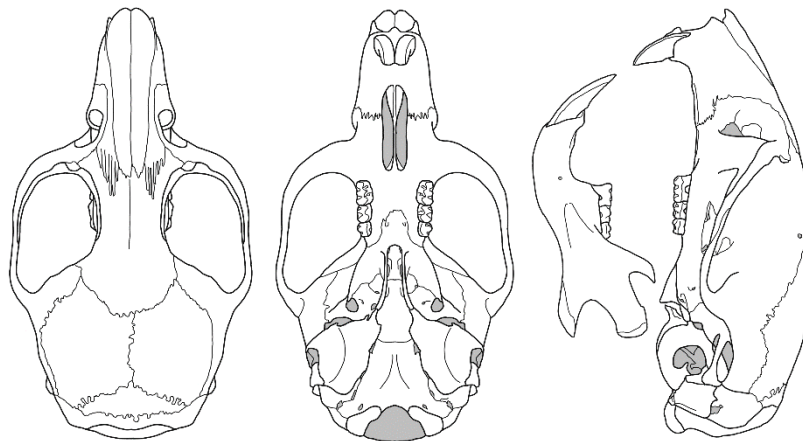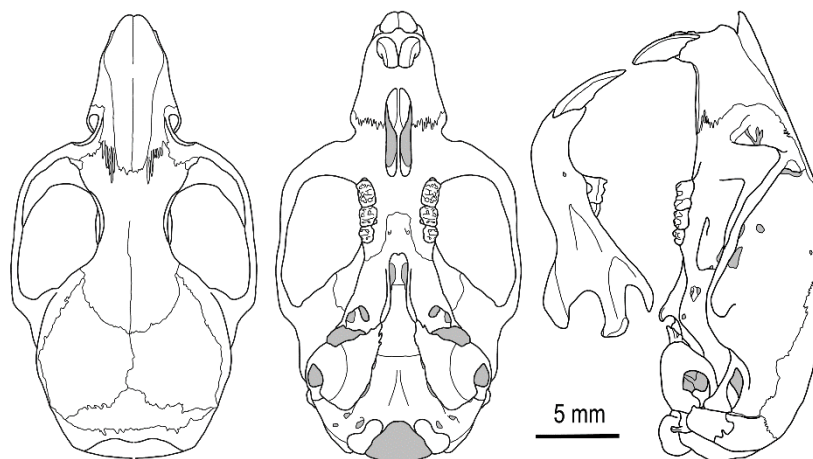
Phodopus roborovskii

Cricetiscus campbelli

Cricetiscus sungorus

5 mm

Figure 114: Skull and mandible in Phodopina hamsters. Top to bottom: *Phodopus roborovskii* (Dundovi Province, Mongolia), *Cricetiscus campbelli* (Dornod Province, Mongolia), and *C. sungorus* (Karasukskiy Rayon, Russian Federation).

Variation and subspecies. Subspecific taxonomy was never comprehensively revised and the number of recognized subspecies varied from 2 subspecies (*roborovskii* and *bedfordiae*) in Argyropulo (1933c), 3 subspecies (*roborovskii, bedfordiae, praedilectus*) in Ellerman & Morrison-Scott (1951) and 4 subspecies (*roborovskii, bedfordiae, praedilectus, przhewalskii*) in Vorontsov & Krjukova (1969b). Many authors, on the other hand,

considered *P. roborovskii* a monotypic species (Bannikov 1954, Gromov et al. 1963, Zhang et al. 1997, Luo et al. 2000, Wang 2003). This is not surprising, given the lack of obvious variation in colour, size and cranial proportions (e.g. Chugunov 1962). Phylogeographic analysis of cyt*b* fragment, however, retrieved significant structuring on the one hand and considerable admixture of up to 4 different lineages in the central

part of the range on the other hand (Meschersky & Feoktisova 2011, Lv et al 2016). Based on these results, Shenbrot (2017a) tentatively admitted 3 subspecies (*roborovskii, praedilectus, przhewalskii*). As shown by an ongoing study (Feoktisova et al., in progress), the situation is even more complex with some 5 lineages as putative subspecies: (1) *roborovskii* lineage with distributional range in Qinghai, Tibet and north-western India; (2) *bedfordiae* lineage which is admixture of several genetic lineages from the central part of geographic range; (3) *praedilectus* lineage from China (north-western Jilin, northern Liaoning and eastern Inner Mongolia); (4) *przhewalskii* lineage in Kazakhstan (eastern Zaysan Depression in the East-Kazakhstan Region) and north-western Xinjiang in China; (5) Tyva lineage from southern Tyva in Russian Federation. Any of these subspecies (or lineages) has so far been defined morphologically. We therefore leave subspecific taxonomic of *P. roborovskii* unresolved, calling for a thorough revision.
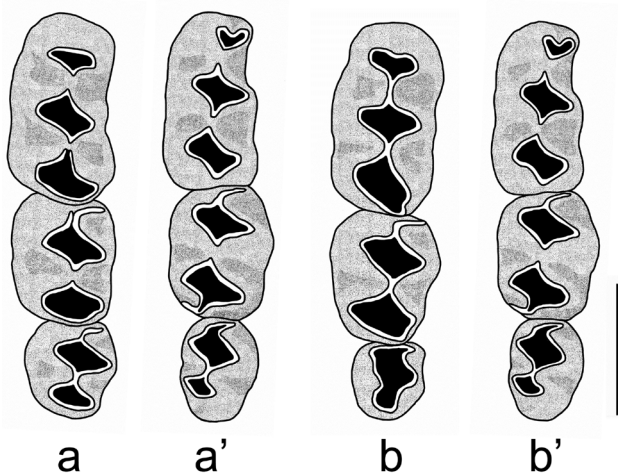

Figure 115: Grinding pattern of upper (a, b) and lower (a', b') molars in desert hamster *Phodopus roborovskii*. Lingual is to the left; scale bar = 1 mm. Voucher (a) originates from 59 km east of Manlai sum, Mongolia, and voucher (b) is from captive stock.

GENUS: *Cricetiscus* Thomas, 1917 – Hairy-footed Hamsters

Cricetiscus Thomas, 1917: 456. Type species is *Cricetulus campbelli* Thomas.

Cricetsicus: Formozov, 1929: 52. Incorrect subsequent spelling of *Cricetiscus* Thomas.

Prodopus: Vorontsov, 1958: 334. Incorrect subsequent spelling of *Phodopus* in combination with *sungorus*.

Etymology. *Cricetus* with diminutive suffix (-iscus) denotes a small (tiny) hamster, which is in allusion to a small size of hairy-footed hamsters.

Taxonomy. *Cricetiscus* was described as a genus in its own right (Thomas 1917), but was only rarely ranked this way (Howell 1929, Allen 1940); the name was usually synonymized with *Phodopus* (Formozov 1929, Tokuda 1941, and subsequent authors); see taxonomic account on Phodopina.

The prevailing view over the 20th century recognized a single hairy-footed hamster (*i. e. sungorus*) and *campbelli* was classified as its subspecies (Kuznetsov 1932, 1965, Argyropulo 1933a, b, Chaworth-Musters 1934, Allen 1940, Ellerman 1941, Tokuda 1941, Kuznetzov 1944, Ellerman & Morrison-Scott 1951, Bannikov 1954, Chugunov 1962, Kuzyakin 1963, Veselovsky et al. 1965, Shubin & Alimbaev 1977, Corbet 1978, Corbet & Hill 1980, 1986, Sokolov & Orlov 1980, Gromov & Baranova 1981, Honacki et al. 1982, Gromov & Erbajeva 1995, Zhang et al. 1997, Luo et al. 2000, Wang 2003); this view was strengthened by chromosomal similarities between *sungorus* and *campbelli* (Gamperl et al. 1977). During the late 1970s, the crossbreeding trials initiated by Yudin et al. (1979) demonstrated male sterility in interspecific hybrids. Sterility of F1 and backcross males was largely the consequence of various anomalies due to meiosis disorder, *e. g.* abnormal synaptonemal complexes, instable bivalents, abnormal pairing of sex chromosomes, and multiple abnormalities during spermatogenesis (Safronova et al. 1992, Sokolov & Vasil'eva 1994, Cherepanova et al. 1998, Levenkova 2003, Ishishita et al. 2015). These aberrations arrested spermatogenesis at the stage of spermatocytes (Bikchurina 2023). Hybrids also showed aberrations in the morphology of seminiferous tubules and underdeveloped caudal parts of epididymis (Bikchurina et al. 2018). Although hybrid females are fertile (Feoktisova et al. 2019), they suffer high mortality rate during pregnancy; besides, their fertility is lower, and the F1 offspring shows developmental anomalies (Cherepanova et al. 1998).

These results necessitated a 2-species solution for *Cricetiscus* (Pavlinov & Rossolimo 1987, Musser & Carleton 1993, Pavlinov et al. 1995), which received further support from molecular analyses (Meshchersky

& Feoktistova 2009, Lebedev et al. 2018a). The 2 species of hairy-footed hamsters diverged at an estimated 0.8±0.1–1.0±0.1 Mya (Neumann et al. 2006).

Morphologically, *sungorus* and *campbelli* differ in fur colouration (Figures 111 & 116), thought the overlap prevents safe classification of all individuals to one or the other species; for *sungorus* cf. Figures 116a & 119b; for *campbelli* cf. Figures 116b & 121a. Putative differences in skull proportions between *sungorus* and *campbelli* (cf. Ross (1992) were not confirmed in recent geometric morphometric study based on 2-dimensional cranial landmarks (Alhajeri 2021). Interspecific differences, however, were reported in physiology, activity patterns, and behaviour. In contrast to *C. sungorus, C. campbelli* starts nocturnal activity earlier and remains active for longer (Wynne-Edwards et al. 1999). It is not so well adapted to cold temperatures (Weiner & Heldmeir 1987) and shows biparental behaviour, while *sungorus* is alloparental (Wynne-Edwards 1995). Additionally, maternal reserves are used differently during reproduction (Wynne-Edwards & Lisk 1987).

Distribution. Steppes of southern Siberia and northern Kazakhstan (eastward of the upper reaches of the Ural and Tobol rivers) and south-eastern Russia as far east as the upper reaches of the River Amur; Mongolia and Nei Mongol (China) south to the Huang He River and the Ordos Loop. *Cricetiscus sungorus* and *C. campbelli* have allopatric ranges with no overlap. In the Early Pleistocene, *Cricetiscus* expanded its range westward and reached Europe (Maul 1990).

Characteristics. Small hamsters with vestigial tail (Figure 111a, b) and short but broad feet; soles and palms are densely haired; the only 3 small interdigital plantar pads are entirely concealed by hair (Figure 109b, c, c'). Ears are fairly short and the eyes are quite large. Tail is hardly projecting from the fur (Figures 113 & 121b) and accounts for 9–15% (mean ≈ 13%) of length of head and body. Pelage is dense and soft. Back is light-to-dark grey with various admixtures of buffy tints. Underside is frequently shaded by grey hair bases and although hairs may be white throughout, the underside is not as purely white as in *Phodopus*; the exception is white winter pelage of *P. sungorus* (Figure 111a2 & 119a). The lateral line is undulating and white fur of the lower side extends up on the flanks forming convex areas on

the cheeks, neck, behind the rib-cage and on a hip (Figure 116). The light lateral patches are separated by narrow strip-like ventral expansions of dark dorsal colouration; the most prominent expansions are behind the shoulders and in front of hips. Tail is densely covered by white hairs that form short terminal pencil; dorsal side is frequently shaded buff. Hairs above the tail base are of same colour as the rest of the back (Figure 113b). Black mid-dorsal line extends from head to rump.
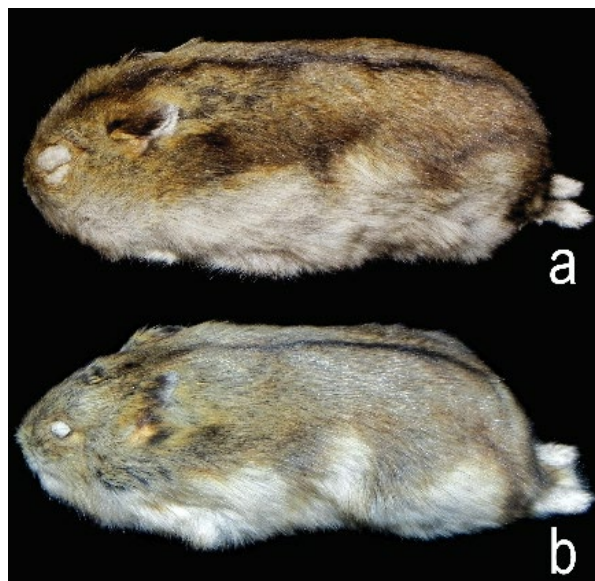

Figure 116: Museum skins of *Cricetiscus sungorus* (a) and *C. campbelli* (b) in semilateral view. *C. sungorus* is characterized by bolder blackish-brown shoulder stripe and wider mid-dorsal stripe on the crown. Note sinuous lateral line and associated upward extensions of the white underside on the cheeks, neck, behind the rib-cage and on hip. Vouchers: a – Krasnoyarsk Region, b – Tuva (Tyva) (both in Russian Federation).

The skull is small and delicate (Figure 114); zygomatic arches are less expanded than in *Phodopus* and zygomatic width accounts for 53.8–61.7% of condylobasal length (mean = 57.5%). The nasals are long and reach behind the level of lacrimals. The anterior edge of the superior maxillary root of zygoma forms a smooth curve at its junction with the rostrum. Zygomatic plate is wider than in *Phodopus*; infraorbital foramen is of myomorphous type, being expanded dorsally and narrowed in its ventral half (Figure 20c). Zygomatic keel and notch are largelly absent. Interorbital region is narrower than in *Phodopus*; supraorbital ridges are absent. Braincase is broad but more of diamond shape than circular. Parietals are les expanded than in *Phodopus*. The profile is bowed but the skull is shallower
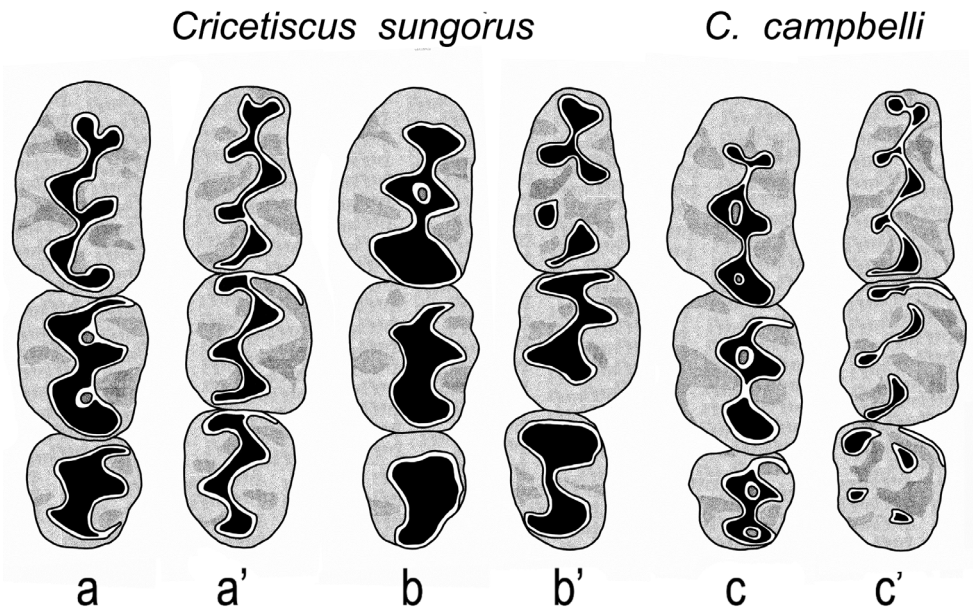
Cricetiscus sungorus   *C. campbelli*

Figure 117: Grinding pattern of upper (a–c) and lower (a'–c') molars in hairy-footed hamsters: a, b – *Cricetiscus sungorus* from Minusinskiy Rayon (a) and Barabinskiy Rayon (b; Russian Federation); c – *C. campbelli* from Chono Karaikhyn gol, Mongolia. Lingual is to the left; scale bar = 1 mm.

than in *Phodopus*. Incisive foramens are narrower but longer than in *Phodopus*, and clearly exceed the length of maxillary tooth-row; posteriorly, they hardly reach the level of M^1. The hard palate, pterygoid fossa and basioccipital bone are narrower than in *Phodopus*. Bullae are flattened, with a characteristic tube-shaped anterior portion; they are comparatively larger than in *Phodopus*. Mandible is the same as in *Phodopus*, though the coronoid process tends to be longer. Upper incisors are orthodont. The occlusal surface of molar cusps resembles condition in *Urocricetus*; the major cusps alternate and there are closed internal fields on the upper molars. The M^3 is of normal size, accounting for *c.* ¼ of the upper tooth-row (Figure 117).

Karyotype: 2n = 28, NF = 51 (males) or 52 (females), NF$_a$ = 48; 11 autosomal pairs are biarmed and 2 pairs are acrocentric; the X chromosome is large metacentric and the Y chromosome is small acrocentric. Conventionally stained karyotypes of *C. campbelli* and *C. sungorus* are identical (Gamperl et al. 1977, Schmidt et al. 1986, Romanenko et al. 2007); interspecific differences become apparent in C-banded chromosomes (Safronova et al. 1992).

Key to species

1a) Dorsal fur is duller (Figures 111a1, 116a); mid-dorsal stripe is bolder and longer (anteriorly reaching the level of eyes), with fuzzy edges; the stripe is widened on the front; a transverse stripe behind shoulders is frequently present; a bold blackish blotch is present on shoulders[1]; winter fur is white (Figures 111a2, 119a); allopatric with respect to *campbelli*, present in Kazakhstan and southern Asiatic Russia (administrative regions of Orenburg, Chelyabinsk, Kurgan, Tyumen, Omsk, Novosibirsk, Altayskiy Kray, Krasnoyarsk and Khakasia; Figure 118) ………………..…… *sungorus*

1b) Dorsal fur paler (Figures 111b, 116b); mid-dorsal stripe narrower and shorter (anteriorly not reaching the level of eyes), with sharp edges; the stripe is usually not widened on the front; transverse stripe behind shoulders usually absent; blotch on shoulders weakly expressed or absent[1]; winter and summer fur are of similar colour; allopatric with respect to *sungorus*, present in Mongolia, China, and southern Asiatic Russia (administrative regions Altai Republic, Tuva, Buryatya and Chita; Figure 120) …………………………………....… *campbelli*

[1] Colour traits vary and the typical condition for one species may be seen as an extreme in the opposite species; for extreme colouration of *sungorus* cf. Figure 119b; for *campbelli* cf. Figure 121a.

Cricetiscus sungorus Pallas, 1773 – Siberian Hairy-footed Hamster

Mus sungorus Pallas, 1773: 703. Type locality: "in campis elatis, aridis, auſtralioribus Irtin [in the elevated dry plains of River Irtysh]". Pallas obtained first specimens at "Gratschefskoi [Gratſcheffkoi; Pallas 1773: 493] (Gratschewsk) on the Irtish [Irtysh] River about 100 kilometres west of Semipalatinsk, S.W. [south-western] Siberia" Chaworth-Musters (1934: 590); in current spelling: Grachevskiy [Грачевский], 100 km west of Semipalatinsk (Semey [Семей]), Abai Region, eastern Kazakhstan (cf. Pavlinov & Rossolimo 1987: 171).

Mus songarus Pallas, 1779: 269. Type locality: "ad Irtin in auſtralibus Barabenſium camporum [Irtysh, especially southward to the Baraba plains]". It is unclear why Pallas was not consistent in spelling the name. As shown by Thomas (1917: 452) and Chaworth-Musters (1934: 590), the 1773 name was not a misprint, hence *songarus* is not an emendation of *sungorus* (as suggested in Pavlinov & Rossolimo 1987: 171); besides, *sungorus* is used also in entomology (as *sungora*; Chaworth-Musters *l. c.*).

M[us] Cricetus songarus: J. F. Gmelin, 1792: 244. Name combination.

Cric[etus] songarus: Brandt, 1859: 211. Name combination.

Phodopus sungorus: Hollister, 1912: 3. Name combination.

Cricetiscus sungorus: Thomas, 1917: 457. First use of the current species name combination.

Cricetulus zongarus: Pidoplitshka, 1928: 416. Incorrect subsequent spelling of *sungorus* Pallas, and name combination.

Phodopus songarus: Argyropulo, 1931: 60. Name combination.

Phodopus subgorus: Sokolov & Orlov, 1980: 118. Incorrect subsequent spelling of *sungorus* Pallas.

Etymology. The species epithet is derived from 'Dzungaria' (also Sungaria or Junggar), which comes from Mongolian 'Zűn Gar' or 'Jüün Gar', meaning 'left hand'. *Cricetiscus sungorus* is absent from Dzungaria as is currently defined (in northern Xinjiang, China), however, its range partly overlapped the historical Dzungar Khaganate of the Oirat Mongols, which included the upper Irtysh River in the present-day Russian Federation.

Taxonomy. In the past, *C. sungorus* frequently comprised *campbelli* as a junior synonym or a subspecies (see taxonomic account on *Cricetiscus*). Trouessart (1904: 395) synonymized *kozlovi* Satunin (now in *Nothocricetulus*) with *C. sungorus*.

Distribution. The range extends over southern Siberia encompassing northern Kazakhstan and adjacent Russia between the upper reaches of the rivers Ural in the west and Yenisei in the east (Figure 118). The range covers surface area of an estimated 677,955 km². Distribution is largely contiguous between the Ural and Ob rivers in Kazakhstan (provinces of northern Qostanay, the entire North Kazakhstan, eastern Aqmola, northern Qaraghandy, Pavlodar, eastern East Kazakhstan; Afanasiev 1960, Shubin & Alimbaev 1977) and southern Russia (provinces of Orenburg, Cheljabinsk, Kurgan, Tyumen, Omsk, Novosibirsk, Altayskiy Kray; Malykova et al. 2005, Snit'ko 2017, Ryabitseva 2020, Modorov & Polyakov 2021). The range is increasingly fragmented further south in Central Kazakhstan (southern Qostanay, southern Aqmola, central Qaraghandy, and southern East Kazakhstan). There is an eastern isolate in Minussinsk Depression (in the Krasnoyarsk and Khakasia provinces); hamsters were recorded on both banks of the Yenisei River (Yudin et al. 1979). The Siberian hairy-footed hamster is also known from a single locality in Kemerovo. The species putatively expanded its range prior to 1940 (Afanasiev 1953).

Inhabitant of zones of forest steppe, steppe and semidesert. Preferred habitat is ungrazed, short-grass steppe on black and brown soils; present also on fixed sands and saline substrate. Also occupies arable land under grain crops and perennial grasses and occasionally also forest clearings (Beljaev 1933, Afanasiev 1953, 1960, Flint 1966b). Not recorded in buildings (Ryabitseva 2020). *Cricetiscus sungorus* is a flatland dweller, found at elevations of 64–898 m (mean = 257 m). Higher elevations reported in older literature, *e.g.* up to 3,000 m in Chuyskaya Steppe, Atlai Republic, Russia (Yudin et al. 1979), relate to *campbelli*.

Characteristics are the same as for the genus. Dimensions: body mass = 19–45 g, length of head and body = 78–102 mm, length of tail = 5–15 mm, length of hind foot = 12–15 mm, length of ear = 11–16 mm,
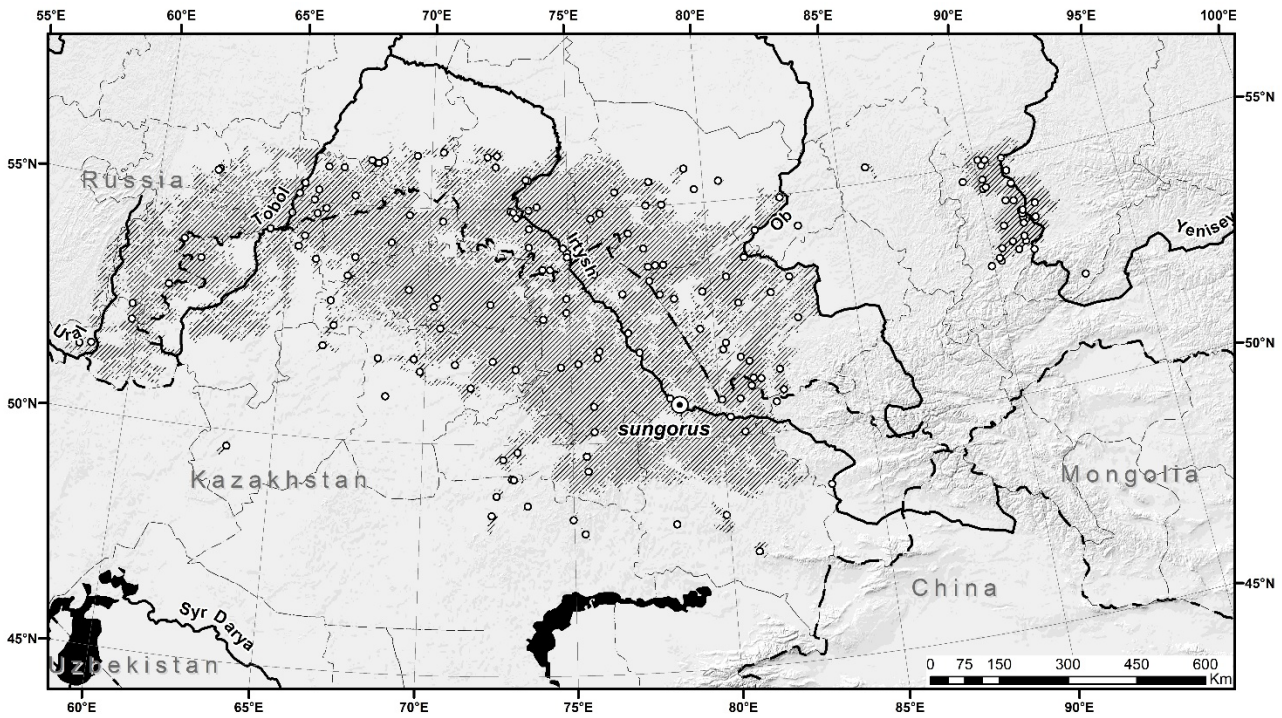
Figure 118: Distributional range of the Siberian hairy-footed hamster *Cricetiscus sungorus*.

condylobasal length of skull = 20.5–25.4 mm, zygomatic width = 12.0–16.1 mm, length of maxillary tooth-row = 3.3–4.1 mm (Shubin & Alimbaev 1977); there is no secondary sex dimorphism. Pelage shows seasonal polyphenism with white winter colouration (Figures 111 & 119). Dorsally, the summer fur is dull ash grey to dark brown (Figures 111a1, 116a); rarely, the back is pale brownish-grey (Figure 119b). The blackish-brown mid-dorsal stripe is normally bold but with fuzzy edges, and extends from the eye level on the front back to tail base. The stripe is usually widened on the front and shoulders (Figures 111a1, 116a). A blackish lateral streak is typically bold and may extend from post-auricular region back to the tights (Figure 116a); its lower edge is irregular. Besides, many individuals show an additional transverse stripe across the shoulders which, however, is less prominent (Figures 111a1). In extreme cases, these black markings may be much less bold and resemble the situation in *C. campbelli* (Figure 119b). White or yellowish postauricular patches are usually present (typically absent in *C. campbelli*). Hairs are white to the base on parts of or the entire underside. Ears are grey to blackish; the paws are greyish-white and the tail is whitish with yellowish shade. Moult into white winter fur proceeds in November–December from the rump and progresses onto the back, the postauricular region, the face and the flanks (the winter moult). The mid-dorsal and the transverse stripes persist throughout winter, albeit in a reduced extent (Figure 111a2);

shoulders in particular may remain grey (Figure 119a). Ventral hairs of winter fur are white to bases. Moult into summer fur occurs in February–March (Shubin & Alimbaev 1977) in a reverse section (Figala et al. 1973). In addition to pigmentation, the winter moult affects the overall length of the hairs (the winter hairs are longer), but not the hair density (Kuhlmann et al. 2003).

Glans penis is egg-shaped with a truncate tip. There are no dorsal or ventral papillae; lingual papilla has forked tip. Baculum has moderately expanded lancelike base; the width of base accounts for ~ 44% of length of proximal stalk. Distal trident is moderately long and cartilaginous; its length approximates ~ 35% of length of proximal baculum (Figure 17a) (Vorontsov 1982). The skull and dentition are the same as in the genus (see above; Figures 114 and 117a, b). Karyotype is as for the genus (Vorontzov 1958, Soldatović et al. 1971, Gamperl et al. 1977, Romanenko et al. 2007).

Variation and subspecies. Kuznetsov (1932) distinguished 2 geographical races in Kazakhstan. He characterized the nominotypical race by light greyish-drab back, white belly, longer spinal stripe (extending from occipital region to sacrum), and pure white paws. This race occupies steppes of western Siberia and north-eastern Kazakhstan. An unnamed race from Central Siberia (regions of Minusinsk, Irkutsk, and Yeniseysk) was characterized by domination of brown

tints, specifically by grey-brown back darkened by black hair tips, a shorter spinal stripe (starting on the front), ventral hairs with grey bases, and brown hairs on the proximal part of hind paws. Because no subspecies were validly proposed, *C. sungorus* is technically still regarded as monotypic species (Ross 1992, Shenbrot 2017c).
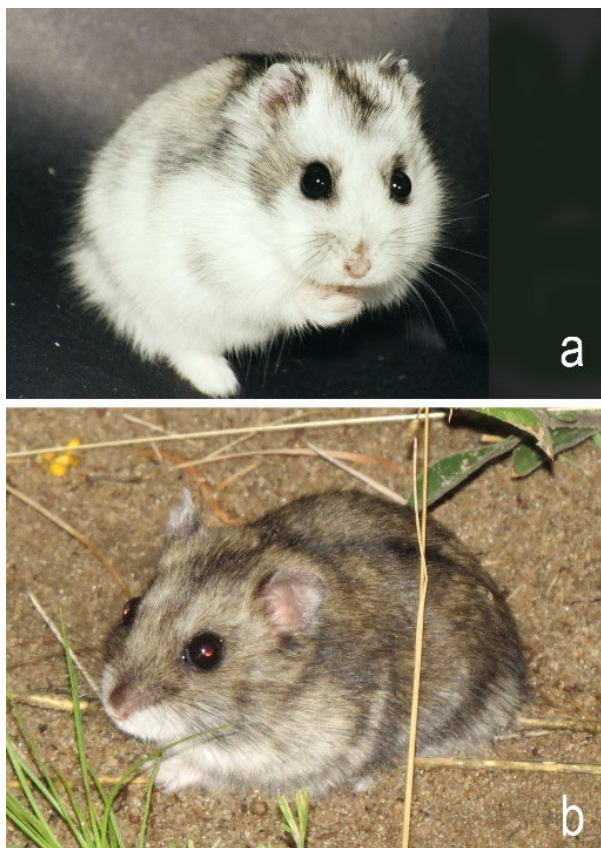

Figure 119: Siberian hairy-footed hamster *Cricetiscus sungorus* in summer fur (b; Altaysky Kray, Russia) and in white winter pelage (a; Khakasia, Russia). Note that specimen (a) still has ample dark summer hairs on head and back; individual (b) represents a light-coloured form with ill-defined dorsal stripe and blotches on shoulders. Photo M. Kabanov (a) and Georgy Shenbrot (b)

Cricetiscus campbelli (Thomas, 1905) – Mongolian Hairy-footed Hamster

Cricetulus Campbelli Thomas, 1905: 322. Type locality "Shaborte, N.E Mongolia (about 42°40' N., 114° E.)" was subsequently amended to "42°40' N., 116°20' E." (Thomas 1908e: 107 footnote). As one can deduct from Campbell's (1903) expeditionary report, the type locality is most probably identical to the current Zhenglanqi, Xilin Gol, Inner Mongolia, China (coordinates 42.6981 north latitude, 116.3576 east longitude) (Shenbrot 2017b: 281). 'Shaborte'

(also Shabarte'), which is a common name for temporary lakes, is frequently incorrectly reported for eastern Mongolia instead for Nei Mongol in China: "approximately 500 km east of Urga (Ulan-Bator-Hoto [Ulaanbaatar]), Mongolia" (Argyropulo 1933c: 136, Bannikov 1954: 453), "42°40' north latitude, 110° east longitude" (Allen 1940: 773), and northern (Ellerman & Morrison-Scott 1951: 627) or north-eastern Mongolia (Ellerman 1941: 437, Musser & Carleton 2005: 1045).

Phodopus crepidatus Hollister, 1912: 3. "Chuisaya [correct spelling is Chuyskaya] Steppe (eight miles [13 km] south of Kosh-Agatch), Altai District, Siberia; altitude 7300 feet [2,225 m]", *i. e.* 13 km south of Kosh-Agach, Kosh-Agachkiy District, Altai Republic, Russian Federation.

P[hodopus] campbelli: Hollister, 1912: 3. Name combination.

Cricetiscus campbelli: Thomas, 1917: 456. First use of the current species name combination.

Cricetiscus crepidatus: G. Allen, 1925: 7. Name combination.

Phodopus (Cricetsicus) [sic] *sungorus campbelli:* Formozov, 1929: 52. Name combination.

P[hodopus] campbell: Mori, 1930: 418. Incorrect subsequent spelling of *campbelli* Thomas.

Phodopus sungorus crepidatus: Chaworth-Musters, 1934: 591. Name combination.

Cricetiscus sungorus campbelli: Allen, 1940: 773. Name combination.

Phodopus cricedatus: Shubin & Alimbaev, 1977: 457. Incorrect subsequent spelling of *crepidatus* Hollister.

Etymology. Species epithet is eponym to Charles William Campbell (1861–1927), the British Consul in China, who organized the 1902 travel to Mongolia (incl. Inner Mongolia; *cf.* Campbell 1903), during which the type and the paratype specimens of *campbelli* were collected.

Taxonomy. Musser & Carleton (1993: 539, 2005: 1045) listed in the synonymy of *campbelli* also "*tuvinicus* Orlov and Iskharova (sic), 1974", referring to "Pavlinov and Rossolimo 1987: 171". Transliteration of the entire paragraph dealing with *tuvinicus* in Pavlinov & Rossolimo (*l. c.*) reads as follows: "?1981. *Phodopus sungorus tuvinicus* 'Orlov et Iskhakova, 1974' anonym[ous], in the book: Catalogue of mammals of

USSR: 158. Tyva ASSR [Autonomous Soviet Socialist Republic] (by tautonomy). Nom[en] nudum (no description, no authorship)." The book from 1981 is obviously the Catalogue by Gromov & Baranova (1981) who on p. 158 indeed listed among synonyms of *C. sungorus* also "*tuvinicus* Orlov et Iskharova (sic), 1974 (Tuva, nomen nudum?)." To best of our knowledge, Orlov & Iskhakova published no joint paper in 1974, but have such a publication in 1975 dealing with the taxonomy of *Cricetulus barabensis*. Noteworthy, Gromov & Baranova (1981: 157) listed another "*tuvinicus* Orlov et Iskharova (sic), 1974", this time as a synonym of *Cricetulus barabensis*. The entire issue with *tuvinicus* is therefore pretty messy and in our firm belief this name was never validly proposed for *Cricetiscus*. The name "*Phodopus sungorus tuvinicus* Orlov & Iskhakova, 1974" as it appeared in Gromov & Baranova (1981) and Pavlinov and Rossolimo (1987) was never properly published and is therefore unavailable name.

In the past, *campbelli* was nearly universally treated as a junior synonym of *C. sungorus* or its subspecies (see taxonomic account on *Cricetiscus*).

Distribution. The range extends across an estimated 969,658 km² in eastern Nei Mongol and Mongolia, from where it marginally also encompasses adjacent parts of Russia (Figure 120). The northern border is tentatively set by the upper reaches of the Irtysh, Ob, Yenisei, Amur and Baikal Lake, and the southern border is on the great loop of the Huang He River. The species is widespread in Mongolia; the only exception is northern Ksövgöl where *C. campbelli* does not occur; in addition, records are scarce to the south of the 45th parallel. In the north-west, the range expands from Bayan-Ölgii and Uvs (Mongolia) into southern Altai Republic and southern Tyva (Russian Federation). Further northward, expansions from Mongolia into Russia are into southern Buryatia and north-eastern Chita. In China, the bulk of range is in eastern and central Nei Mongol with slight extensions into north-western Hebei and Ningxia, with the most exposed southern record for the species.

The Mongolian hairy-footed hamster inhabits high-elevation steppe with *Artemisia* and *Festuca*, stabilized sand dunes dominated by *Caragana* shrubs, river valleys, sandy or saline banks of lakes, and cultivated land (Bannikov 1954, Chugunov 1962, Flint 1966b). Elevational range is 145–3,390 m (mean = 1,322 m).

Characteristics. Size and proportions are as in *C. sungorus*. Dimensions: body mass = 13–43 g, length of head and body = 85–103 mm, length of tail = 5–16 mm, length of hind foot = 10–15 mm, length of ear = 8–17 mm, condylobasal length of skull = 20.8–25.5 mm,
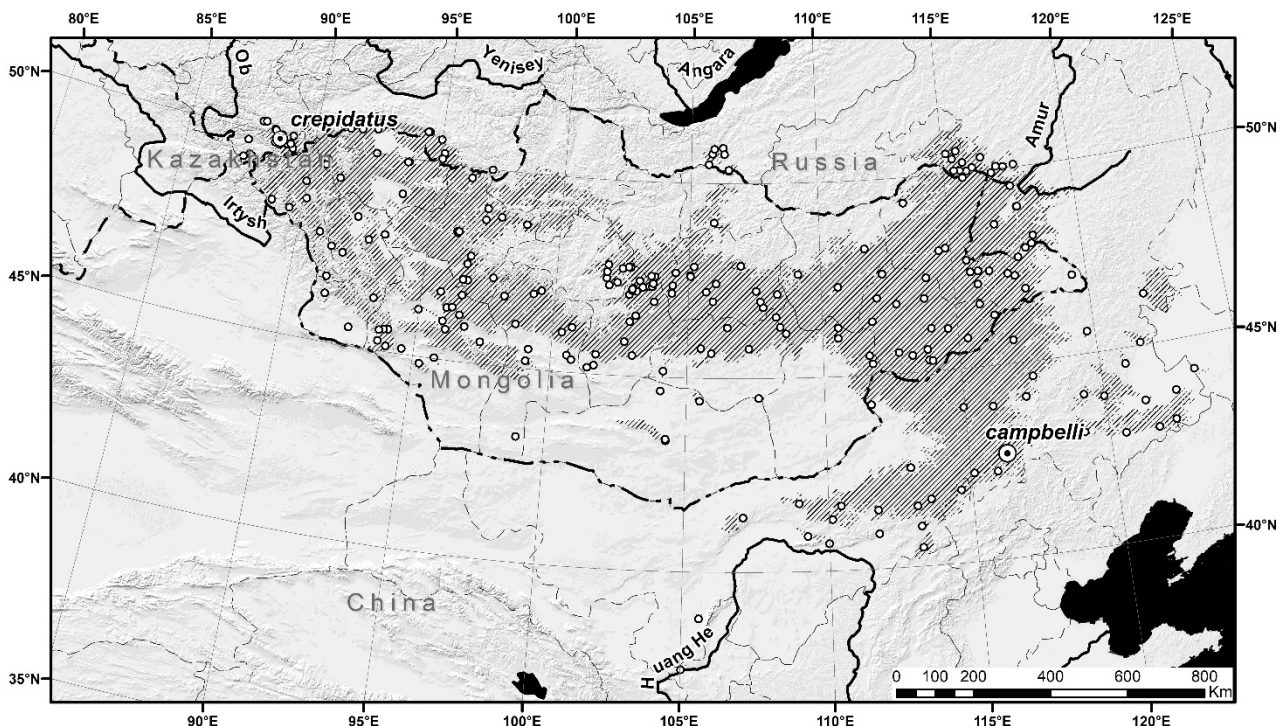

Figure 120: Distributional range of the Mongolian hairy-footed hamster *Cricetiscus campbelli*.

zygomatic width = 11.7–15.1 mm, length of maxillary tooth-row = 3.3–4.3 mm. Colouration is on average paler than in *sungorus*. Dorsal pelage is grey-buff tipped with black; the face, the area around the ears, the shoulders, and the flanks may have more buffy tint; the lips and cheeks are cream-white. The blackish mid-dorsal stripe is on average narrower than in *C. sungorus*; variation is, however, considerable and the stripe varies from a faded line in light-coloured individuals (Figure 121b) to a bold one in those with brighter colouration (Figure 121a). As a rule, the stripe is not bold on the front and terminates before the tail base; it is the boldest between the shoulders and the rump. The lateral streak is typically absent (Figure 121b) and only rarely prominent (Figure 121a); the majority of hamsters show a yellow or buffy dividing line between the dorsal and the ventral pelage (Figure 116b). The transverse stripe across the shoulders is absent. Hairs on the underside have slate bases and white to creamy-buff tips; the paws and the tail are silvery-white or cream-buff, and the ears are grey. Winter pelage does not differ essentially from the summer one.

The skull and dentition are as in the genus (see above; Figures 114 & 117c). The same also holds for the karyotype (Safronova et al. 1992, Romanenko et al. 2007, Ishishita et al. 2015).

Variation and subspecies. Phylogeographic analysis based on partial *mt*DNA sequences retrieved three lineages (the East, the West, and the Kosh-Agach lineages). The major division is between the West and the East lineages in the Khangai mountain range (at approximately 100–102nd eastern meridian) and dates back to around 0.45–0.55 Mya. There is an outlier of the West lineage in Dauria (south-eastern Transbaikalia, Russia), deeply inside the range of the East lineage. The Kosh-Agach lineage is nested inside the West lineage and diverged approximately 0.34–0.42 Mya (Meshchersky & Feoktisova 2009). The major phylogenetic lineages are classified as distinct subspecies, the nominotypical subspecies (lineage East) and *crepidatus* (lineage West with the inclusion of lineage Kosh-Agach) (Shenbrot 2017b). Due to the low sampling density, in addition to the presence of an obvious outlier, the proposed classification has to be taken with caution. On the other hand, the two subspecies were recognized already on morphological

ground (Allen 1925, Chaworth-Musters 1934, Ross 1992) and Ross (*l. c.*) strongly argued that *crepidatus* is sufficiently distinct to merit subspecific status at least.
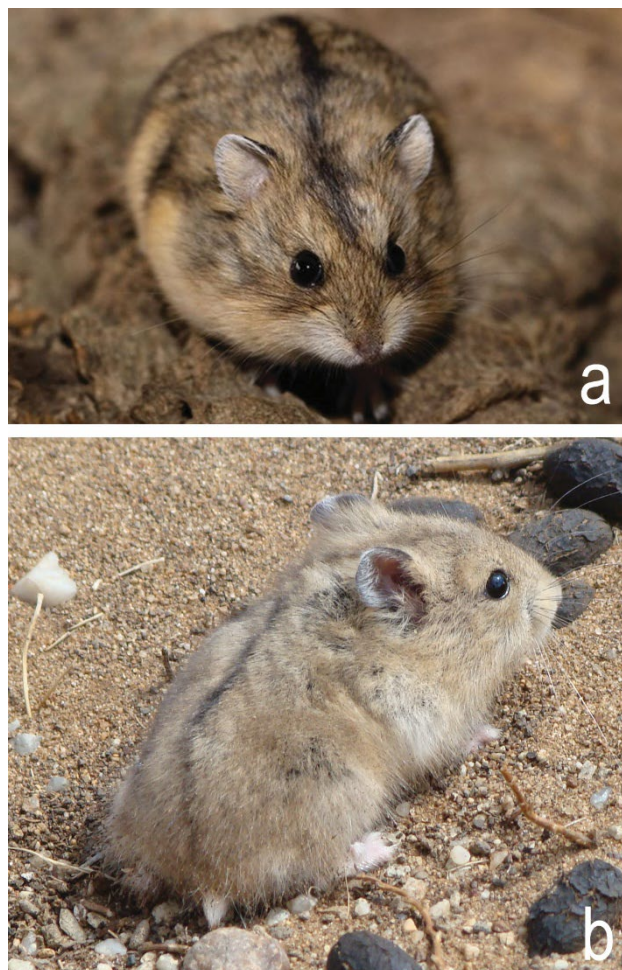

Figure 121: Mongolian hairy-footed hamster *Cricetiscus campbelli* from Mongolia. Note differences in fur colouration. Photo courtesy by Konstantin A. Rogovin (a) and Nedko Nedyalkov (b)

Cricetiscus campbelli campbelli (Thomas, 1905)

Distribution. Central and eastern Mongolia and China (Inner Mongolia, western Ningxia and northern Hebei) (Shenbrot 2017b).

Characteristics. Dorsal pelage is greyish-buff, the mid-dorsal stripe runs from between the ears to the tail base; the tail, tips of the ears, and forearms are washed beige. The skull is on average shorter and wider; auditory bullae are more flattened and the eustachian tube is more elongated. The transverse ridge formed by the anterocone of M^1 is narrower than the width across the paracone–protocone; in a worn stage, the anterior

medial fold separating the lingual and the buccal anterocones persists for longer than in *crepidatus* (Ross 1992).

Cricetiscus campbelli crepidatus (Hollister, 1912)

Etymology. The Latin word 'crepidatus' originates from 'crepida' (sandal) and means 'wearing sandals', in allusion to heavily hairy soles in *Cricetiscus*.

Distribution. South-eastern Siberia in Russian (Altai Mts., Tyva, Buryatia, Chita) and north-western Mongolia (Shenbrot 2017b); there is an isolate of the West lineage in Dauria (south-eastern Transbaikalia, Russia), on the eastern edge of the presumed range of the nominotypical subspecies.

Characteristics. Dorsal pelage is wood-brown, the mid-dorsal stripe runs from the shoulder to approximately 2–3 cm above the tail base; the tail, tips of the ears, and forearms are white with no beige tint. The skull is on average longer and narrower; auditory bullae are more swollen and the eustachian tube is more rounded. In a worn stage of M^1, the ridge formed by the anterocones lacks the anterior medial fold, separating the lingual and the buccal cones (Ross 1992).

References

Transliteration

The papers quoted below have been published in various languages and scripts found across the Palaearctic Region. Many important works are in Slavic languages (in particular Russian), Chinese, Korean, and Japanese, to mention just the main linguistic groups. Whenever these papers have a title written in English or another language widely used in the past by the zoological community (Latin, German, French and so on), we quoted it. The remaining titles were translated and are in square brackets.

The names of the authors were not always consistently transliterated into the Latin script. We have retained transliterations as they were originally used in the quoted papers. For this reason, the spelling of the same name may vary in the list of references (e.g. Kozlovsky or Kozlovskij; Meier or Meyer; Ognev or Ogneff, etc.). To assist the reader, we inserted the most widely used spelling in square brackets after the quoted name.

Abbreviations

AN USSR   Academy of Sciences, Union of the Soviet Socialist Republics (in use before 1991); national academies used the name of a Republic followed by the SSR (the Soviet Socialist Republic; e.g. Belorussian SSR or BSSR) or ASSR (Autonomous Soviet Socialist Republic)

ICZN   International Commission on Zoological Nomenclature

RAS   Russian Academy of Sciences (in use after 1991)

Afanasiev A.V. (1953). [Subfamily Hamsters - Cricetinae]. In: Afanasiev A.V., Bazhanov V.S., Korelov M.N., Sludskiy A.A. & Strauman E.I. [*Mammals of Kazakhstan*]. AN KazSSR, Alma-Ata [Almaty], pp. 228–238 [in Russian].

Afanasiev A.V. (1960). [*Zoogeography of Kazakhstan.*] AN KazSSR, Alma-Ata, 259 pp. [in Russian].

Agadjianian A.K. & Orlov V.N. (Eds.) (2000). *Systematics and phylogeny of the rodents and lagomorphs.* A.N. Severtsov Institute of Ecology and Evolution and Paleontological Institute RAS, Moscow [In Russian with Eng. front page].

Agrawal V.C. (2000). Taxonomic status on Indian Muridae and Hystricidae (Mammalia: Rodentia). Zool. Surv. India 180: viii + 1–186.

Aharoni B. (1932). Die Muriden von Palästina und Syrien. Z. Säugetierkunde 7 (5): 166–240.

Aidek A. & Zuhair S.A. (2021). A new locality record for the Syrian hamster, *Mesocricetus auratus*. Mammalia 85 (6): 601–602.

Aidek A.E., Ibrahim A., Amr Z., Hutterer R., Kryštufek B., Serra G., Benda P., Shkaky Y., Barbanera F. & Al-Sheikhly O.F. (2025). Checklist of the mammals of Syria (Chordata: Mammalia). Zootaxa (accepted).

Ainsworth W. (1838). *Researches in Assyria, Babylonia, and Chaldæa; Forming part of the labours of the Euphrates Expedition.* John W. Parker, London.

Alekperov Kh.M. (1966). [*Mammals of south-western Azerbaijan.*] AN AzSSR, Baku [in Russian].

Alhajeri B.H. (2021). A morphometric comparison of the cranial shapes of Asian dwarf hamsters (*Phodopus*, Cricetinae, Rodentia). Zool. Anz. 292: 184–196.

Allen G.M. (1925). Hamsters collected by the American Museum Asiatic expeditions. Am. Mus. Nov. 179: 1–7.

Allen G.M. (1928). A new cricetine genus from China. J. Mammal. 9 (3): 244–246.

Allen G.M. (1940). *The mammals of China and Mongolia. Natural History of Central Asia.* Am. Mus. Nat. Hist., NY, 11 (2): 621–1350.

Allen G.M. & Andrews R.C. (1913). Mammals collected in Korea. Bull. Am. Mus. Nat. Hist. 32: 427–436.

Alpaslan F.S., Ünay E. & Ay F. (2010). The Rodentia and Lagomorpha (Mammalia) from the Early Pliocene from İğdeli (Gemerek, Sivas): biochronological and paleogeographical implications. Fen Bilim Dergisi 31: 1–29 [in Turkish with Eng. abstract].

Al-Sheikhly O.F., Haba M.K., Barbanera F., Csorba G. & Harrison D.L. (2015). Checklist of the mammals of Iraq (Chordata: Mammalia). Bonn. zool. Bull. 64 (1): 33–58.

Alston E.R. (1873). Mammalia. Zool. Record for 1873, 10: 1–20.

Alston E.R. (1876). On the classification of the order Glires. Proc. Zool. Soc. Lond. 1876: 61–98.

Amr Z.S., Abu Baker M.A., Qumsiyeh M. & Eid E. (2018). Systematics, distribution and ecological analysis of rodents in Jordan. Zootaxa 4397 (1): 1–94.

Anděra M. & Gaisler J. (2019). [*Mammals of Czech Republic. List, distribution, ecology, conservation.*] Academia, Prague [in Czech].

Anderson J. (1891). *Catalogue of Mammalia. Indian Museum. Part II. Order Rodentia.* Trustees Indian Museum, Calcutta [Kolkata].

Anderson R.R. & Sinha K.N. (1972). Number of mammary glands and litter size in the golden hamster. J. Mammalogy 53 (2): 382–384.

Anonymous (1875). MM. H. and E. [typographical error for A.] Milne-Edwards's new work on mammals. Nature 11: 463–464.

Argyropulo A.J. (1931). [*A key to rodents of the Uralsk Oblast and adjacent regions.*] [State Agricultural Publisher, Moscow] [in Russian].

Argyropulo A.I. (1933a). Matériaux pour servir a la connaissance des Rongeurs de l'Asie Centrale. III. Une sousespèce nouvelle de l'Hamster (*Cricetus cricetus* L.) de la région de Sémiretchie. Trav. Inst. Zool. Acad. Sci. URSS (1932) 1: 235–237 [in Russian with French title].

Argyropulo A.J. (1933b). Die Gattungen und Arten der Hamster (Cricetinae) der Palaearktis. Trav. Inst. Zool. Acad. Sci. URSS (1932) 1: 239–248 [in Russian with German abstract].

Argyropulo A.I. (1933c). Die Gattungen und Arten der Hamster (Cricetinae Murray, 1866) der Paläarktik. Z. Säugetierkunde 3 (3): 129–148.

Argyropulo A.I. (1936). [Subfamily Cricetinae (Murray, 1866) – Hamsters.] In: Vinogradov B.S., Argyropulo A.I. & Heptner V.G. (Eds.): *Rodents of Central Asiatic part of USSR.* AN USSR, Moscow, pp. 116–122 [in Russian with Eng. title].

Argyropulo A.I. (1941a). [Subfamily Cricetinae – Hamsters.] In: Vinogradov B.S. & Argyropulo A.I.: *Faune de l'URSS. Mammifères. Tableaux analytique des rongeurs.* AN URSS, Moscow, pp. 165–173 (in Russian, title in French).

Argyropulo A.I. (1941b). Quaternary fauna of Binagady (Apsheron Peninsula): Rodents and insectivores. Priroda 3: 88–91 [in Russian; quoted from Vereshchagin 1959].

Aristov A.A. (1988). Homology, convergence and parallelism in muscular structure of cheek pouches in rodents. Zool. Zh. 67 (2): 200–204 [in Russian with Eng. abstract].

Arslan A. & Zima J. (2014). Karyotypes of the mammals of Turkey and neighbouring regions: a review. Folia Zool. 63 (1): 1–62.

Aşan N. (2012). Nucleolar organizer regions in *Mesocricetus brandti* (Nehring, 1898) (Mammalia: Rodentia) from the Yozgat and Tohat provinces of Turkey. Turk. J. Zool. 36: 255–257.

Atallah S.I. (1977). Mammals of the eastern Mediterranean region; their ecology, systematics and zoogeographical relationships. Säugetierkdl. Mitt. 25: 241–320.

Atanassov N. & Peschev Z. (1963). Die Säugetiere Bulgariens. Säugetierkdl. Mitt. 11 (3): 101–112.

Ausländer D. & Hellwing S. (1957). Observations ecologiques sur les petits Mammiferes des ecrans forestiers de protection, de "Valul Traian" references speciales concernant leur dynamique. Trav. Mus. Hist. Nat. Gr. Antipa 1: 111–139.

Averianov A. & Abramson N. (2003). *Systematics, phylogeny and paleontology of small mammals.* Zoological institute RAS, Sankt Petersburg.

Ayzin B.M. (1979). [*Rodents and lagomorphs of Kirgizia.*] Ilim, Frunze, 199 pp. [in Russian].

Bakhrushev A.V., Karsakov N.G. & Mal'kova N.G. (2005). [Grey hamster *Cricetulus migratorius* (Pallas, 1773).] In: Sidorov G.N. & Rusakov V.N. (Eds.): [*Red Book of Omsk Oblast.*] OmGPU Press, Omsk, pp. 227–228 [in Russian].

Bannikov A.G. (1954). [*Mammals of Mongolian People's Republic*]. AN USSR, Moscow [in Russian].

Baranova G.I. & Gromov I.M. (2003). [*Catalogue of type specimens in the Collection of Zoological Institute of RAN. Mammals (Mammalia) 4. Rodents (Rodentia)*]. RAS, Sankt-Petersburg [In Russian].

Barrett-Hamilton G.E.H. (1900). On a small collection of mammals obtained by Captain Deasy in South Chinese Turkestan and Western Tibet. Proc. Zool. Soc. Lond. 1900: 196–197.

Baryshnikov G.F. & Baranova G.I. (1983). [Rodents of the early Palaeolith of the Greater Caucasus.] Trav. Inst. Zool. Acad. Sci. URSS 119: 100–138 [in Russian].

Bate D.M.A. (1943). Pleistocene cricetins from Palestine. Ann. Mag. Nat. Hist. 11, 10, 72: 813–838.

Bauer K. (1960). Die Säugetiere des Neusiedlersee-Gebietes. Bonn. zool. Beitr. 11: 141–344.

Bazhenov Yu.A. (2022). Synanthropic rodent fauna of eastern Transbaikalia in the early 21st century. IOP Conf. Series: Earth and Environmental Science 962 (2022) 012008, doi:10.1088/1755-1315/962/1/012008

Bechstein J.M. (1801). *Gemeinnützige Naturgeschichte Deutschlands nach allen drei Reichen. Vol. 1.* Siegfried Lebrecht Erusius, Leipzig, Germany.

Becvar T., Vojtkova B., Pacakova L., Vomackova Kykalova B., Ticha L., Volf P. & Sadlovaet J. (2024). Steppe lemmings and Chinese hamsters as new potential animal models for the study of the leishmania subgenus *Mundinia* (Kinetoplastida: Trypanosomatidae). PLoS Negl Trop Dis. 2024 May 13;18(5):e0011897.

Beljaev A.M. (1933). Les rongeurs du Kazakstan (Mammalia, Rodentia).] Trav. Inst. Zool. AS USSR 2: 29–40. [in Russian with French title].

Berdyugin K.I. & Bolshakov V.N. (1998). The common hamster (*Cricetus cricetus* L.) in the eastern part of the area. Pp. 43–79 In: Stubbe & Stubbe (1998).

Bescós G.C. (2003). Análisis filogenético de *Allocricetus* del Pleistoceno (Cricetidae, Rodentia, Mammalia) *Allocricetus* (Cricetidae, Rodentia, Mammalia). Col. Paleont. 1: 95–113.

Bihun C. & Bauck L. (2005). Basic anatomy, physiology, husbandry, and clinical techniques. In: Quesenberry K.E. & Carpenter J.W. (Eds.): *Ferrets, rabbits, and rodents. Clinical medicine and surgery. 2nd ed.* Saunders, St. Louis, Missouri, pp. 286–298.

Bikchurina T.I. (2023). [Cytogenetic mechanisms of sterility in hybrids between certain species from hamster family (Cricetidae).] Unpublished Ph.D. Thesis, Federal Research Institute for cytology and genetics, Russian Acad. Sci., Siberian branch, Novosibirsk [in Russian].

Bikchurina T.I., Tishakova K.V., Kizilova E.A., Romanenko S.A., Serdyukova N.A., Torgasheva A.A. & Borodin P.M. (2018). Chromosome synapsis and recombination in male-sterile and female-fertile interspecies hybrids of the dwarf hamsters (*Phodopus*, Cricetidae). Genes (Basel) 9, 227; doi: 10.3390/genes9050227.

Bittera v. J. (1918). Einiges über die männlichen Copulationsorgane der Muriden und deren systematische Bedeutung. Zool. Jahrb., Abt. Syst. Georg. Biol. Tiere 41: 399–418 + Table 3–18.

Blanford W.T. (1875). List of Mammalia collected by late Dr. Stoliczka when attached to the embassy under Sir D. Forsyth in Kashmir, Ladák, Eastern Turkestan, and Wakhán, with description of a new species. J. Asiatic Soc. Bengal 14: 105–112.

Blasius J.H. (1857). *Fauna der Wirbelthiere Deutschlands und der angrenzenden Ländern von Mitteleuropa. Erster Band. Säugethiere.* Friedrich Vieweg und Sohn, Brunschweig.

Bobrov V.V., Varshavskiy A.A. & Hlyap L.A. (2008). [*Alien mammal species in ecosystems of Russia.*] KMK, Moscow [in Russian].

Bogdanov M.N. (1871). [Birds and mammals of the chernozem strip of the Volga catchment and the valley of the middle and lower Volga (biogeographical materials)]. Trudy Obshchestva Estestvoispytatelei pri Imperatorskom Kazanskom Universitete 1: 1–226 [in Russian].

Bonhote J.L. (1905a). [Mr. J. Lewis Bonhote, F.Z.S., communicated a paper on the mammals brought back by the Tibet Misson.] Abstr. Proc. Zool. Soc. Lond. Nov 14th 1905, p. 14.

Bonhote J.L. (1905b). On a collection of mammals brought home by the Tibet Frontier Commission. Proc. Zool. Soc. Lond. 1905(2): 302–308.

Bont de R. (2021). Hamster numbers: Biopolitics and animal agency in the Dutch fields, circa 1870–present. HPLS 43: 50, https://doi.org/10.1007/s40656-021-00398-3

Bontzorlos V. (2009). *La ecologia trofica de la lechuza comun en los ecosistemas agricolas de Grecia Central: Su aplicacion a la distribucion y abundancia de sus presas*. Unpublished Ph.D. Thesis, University of Salamanca, Salamanca, Spain, 30 January 2009.

Bontzorlos V., Vlachopoulos K. & Xenos A. (2023). Distribution of four vole species through the barn owl *Tyto alba* diet spectrum: Pattern responses to environmental gradients in intensive agroecosystems of Central Greece. Life 2023, 13, 105. https://doi.org/10.3390/life13010105

Borisov Yu.M. (2012). The polymorphism and distribution of B chromosomes in germline and somatic cells of *Tscherskia triton* de Winton (Rodentia, Cricetinae). Russ. J. Gen. 48 (5): 539–542.

Borisova N.G., Abramov A.V., Starkov A.I., Boronoeva G.I. & Dagdunova A.A. (2001). Mammal fauna of the Republic of Buryatia. Proc. Zool. Inst. St. Petersburg 288: 48–95 [in Russian with Eng. abstract].

Borissenko A.V., Kruskop S.V., Pavlinov I.Ya. & Spasskaya N.B. (2001). Class Mammalia. In: Pavlinov I.Ya. & Borissenko A.V. (Eds.) *Types of vertebrates in the Zoological Museum of Moscow University*. Moscow Univ. Publ., Moscow, pp. 163–228.

Brandler O.V. (1999). [New chromosomal form of the grey hamster *Cricetulus migratorius* Pallas, 1773 from the Tien Shan]. In: Abstracts of VI Congress of Theriological Society, Moscow, p. 37 [In Russian].

Brandler O.B. & Blekman A.V. (2024). Karyotype and molecular genetic differentiation of a 24-chromosomal form of the gray hamster *Nothocricetulus migratorius* from the Tien Shan. Russ. J. Gen. 60 (7): 982–986.

Brandt J.F. (1835). Mammalium rodentium exoticorum novorum vel minus rite cognitorum Musei Academici zoologici descriptions et icons. Mém. Acad. Impériale sci. St. Pétersbourg 6ème sér., 3 (2): 367–442 + 10 plates.

Brandt J.F. (1859). Quelques remarques sur les espèces du genre *Cricetus* de la faune de Russie. Mél. Biol. Acad. St. Pétersb. 3: 205–212.

Brants A. (1827). *Het geslacht der muizen door Linneaus opgesteld, volgens de tegenswoordige toestand der wettenschap in familien, geslachten en soorten*. Akademische Boekdrukkery, Berlyn [Berlin] [in Dutch].

Buchtová M., Matulová P., Witter K. & Tichý F. (2005). Morphogenesis of palatal ridges in the golden hamster (*Mesocricetus auratus*, Rodentia). Acta Vet. Brno. 74: 319–327.

Bugge J. (1970). The contribution of the stapedial artery to the cephalic arterial supply in muroid system. Acta anat. 76: 313–336.

Bugge J. (1985). Systematic value of the carotid arterial pattern in rodents. In: Luckett W.P. (Ed.) *Evolutionary relationships among rodents*. Springer, New York, pp. 355–379.

Buhle Ch.A. (1821). *Naturgeschichte des Hamsters nebst Angabe mehrerer Mittel zu seiner Verminderung, besonders einer neu erfundenen Falle*. Joseph Georg Trassler, Brünn [Brno], 104 pp. + 2 plates.

Bukhnikashvili A. (2004). *On cadastre of small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) of Georgia*. Tbilisi State Univ., Tbilisi.

Burgin C.J., Wilson D.E., Mittermeier R.A., Rylands A.B., Lacher T.E. & Sechrest W. (2020). *Mammals of the World. Vol. 1. Monotremata to Rodentia*. Lynx, Barcelona.

Călinescu R.I. (1931a). Verzechnis und Bibliographie der Säugetiere Rumaniens. Z. Säugetierkunde 6 (1): 78–84.

Călinescu R.I. (1931b). Die Säugetiere Rumaniens. Verbreitung und biogeographischen-ökonomischen Betrachtungen. Regia M. O., Imprimeria Naţională, Bucureşti, 103 pp. [in Romanian with German summary].

Callery R. (1951). Development of the os genital in the golden hamster, *Mesocricetus (Cricetus) auratus*. J. Mammalogy 32 (2): 204–207.

Çam P., Yiğit N. & Çolak E. (2015). Chromosomal arrangements of hybrid individuals of *Mesocricetus brandti* (Nehring, 1898) (Mammalia: Rodentia). Marmara Fen Bilimleri Dergisi 3: 93–96.

Campbell C.W. (1903). Journeys in Mongolia. Geogr. J. 22 (5): 485–518 + 2 maps.

Carleton M.D. & Musser G.G. (1984). Muroid rodents. In: Anderson S.K. & Jones J.K. (Eds.): *Recent mammals of the world*. John Wiley and Sons, New Yank, pp. 289–314.

Chang A., Diani A. & Connell M. (1987). The Chinese hamster: biology and care. In: Van Hoosier G.L. & McPherson C.W. (Eds.): *Laboratory hamsters*. Academic Press, San Diego, pp. 305–320.

Charleman E. (1915). *The mammals of the vicinity of Kiev*. Izdanie Kievskago Ornitologicheskago obschestva imeni K. F. Kesslera, Kiev [in Russian with title in Eng.].

Chaworth-Musters J.L. (1933). A note on the synonymy of *Cricetulus barabensis* Pallas. Ann. Mag. Nat. Hist. 10, 12: 221–223.

Chaworth-Musters J.L. (1934). A note on the nomenclature of *Phodopus sungorus* (Pallas) and its geographical races. Ann. Mag. Nat. Hist. 10, 13: 590–591.

Cheesman R.E. (1921). Report on a collection of mammals made by Col. J. E. B. Hotson in Shiraz, Persia. J. Bombay Nat. Hist. Soc. 27 (3): 33–41.

Chen F. & Min Z. (1982). Taxonomic review of several species in rodents. Zool. Res. 3 (sup.): 369–371 [in Chinese with Eng. title].

Chen W., Gao W. & Fu B.Q. (2002). *[The Fauna of Beijing: Mammals]*. Beijing Publ. House, Beijing [in Chinese].

Cherepanova E., Safronova L. & Vasilieva N. (1998). Reproductive isolations between *Ph[odopus] sungorus* and *Ph. campbelli*: The consequences of allopatric speciation. In: [Proc.] Euro-Amer. Mamm. Congress, Santiago de Compostella, Spain, July 19–24 1998, p. 350.

Chernova O.F., Kupriyanova V.P., Feoktistova N.Yu. & Surov A.V. (2022a). Peculiarities of the structure of the skin and its derivatives in some member of the subfamily Cricetinae (Cricetidae, Rodentia): Why it is important to know. Biol. Bull. 49 (8): 1216–1231 [Eng. translation of Russian original published in Zool. Zh. 2021, 100 (11):1288–1304].

Chernova O.F., Khatsaeva R.M., Kupriyanova V.P., Feoktistova N.Yu. & Surov A.V. (2022b). Structural features of the skin, hair, and specific skin glands of the common hamster (*Cricetus cricetus*, Cricetidae, Rodentia). Biol. Bull. 49 (9): 1352–1356 [Eng. translation of Russian original published in Zool. Zh. 2022, 101 (1): 101–116].

Ching-Mei M. & Anderson R.R. (1975). Papillae and galactophore numbers in mammae of *Cricetus auratus, Meriones unguiculatus, Spermophilus tridecemlineatus*, and *Chinchilla laniger*. J. Mammalogy 56 (1): 247–250.

Chişamera G.B., Birău A.C., Cobzaru J. & Gavril V.D. (2023). Atypical melanistic color in common hamsters *Cricetus cricetus* (Rodentia: Cricetidae) in Romania. North-West. J. Zool. 19: 57–61.

Chugunov Yu.D. (1962). Mammals of the Gobi Altai. Part I. Gerbillinae, hamsters, voles. Zool. Zh. 41 (11): 1719–1730 [in Russian with Eng. abstract].

Chunkov M.M. (2018). [Influence of land use patterns on the Ciscuacasian golden hamster (*Mesocricetus raddei avaricus*) in the inner mountaineous Dagestan, particularly in the vicinity of the natural park "Khunzakhsky"]. In: Dzhamalov Sh.D., Magomedov I.M., Ataev Z.V. & Radzhabova R.T. (Eds.): *Proceedings from a Conference "Actual problems of specifically protected areas."* Ministry of Natural Resources and Ecology of the Republic of Dagestan, Makhachkala, pp. 108–109 [in Russian].

Chunkov M.M. (2020). [*Ecological characteristics of Radde's hamster (Mesocricetus raddei avaricus) under condition of land-use changes in the mountains of Dagestan.*] Ph.D. Thesis, IPEE of A.A. Severtsov RAS, Moscow [in Russian].

Chunkov M.M. & Omarov K.Z. (2020). [Preliminary results from a study of summer activity of Radde's hamster (*Mesocricetus raddei avaricus*) in agrocenoses of the mountain Dagestan using telemetry and Fais system.] Obshchaya Biolog. 79: 6–11 [in Russian].

Conroy C.J. & Cook J.A. (1999). MtDNA evidence for repeated pulses of speciation within arvicoline and murid rodents. J. Mamm. Evol. 6: 221–245.

Corbet G.B. (1978). *The mammals of the Palaearctic region: a taxonomic review.* Brit. Mus. (Nat. Hist.), London.

Corbet G.B. & Hill J.E. (1980). *A world list of Mammalia species.* Brit. Mus. (Nat. Hist.), London.

Corbet G.B. & Hill J.E. (1986). *A world list of Mammalia species. 2nd ed.* Brit. Mus. (Nat. Hist.), London.

Corbet G.B. & Hill J.E. (1992). *The mammals of the Indomalayan Region: systematic review.* Oxford Univ. Press, Oxford.

Cuvier [G.] (1817). *Le règne animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Tome I. L'introduction, les mammifères et les oiseaux.* Deterville, Paris.

Dahl F. (1894). Tierwelt Schleswig-Holsteins. III. Säugetiere. Die Heimat 4: 113–141.

Dal' S.K. (1954). [*Animal world of the Armenian SSR. Vol. 1. Vertebrates.*] AN ASSR, Erevan, 415 pp. [in Russian].

Danford C.G. & Alston E.R. (1877). On the mammals of Asia Minor. Proc. Zool. Soc. Lond. 1877: 270–281.

Danford C.G. & Alston E.R. (1880). On the mammals of Asia Minor. Part II. Proc. Zool. Soc. Lond. 1880: 50–64.

Danini E.S. & Olschwang N.A. (1936). Contributions to the ecology and biology of rodents of the Troitsk district, form[er] Ural province. 3. Notes on the anatomy and biology of *Cricetulus eversmanni* Br[andt]. Izv. Biol. Nauchno-issled. Inst. Permsk. Gos. Univ. 10: 115–124 [in Russian with Eng. summary].

David A. (1871). Report addresé a mm. les professeurs-administrateurs du Muséum d'histoire naturelle. Bull. Nouv. Arch. Mus. 7: 75–100.

Davydov G.S. (1988). *Fauna of the Tadjik Soviet Socialist Republic. Vol. XX, Part 3. Mammalia (Rodentia).* AN Tadjik SSR, Dushanbe [in Russian with Eng. title page].

Desmarest M.A.G. (1820). *Mammalogie ou descriptions des espèces des mammifères. 1er partie.* Veuve Agasse, Paris.

Didier R. (1953). Etude systématique de l'os penien des mammifères. Mammalia 17 (4): 260–269.

Ding L. & Liao J. (2019). Phylogeography of the Tibetan hamster *Cricetulus kamensis* in response to uplift and environmental change in the Qinghai–Tibet Plateau. Ecol. Evol.; 00:1–16. https ://doi.org/10.1002/ece3.5301

Ding L., Wenjia L. & Jicheng L. (2016a). Mitochondrial genome of *Cricetulus migratorius* (Rodentia: Cricetidae): Insights into the characteristics of the mitochondrial genome and the phylogenetic relationships of *Cricetulus* species. Gene 595 (1): 121–129.

Ding L., Li W. & Liao J. (2016b). Characterization of the complete mitochondrial genome of *Phodopus roborovskii* (Rodentia: Cricetidae) and systematic implications for Cricetinae phylogenetics. Biochem. Syst. Ecol. 69: 226–235.

Ding L., Zhou Q., Sun Y., Feoktisova N.Yu. & Liao J. (2020). Two novel cricetine mitogenomes: Insight into the mitogenomic characteristics and phylogeny in Cricetinae (Rodentia: Cricetidae). Genomics 112 (2): 1716–1725.

Djakonov A. (1926). Zur Kentniss der Geometriden Fauna des Minussinsk - Bezirks (Sibirien Jenissei Gouv.). Jahrbuch des Martjanov'schen Staatsmuseums in Minussinsk (Sibirien) 4 (1): 1–78 [in Russian with German summary].

Doğramacı S., Kefelioğlu H. & Gündüz İ. (1994). Karyological analysis of the species of *Mesocricetus* (Mammalia: Rodentia) in Anatolia. Turk. J. Zool. 18: 41–45. [in Turkish with Eng. summary].

Dombrowski v. R. (1907). *Mesocricetus newtoni*, Nehring. Monographische Studie. Bull. Soc. Stiinţe (Bucureşti) 16 (1–2): 94–101.

Ellerman, J.R. (1941) *The families and genera of living rodents. Volume II. Family Muridae.* Brit. Mus. (Nat. Hist.), London, xii + 690 pp. [with a list of named forms (1758–1936) by R. W. Hayman and G. W. C. Holt].

Ellerman J.R. (1947). A key to the rodents inhabiting India, Ceylon, and Burma, based on collections in the British Museum. I. J. Mammalogy 28: 249–278.

Ellerman J.R. (1948). Key to the rodents of South-west Asia in the British Museum Collection. Proc. Zool. Soc. Lond. 118: 765–816.

Ellerman J.R. (1961). *Rodentia. The fauna of India including Pakistan, Burma and Ceylon. Mammalia. 2nd ed., part 1*, Zool. Survey India, Calcutta [Kolkata].

Ellerman J.R. & Morrison-Scott T.C.S. (1951). *Checklist of Palaearctic and Indian mammals 1758 to 1946.* Brit. Mus. (Nat. Hist.), London.

Erbajeva M.A., Borisova N.G. & Alexeeva N.V. (2021). The history of small mammal fauna of Western Transbaikalia: a brief review. IOP Conf. Ser.: Earth Environ. Sci. 908 (2021) 012017, doi:10.1088/1755-1315/908/1/012017.

Erdal O., Erturaç M.K., Dalfes H.N. & Sen S. (2018). Rodents from the Middle Pleistocene of Niksar Basin (Tokat-Turkey): implications on palaeoenvironment and the North Anatolian Fault. N. Jb. Geol. Paläont. Abh. 289/1: 77–111.

Erxleben J.C.P. (1777). *Systema regni animalis per classes, ordines, genera, species, varietates cum synonymis et historia animalium. Classis I Mammalia.* Impensis Weygandianis, Lipsiae [Leipzig].

Esfandiari B., Nahrevanian H., Pourshafie M.R., Gouya M.M., Khaki P., Mostafavi E., Darvish J. & Hanifi H. (2017). Epidemiological distribution of rodents as potent reservoirs for infectious diseases in the Provinces of Mazandaran, Gilan and Golestan, Northern Iran. Infect. Dis. Rep. 9(2):6900. doi: 10.4081/idr.2017.6900. PMID: 28626537; PMCID: PMC5472340.

Eversmann E. (1850). [*The natural history of mammals of Orenburg Kray*]. Kazan' [in Russian].

Evstafiev I.L. (2015). The common hamster (*Cricetus cricetus*): a case of unusual aggressive behavior. Novitates Theriol. 9: 132–134 [in Russian with Eng. abstract].

Evstafiev I.L. (2016). Results of a 30-years-long investigation of small mammals in Crimea. Part 2. Ecology of species. Proc. Theriol. School 14: 103–120 [in Russian with Eng. abstract].

Fahlbusch V. (1969). Pliozäne und Pleistozäne Cricetinae (Rodentia, Mammalia) aus Polen. Acta Zool. Cracov. 15 (5): 99–138.

Falk J.P. (1786). *Beyträge zur topographischen Kentniß des rußischen Reichs. Dritter Band, welcher Beyträge zur Thierkenntniß und Völkerbeschreibung enthält.* Kayserl. Akademie der Wißenschaften, St. Petersburg.

Feeny W.P. (2012). The Chinese or striped-backed hamster. In: Suckow M.A., Stevens K. & Wilson R. (Eds.), *The laboratory rabbit, guinea pig, hamster, and other rodents.* Elsevier Inc., Pp. 907–922.

Feoktisova N.Yu. (2008). *Dwarf hamsters (Phodopus, Cricetinae): systematics, phylogeography, ecology, physiology, behaviour, chemical communication.* KMK, Moscow [in Russian with Eng. abstract].

Feoktistova N.Y., Meschersky I.G., Bogomolov P.L., Sayan A.S., Poplavskaya N.S. & Surov A.V. (2017). Phylogeographic structure of the common hamster (*Cricetus cricetus* L.): late Pleistocene connections between Caucasus and Western European populations. PLoS One 12:e0187527.

Feoktistova N.Y., Meschersky I.G., Bogomolov P.L., Meschersky S.I., Sayan A.S., Sitnikova E.F., Vlasov A.A. & Surov A.V. (2018). About the border between two phylogroups of the common hamster (*Cricetus cricetus*) (Cricetinae, Rodentia). Povolzhskiy Ecol. J. 4: 485–494.

Feoktistova N.Y., Kropotkina M.V., Potashnikova E.V., Gureeva A.V., Kuznetsova E.V. & Surov A.V. (2019). Speciation in allopatric species of the hamster subfamily Cricetinae (Rodentia, Cricetidae). Biol. Bull. Rev. 9: 230–242.

Feoktistova N.Yu., Meschersky I.G., Shenbrot G.I., Puzachenko A.Yu., Meschersky S.I., Bogomolov P.L. & Surov A.V. (2022). Phylogeography of the common hamster (*Cricetus cricetus*): paleoclimatic reconstructions of Late Pleistocene colonization. Integr. Zool. 18(3): 581–599.

Feoktistova N.Yu., Meschersky I.G., Katsman E.A., Meschersky S.I., Gureeva A.V., Kupriyanov V.P., Bogomolov P.L., Kropotkina M.V., Davydov I.D., Leonov A.G. & Surov A.V. (2023). Genetic differentiation within two large phylogroups of the common hamster (*Cricetus cricetus*) (Cricetidae, Rodentia), the boundary between them, and the population abundance. Povolzhskiy J. Ecol. 2023 (4): 481–497 [in Russian with Eng. summary].

Field K.J. & Sibold A.L. (1999). *The laboratory hamster and gerbil.* CRC Press, Boca Raton, Florida.

Filippi F. de (1865). *Note di un Viaggio in Persia nel 1862. Vol. 1.* G. Daelli & C., Milano.

Fischer G. (1817). Adversaria zoologica. Fasciculus primus. Quaedam ad Mammalium systema et genera illustranda. Mem. Soc. imper. natural. Moscou 5: 357–424.

Fitzinger L.J. (1867). Versuch einer natürlichen Anordnung der Nagethiere (Rodentia). Sitzungsber. Akad. Wiess. math-natur. Klasse 56: 57–168.

Flerov K.K. (1929). Sur le faune des Mammifères du Karadagh (Crimée). Ann. Mus. Zool. l'Acad. Sci. URSS, 30: 371–404.

Flint V.E. (1960). On the biology of the Roborovsky hamster. Trans. Moscow Soc. nat. 65 (5): 98–101 [In Russian with Eng. title].

Flint V.E. (1966a). [On biology of long-tailed dwarf hamster.] Zool. Zh. 45 (3): 471–474 [in Russian].

Flint W.E. (1966b). *Die Zwerghamster der Palaärktischen Fauna.* Neue Brehm-Bücherei, Wittenberg.

Flint V.E., Chugunov Yu.E. & Smirin V.M. (1965). [*Mammals of the USSR*]. Mysl', Moscow [in Russian].

Flower W.H. & Lyddeker R. (1891). *An introduction to the study of mammals living and extinct.* Adam and Charles Black, London.

Formozov A. (1929). [Mammals of Northern Mongolia collected during the 1926 Expedition]. AN USSR, Moscow [in Russian].

Fu H., Wu X. & Yang Z. (2005). Diversity of small mammals communities at different habitats in Alashan Region, Inner Mongolia. Acta Theriol. Sin. 25 (1): 32–38.

Fulton G.P. (1968). The golden hamster in biomedical research. In: Hoffman et al. (1968), pp: 3–13.

Gamperl R., Victorin G. & Rosenkrantz W. (1977). New observations on the karyotype of the Djungarian hamster, *Phodopus sungorus*. Experientia 33 (8): 1020–1021.

Gamperl R., Vistorin G. & Rosenkranz W. (1978). Comparison of chromosome banding patterns in five members of Cricetinae with comments on possible relationships. Caryologia 31 (3): 343–353.

Gattermann R., Fritzsche P., Neumann K., Al-Husseyin I., Kayser K., Abiad M. & Yakti, R. (2001). Notes on the current distribution and the ecology of wild golden hamsters (*Mesocricetus auratus*). J. Zool. Lond. 254: 359–365.

Gavril V.D., Vasiliu O.C., Cobzaru I., Murariu D., Sahlean T.C., Chişamera G.B. & Nicoară R.G. (2023). Preliminary observations on the food availability and diet composition of the Romanian hamster *Mesocricetus newtoni* (Rodentia, Cricetidae). Trav. Muséum Nat. d'Hist. Nat. "Grigore Antipa" 66 (1): 197–209.

Geoffroy Saint-Hilaire É. (1803). *Catalogue des mammifères du Museum nationale d'histoire naturelle.* Paris.

Georgi J.G. (1775). *Bemerkungen einer Reise im Russischen Reich im Jahre 1772.* Kayserl. Academie der Wissenschaften, St. Petersburg.

Gershenson S. (1945). Evolutionary studies on the distribution and dynamics of melanism in the hamster (*Cricetus cricetus* L.). I. Distribution of black hamsters in the Ukrainian and Bashkirian Soviet Socialist Republics (U.S.S.R.). Genetics 30: 207–232.

Gershenson S. (1946). [The role of natural selection in distribution and dynamics of melanism in common hamster (*Cricetus cricetus* L.).] J. General Biol. 7 (2): 97–127 [in Russian].

Gershenson S. & Polevoy V. (1941). [Inheritance of black coat colour in the common hamster (*Cricetus cricetus* L.)]. Dokl. AN SSSR 29: 608–609 [in Russian].

Gervais P. (1854). *Histoire naturelle des mammifères. Primates, chiroptères, insectivores et rongeurs.* L. Curmer, Paris.

Gervais P. (1859) *Nouvelles recherches sur les animaux vertébrés. 2nd ed.* Librarie de la Société Géographique, Paris.

Gesner C. (1602). *Medici tigurini historiae animalium. Liber primus, De quadrupedibus viulparis.* Bibliopolio Cambieriano, Francofurti [Frankfurt a. M.].

Giebel C.G. (1855). *Die Säugethiere in zoologischer, anatomischer in palæontologischer Beziehung.* Ambrosius Abel, Leipzig.

Gilibert M.J.E. (1805). *Abrégé du system de la nature, de la Linné, Histoire dés mammaires ou des quadrupèdes et cétacées.* Lyon.

Gloger C.W.L. (1835). Jahrbücher für wiessenschaftliche Kritik, 8: 718–719.

Gmelin J.F. (1788). *Caroli a Linné, Equitis aurati de stella polari, arciatri regii, med. et botan. profess. Upsal. Acad. Paris. Upsal. Holm. Petropo. Berolin. Imper londin. Angl. Mosp. Tolos. Florent. Edinb. Bern. Soc. Systema naturae per regna tria naurae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Edition decima tertia, aucta, reformata.* Impensis Georg. Emanuel. Beer, Lipsiae [Leipzig], 11 + 500 pp.

Gmelin J.F. (1792). *The animal kingdom or Zoological system, of the celebrated Sir Charles Linnaeus. Class I: Mammalia.* A. Strahan, London.

Gmelin J.F. (1805). *Abrégé du system de la nature, de Linné, Histoire des mammaires ou des quadrupèdes et cétacés.* Lyon.

Graphodatsky A. (2006a). *Cricetulus longicaudatus* (Lesser long-tailed hamster). In: O'Brien S.J., Menninger J.C. & Nash W.G. (2006), p. 214.

Graphodatsky A. (2006b). *Mesocricetus raddei* (Ciscuacasian hamster). In: O'Brien S.J., Menninger J.C. & Nash W.G. (2006), p. 220.

Gray J.E. (1821). On the natural arrangement of vertebrose animals. London Med. Reposit. 15: 296–310.

Gray R.E. (1825). An outline of an attempt at the disposition of Mammalia into tribes and families, with a list of the genera apparently appertaining to each tribe. Ann. Phil. N.S. 10: 337–344.

Gray J.E. (1873). Notes on the rats; with the description of some new species from Panama and the Aru Islands. Ann. Mag. Nat. Hist. 4: 416–419.

Gromov I.M. & Baranova G.I. (1981). [*Catalogue of the mammals of USSR (Pliocene–Recent)*]. Nauka, Leningrad [St. Petersburg] [in Russian].

Gromov I.M. & Erbajeva M.A. (1995). [*The mammals of Russia and adjacent territories. Lagomorphs and Rodents*]. Nauka, Leningrad [St. Petersburg] [in Russian].

Gromov I.M., Gureev A.A., Novikov G.A., Sokolov I.I., Strelkov P.P. & Chapsky K.K. (1963). [*Mammals in the Fauna of the Soviet Union. Part 1*]. Nauka, Moscow [in Russian].

Grulich I. (1978). Standorte des Hamsters (*Cricetus cricetus* L., Rodentia, Mamm.) in der Ostslowakei. Acta Sc. Nat. Brno 12 (1): 1–42.

Grulich I. (1987a). Variability of *Cricetus cricetus* in Europe. Acta Sc. Nat. Brno 21 (7): 1–53.

Grulich I. (1987b). Contribution to the sexual dimorphism of the hamster (*Cricetus cricetus*, Rodentia, Mammalia). Folia Zool. 36 (4): 291–306.

Gu J., Ma Y. & Sun Y.-H. (2005). A rediscussion of the taxonomic status of *Cansumys canus*. Chinese J. Zoo. 40 (3): 116–120.

Günther, A. (1871). Mammalia. Zool. Record for 1871, 8: 1–22.

Gureeva A.V. (2022). [Phylogeography and systematics of the genus *Allocricetulus* (Rodentia, Cricetinae)]. Unpublished Thesis, Russian Acad. Sci., Dept. Biol. Sci., Moscow [in Russian].

Gureeva A.V., Feoktistova N.Yu., Matveevsky S.N., Kolomiets O.L. & Surov A.V. (2016). Speciation of Eversman and Mongolian hamsters (*Allocricetulus*, Cricetinae): Experimental hybridization. Biol. Bull. 43 (7): 736–742 [Russian version published in Zool. Zh. 2015, 94 (5): 614–620].

Gureeva A.V., Lebedev V.S., Feoktisova N.Yu. & Surov A.V. (2020). Geographical variability of cranial characteristics and the systematics of the genus *Allocricetulus* (Cricetidae). Zool. Zh. 99 (12): 1424 –1433 [in Russian with Eng. abstract].

Hamar M. (1958). [Fauna and distribution of rodents in the Rumanian National Republic.] Sci. reports High School (Biol. Sci.) 4: 50–56 [in Russian].

Hamar M. & Schutowa M. (1961). [On the question of systematics and ecology of the Asia Minor (*sic*) hamster in Romania]. 1st All-Union Conference on Mammals, Book of Abstracts, Moscow, p. 140 [in Russian].

Hamar M. & Schutowa M. (1966). Neue Daten über die geographische Veränderlichkeit und die Entwicklung der Gattung *Mesocricetus* Nehring, 1898 (Glires, Mammalia). Z. Säugetierkunde 31: 237–251.

Handler A.H. & Shepro D. (1968). Cheek pouch technology: Uses and applications. In: Hoffman et al. (1968), pp. 195–201.

Hansson H.G. (not dated). Henri Milne-Edwards. In: Biographical etymology of marine organism names. Göteborgs Universitet. Retrieved 12 February 2024. Accessed at: https://web.archive.org/web/20120205205939/http://www.tmbl.gu.se/libdb/taxon/personetym/petymol.m.html

Harrison D.L. & Bates P.J.J. (1991). *The mammals of Arabia*. Harrison Zool. Mus. Publ., Sevenoaks, UK.

Haslauer, R. (2017a). 8. Gray dwarf hamster *Cricetulus migratorius*. In: Pardiñas et al. (2017), pp. 283–284.

Haslauer, R. (2017b). 9. Long-tailed dwarf hamster *Cricetulus longicaudatus*. In: Pardiñas et al. (2017), pp. 284.

Haslauer, R. (2017c). 12. Ladakh dwarf hamster *Cricetulus alticola*. In: Pardiñas et al. (2017), pp. 285.

Haslauer, R. (2017d). 13. Tibetan dwarf hamster *Cricetulus kamensis*. In: Pardiñas et al. (2017), pp. 285.

Heptner V.G. & Formozov A.N. (1941). Les mammiféres du Dagestan (Caucase oriental). Arch. Mus. Zool. Univ. Moscou 6: 3–74 [in Russian with Frenc title].

Heptner V.G. (1926). [*Key to Mammals of Dagestan*]. [Scientific and Research Inst. Dagestan], Makhach-Kala [in Russian].

Herskovitz P. (1962). Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Field. Zool. 46: 1–524.

Ho H.J. (1935). A new subspecies of Cricetidae from Shensi. Contr. Biol. Lab. Soc. China 10: 288–291.

Hoffman R.A., Robinson P. & Magalhaes H. (1968). *The golden hamster, its biology and use in medical research*. Iowa State Univ. Press, Ames, Iowa.

Hollister N. (1912). New mammals from the highlands of Siberia. Smith. Misc. Coll. 60: 1–6.

Honacki J.H., Kinman K.E. & Koeppl J.W. (1982). *Mammal species of the world: a taxonomic and geographic reference*. Allen Press, Lawrence, KS.

Hooper E.T. (1952). A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Misc. Publ. Mus. Zool., Univ. Michigan 77: 1–255 + 9 plates.

Horáček I. & Lebedová K. (2022). Cricetinae in the Quaternary fossil record of the Czech Republic and Slovakia (Rodentia: Cricetidae). Lynx, n. s. (Praha) 53: 565–545.

Howell A.B. (1929). Mammals from China in the collections of the United States National Museum. Proc. Wash. Acad. Sci. 75: 1–82.

Hu Y., Yao Z., Huang Z., Tian Y., Li H., Pu Q., Yang D. & Hu H. (2014). Mammalian fauna and its vertical changes in Mt. Qomolangma National Nature Reserve, Tibet, China. Acta. Theriol. Sin. 34 (1): 28–37 [in Chinese with Eng. abstract].

Huang W., Xia L., Yang Q. & Feng Z. (2008). Distribution pattern and zoogeographical division of mammals on Qinghai-Tibet Plateau. Acta Theriol. Sin. 28 (4): 375–394 [in Chinese with Eng. abstract].

Husson A.M. (1959). On the systematic position of the western hamster, *Cricetus cricetus canescens* Nehring (Mammalia: Rodentia). Bijdragen tot de dierkunde 29 (1): 187–201.

Hutterer R. & Kryštufek B. (2020). A history of mammal research in Europe. In: Hackländer K. & Zachos F. (Eds.) *Mammals of Europe - Past, present, and future. Handbook of the mammals of Europe*. Springer, Cham. https://doi.org/10.1007/978-3-030-00281-7_5

ICZN (1964). *International code of zoological nomenclature adopted by the XV Congress of Zoology*. Int. Trust Zool. Nomencl., London.

ICZN (1999). *International code of zoological nomenclature, 4th ed*. Int. Trust Zool. Nomencl., London.

ICZN (2003). Declaration 44. Amendment of article 73.7.3. Bull. Zool. Nomencl. 60: 263.

Illiger C. (1811). *Prodromus systematis mammalium et avium [...]*. Sumptibus C. Salfeld, Berolini [Berlin].

Ishishita S., Tsuboi K., Ohishi N., Tsuchiya K. & Matsuda Y. (2015). Abnormal pairing of X and Y sex chromosomes during meiosis I in interspecific hybrids of *Phodopus campbelli* and *P. sungorus*. Sci. Rep. 5: 9435 | DOI: 10.1038/srep09435

Iskhakova E.N. (1974). Taxonomy of the group *Cricetulus barabensis* (Rodentia) according to the karyological data. In: Yablokov A.V. (Ed.) *First Int. Theriolog Congress. I (A–M)*. Nauka, Moscow, pp. 231–232.

Ivanov V.G. (1969a). The chromosome complements of *Mesocricetus* of Kaukasus and their taxonomic position. Pp. 105–106 in Vorontsov (1969).

Ivanov V.G. (1969b). The karyotype of *Cricetus cricetus stavropolicus* Satunin, 1907. Pp. 104 in Vorontsov (1969).

Janushevich A.I., Ayzin B.M., Kydyraliev A.K., Umrikhuna G.S., Fedjanina T.F., Shukurov Z.A., Grebenyuk R.V. & Tokobaev M.M. (1972). [*Mammals of Kyrgysia*.] Ilim, Frunze, 461 pp. [in Russian].

Jiang, Z., Ma, Y., Wu, Y., Wang, Y., Zhou, K., Liu, S. & Feng, Z. (2015). *China's mammal diversity and geographic distribution*. Sichuan Sci. & Technol. Press, Chengdu (Sichuan).

Jiang H., Wang X., Yang Y., Pan X., Liu S. & Lu J. (2024). *Tscherskia ningshaanensis*: a neglected species based on phylogenetic and taxonomic analysis of *Tscherskia* and *Cansumys* (Cricetidae, Rodentia). Zoosyst. Evol. 100 (4): 1231–1241.

Jo Y.S., Kim T.W., Choi B.J. & Oh H.S. (2012). Current status of terrestrial mammals on Jeju Island. J. Species Res. 1 (2): 249–256.

Jo Y.-S., Baccus J.T. & Koprowski J.L. (2018). Mammals of Korea: A review of their taxonomy, distribution and conservation status. Zootaxa 4522: 1–216.

Jones J.K. & Johnson D.H. (1965). Synopsys of the lagomorphs and rodents of Korea. Univ. Kansas Publ., Mus. Nat. Hist. 16: 357–407.

Jugder D., Gantsetseg B., Davaanyam E. & Shinoda M. (2018). Developing a soil erodibility map across Mongolia. Nat. Hazards 92 (Suppl. 1): 71–94.

Jurgenson [Yurgenson] P.B. (1938). [Contribution â l'étude des mammifères de la région du Lac Teletzky de la Réserve d'état d'Altaï.] Trav. de la Réserve d'état d'Altaï 1: 92–170 [in Russian with French abstract].

Kalabuchow N. & Rajewskij W. (1930). Säugetiere (Mammalia) des Kreise Donez (Nord-Kaukasus). Izvestya Severo-Kavkazskoy Kraevoy Stanitsi Zaschiti Rasteniy 5: 129–148.

Kalthoff D.C. (2006). Incisor enamel microstructure and its implications to higher-level systematics of Eurasian Oligocene and Early Miocene hamsters. Palaeontographica A 277 (1–6): 67–80.

Kamimura E., Uno Y., Yamada K., Nishida C. & Matsuda Y. (2022). Molecular cytogenetic characterization of C-band-positive heterochromatin of the greater long-tailed hamster (*Tscherskia triton*, Cricetinae). Cytogen. Gen. Res. 162 (6):323–333.

Kandaurov A.S., Morgilevskaya I.E. & Bukhnikashvili A.K. (1994). [Knowledge on the systematics of small mammals (Insectivora, Rodentia) in Georgia.] In: [*Biodiversity: Degree of taxonomic knowledge*], Nauka, Moscow, pp. 126–141 [in Russian].

Kang, C., Yue, H., Liu, M., Huang, T., Liu, Y., Zhang, X., Yue, B., Zeng, T. & Liu, S. (2016). The complete mitochondrial genome of *Cricetulus kamensis* (Rodentia: Cricetidae). Mitochondrial DNA A: DNA Mapp Seq Anal. 27 (2): 976–977.

Karaseva E.V. (1963). [Materials to the knowledge of geographical distribution and biology of selected small mammal species of northern and central Kazakhstan]. Trans. Moscow Soc. Natural. 10: 194–219 [In Russian].

Kartavtsev Y.F., Kartavtseva I.V. & Vorontsov N.N. (1984a). Population genetics and genogeography of wild manuals. IV. Level of heterozygosity in five species of Palearctic hamsters (Mammalia, Cricetini). Genetika, 20: 954–960 [in Russian; English translation published by Plenum Publishing Corp. 1984].

Kartavtsev Y, Kartavtseva I.V. & Vorontsov N.N. (1984b). (Population genetics and genogeography of wild mammals. V. Genetic distances between representatives of different genera of Palearctic hamsters (Rodentia, Cricetini).) Genetika 20: 961–966 [in Russian, English version published by Plenum Publishing Corp. 1984].

Kartavtseva I.V. (1985). [Intraspecific chromosomal polymorphism of wide-ranging species: the Libyan gerbil and the gray hamster]. In: [Phenetics of populations], Saratov, pp. 84—85 [in Russian].

Kartavtseva I.V. & Alekseeva E.V. (1987). [Subspecies of the greater long-tailed hamster *Tscherskia triton* de Winton, 1899 (Rodentia, Cricetidae) on the territory of the Far Eastern USSR and its remnants excavated in southern Primorye.] In: Freiman L.V. & Yakimenko A.I. (Eds.): [*Issues of evolutionary zoology and genetics of mammals.*], DVO AN SSSR, Vladivostok, pp. 96–106 [in Russian].

Kartavtseva I.V. & Vorontsov N.N. (1992). Chromosome differences among subspecies of hamster *Allocricetulus eversmanni* (Rodentia, Cricetidae) and the new taxon of subspecific rank description. Chromosome Inform. Service 53: 8–10.

Kartavtseva I.V. & Surov A.V. (2005). G-, C-, and NOR-stained karyotype of the Eversmann's hamster *Allocricetulus eversmanni* and comparison with the karyotype of *Cricetulus* species. Mamm. Stud. 30: 89–91.

Kartavtzeva [Kartavtseva] I.V., Borisov Yu.M., Lyapunova E.A., Vorontsov N.N. & Korablev V.P. (1980). Accessory chromosomes in the rat-like hamster (*Tscherskia triton*) and its taxonomic status. Zool. Zh. 59 (6): 899–904 [in Russian, with Eng. summary].

Kashchenko N.Th. (1910). Description d'une collection des mammifères, provenant de la Transbaikalie. Ann. Mus. Zool. Acad. Imp. Sci. St. Pétersbourg 15: 267–298.

Kashkarov D.N. (1926). [A key to rodents of Turkestan]. Izd. UZOSTAZRA, Tashkent [in Russian].

Kashkarov D.N., Korovin A. & Kurbatov V. (1923). [Rodents of Western Tien-Shan. Based on collections from summer 1921 and summer 1922]. Trans. Sci. Soc. Turkestan 1: 195–218 [In Russian].

Kaup J.J. (1835). *Das Thierreich in seinen Hauptformen systematisch beschrieben*. Johann Philipp Diebl, Darmstadt.

Kayser A. & Stubbe M. (2000). Colour variation in the common hamster *Cricetus cricetus* in the north-eastern foot-hills of the Harz Mountains. Acta Theriol. 45: 377–383.

Kerr, R. (1792). *The animal kingdom, or zoological system, of the celebrated Sir Charles Linnéus. Class I. Mammalia: containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young; being a translation of that part of the Systema Naturé, as lately published, with great improvements, by Professor Gmelin of Goettingen*. J. Murray, London, UK.

Kessler K.F. (1851). [*Natural history of the governments of the Kiev educational district. Part I.*] Kiev [in Russian].

Keyes P.H. & Dale P.P. (1944). A preliminary survey of the pouches and dentition of the Syrian hamster. J. Dent. Res. 23 (6): 427–438.

Kishida K. (1929). A synopsis of Corean hamsters. Lansania 1: 1–160.

Kishida, K. & Mori, T. (1931). On the distribution of terrestrial mammals of Korea. Zool. Mag. 43: 372–391 [in Japanese].

Kittel R. (1984). *Der Goldhamster*. Die Neue Brehm Bücherai. A Ziemsen Verlag, Wittemberg Lutherstadt., Germany.

Kobayashi S. (1984). Tooth eruption of the Chinese hamster (*Cricetulus griseus*). J. Kyushu Dent. Soc. 38 (2): 359–364.

Koh H.S., Eger J., Oh J.G., Lim B., Lee B.K., Jang K.H., In S.T., Lee J.H., Kim K.S. & Kweon G.H. (2013). Genetic distinctiveness of the greater long-tailed hamster, *Tscherskia triton nestor* (Rodentia: Mammalia), from Jeju Island, Korea: cytochrome oxidase I and cytochrome *b* sequence analyses. Anim. Cells Syst. 17 (1): 31-35.

Korablyov V.P., Pavlenko M.V., Kiriliuk M.V. & Bazhenov Yu.A. (2013). Distribution of different chromosomal forms of the striped-back hamsters of the superspecies *Cricetulus barabensis* in Transbaikalia. Zool. Zh. 92: 596–601 [in Russian with Eng. abstract].

Korbut Z., Rusin M., Neumann K. & Banaszek A. (2019). Filling the gap: the common hamster, *Cricetus cricetus*, phylogeography – a case study of Ukraine as potential refugial area. Folia Zool. 68: 48–58

Kostenko V.A. (1984). [IV. Order Rodentia Bowdich, 1821 – Rodents]. In: Krivosheev V.G. (Ed.): [*Terrestrial mammals of Far East of the Soviet Union*]. Nauka, Moscow, pp. 118–215 [In Russian].

Kotschy Th. (1858). *Reisen in den Cilicischen Taurus über Tarsus*. J. Berthes, Gotha.

Kouznetzof [Kuznetsov] B.A. (1928). Mammifères de la région des steppes de l'Oural méridional. Bul. Soc. Nat. Moscou, Sec. Biol. 37 (3–4): 250–311 [in Russian with French summary].

Kowalski K. (2001). Pleistocene rodents of Europe. Folia Quatern. 72: 3–389.

Kozhantschikov V.D. (1926). Materialien zur Macrolepidopteren Fauna des Minussinsk-Bezirks. Jahrbuch des Martjanov'schen Staatsmuseums in Minussinsk (Sibirien) 4 (1): 79–82 [in Russian with German summary].

Král B., Radjabli S.L., Grafodatsky A.S. & Orlov V.N. (1984). Comparison of karyotypes, G-bands and NORs in three *Cricetulus* spp. (Rodentia, Cricetidae). Folia Zool. 33 :85–96.

Krištofík J. & Danko Š. (2012). *Mammals of Slovakia. Distribution, bionomy and protection*. Veda, Bratislava [in Slovak with Eng. summary].

Krsmanović L., Purger J.J. & Šoti J.P. (1988). Colour variations of fur in common hamster *Cricetus cricetus* (Linnaeus, 1758) and common vole *Microtus arvalis* (Pallas, 1779). Arch. Biol. Sci. (Belgrade) 40 (1–4): 15P–16P.

Krulikovsky L. (1915). Petites notices zoologiques. Bull. Soc. Ouralienne d'amis des sciences naturelles, placèe sous la très auguste protection de son Altesse Impériale Monseigneur le Grand-Duc Nicolas Mikhaĭlovitch 35: 5–8 [in Russian with French abstract].

Kryltzov A.I. (1964). Moult topography of Microtinae, other rodents and lagomorphs. Z. Säugetierkunde 29: 1–17.

Kryštufek B. (1991). *Mammals of Slovenia*. Slov. Mus. Nat. Hist., Ljubljana [in Slovene with Eng. summary].

Kryštufek B. (2017a). 4. Golden hamster *Mesocricetus auratus*. In: Pardiñas et al. (2017), pp. 282.

Kryštufek B. (2017b). 5. Ciscaucasian hamster *Mesocricetus raddei*. In: Pardiñas et al. (2017), pp. 282.

Kryštufek B. (2017c). 6. Brandt's hamster *Mesocricetus brandti*. In: Pardiñas et al. (2017), pp. 282–283.

Kryštufek B. (2017d). 7. Romanian hamster *Mesocricetus newtoni*. In: Pardiñas et al. (2017), pp. 283.

Kryštufek B. (2017e). 18. Common hamster *Cricetus cricetus*. In: Pardiñas et al. (2017), pp. 286–288.

Kryštufek B., Pozdnyakov A.A. (2018). Common names for *Cricetus cricetus* (Rodentia: Cricetidae). Lynx, n. s. (Praha), 49: 177–192.

Kryštufek B. & Shenbrot G. (2022). Voles and lemmings (Arvicolinae) of the Palaearctic region. University of Maribor Press, Maribor (Slovenia), 424 pp., doi: 10.18690/um.fnm.2.2022

Kryštufek B. & Shenbrot G. (2023). The name-bearing type is essential for the objective identification of a taxonomic name: the message from the lectotypification of *Lemmus obensis bungei*. Mammalia 87 (3): 276–282.

Kryštufek B. & Vohralík V. (2009). *Mammals of Turkey and Cyprus. Rodentia II. Cricetinae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae*. Annales, Koper, Slovenia.

Kryštufek B., Pozdnyakov A.A., Ivajnšič D. & Janžekovič F. (2016). Low phenotypic variation in eastern common hamsters *Cricetus cricetus*. Folia Zool. 65 (2): 148–156.

Kryštufek B., Hoffmann I.E., Nedyalkov N., Pozdnyakov A.A. & Vohralík V. (2020). *Cricetus cricetus* (Rodentia: Cricetidae). Mamm. Species 59 (988): 10–26.

Kuhlmann M.T., Clemen G. & Schlatt S. (2003). Moulting in the Djungarian hamster (*Phodopus sungorus* Pallas): seasonal or continuous process? J. Exp. Zool. 285 A: 160–171.

Kulik I.L. (1962). Materials pertaining to the ecology of a common hamster in the Altai area. Bul. Soc. Nat. Moscou, Sec. Biol. 67 (4): 16–25 [in Russian with Eng. abstract].

Kumerloeve H. (1975). Die Säugetiere (Mammalia) der Türkei. Veröffentlich. Zool. Staatssamml. München 18: 71-158.

Kurashvili B.E., Kokhy S.S., Arabuli A.B., Rodonaya T.E., Chlaidze Z.I., Kalanadze A.D. & Matsaberidze G.B. (1981). [*Mammals of Georgia. Atlas.*] Metcniereba, Tbilisi, 109 pp [in Russian and Georgian].

Kuroda N. (1934). Korean mammals preserved in the collection of marquis Yamashina. J. Mammalogy 15 (3): 229–239.

Kuroda N. (1939). Mammal fauna of Manchoukuo preserved in the collection of Marquis Yamasina. Bull. Biogeographical Soc. Japan 9: 1–50.

Kuznetsov B.A. (1932). [Rodents of the Semipalatinsk district, Kazakhstan]. Trans. Moscow Soc. nat. 41 (1–2): 60–120 [in Russian].

Kuznetsov B.A. (1948). [*Mammals of Kazakhstan*]. Soc. Nat. Moscou, Moscow [In Russian].

Kuznetsov B.A. (1965). [Order rodents. Ordo Rodentia]. In: Bobrinskii N.A., Kuznetzov B.A. & Kuzyakin A.P. (Eds.): [*Key to the Mammals of the USSR*]. Prosveshenie, Moscow [In Russian].

Kuznetsov B.A. (1975). [*Key to vertebrate fauna of the USSR*]. Prosveschenie, Moscow [in Russian].

Kuznetzov [Kuznetsov] B.A. (1944). [VIII. Order Rodents. Order Rodentia]. In: Bobrinsky N., Kuznetzov B. & Kuzykin A. (Eds.): [*Mammals of USSR*]. Sovietskaya Nauka, Moscow, pp. 262–362 [in Russian with title page in Eng.].

Kuzyakin A.P. (1963). [On the systematics of rodent fauna of the USSR]. Trans. Moscow Soc. Nat. 10: 105–115 [in Russian].

Lacépède B.G.É. de la V. (1799). Tableau des divisions, sousdivisions, ordres et genres des mammifères. In: *Discours de l'ouverture et de clôture du cours d'histoire naturelle donné dans le Muséum national d'Histoire naturelle, l'an VII de la République, et tableaux méthodiques des mammifères et des oiseaux*. Plassan, Paris, France, pp. 1–20.

Laptev I.P. (1958). [*Mammals in the taiga zone of western Siberia.*] [Tomsk University Press], Tomsk [in Russian].

Lay D.M. (1967). A study of the mammals of Iran resulting from the Street expedition of 1962-63. Field. Zool. 54: 1–282.

Lebedev V.S. (2000). [A morphometric study of geographic variability in migratory hamsters (*Cricetulus migratorius* Pall.).] In: Agadjianian A.K. & Orlov V.N. (2000), pp. 82–84 [in Russian].

Lebedev V.S. (2012). Subfamily Cricetinae s. str. In: Pavlinov I.Yu. & Lissovsky A.A. (Eds.): *The mammals of Russia: A taxonomic and geographic reference*. KMK, Moscow, pp. 211–220.

Lebedev V.S. & Koval'skaya Yu.M. (2003). New data on the distribution of the chromosomal races of the *Cricetulus barabensis* species complex (Rodentia, Muridae) in the Selenga River Basin. In: Averianov A. & Abramson N. (2003), pp. 119–120 [in Russian with Eng. abstract].

Lebedev V.S., & Lisovsky A.A. (2008). The geographical variability of cranial characteristics and systematics of striped-back hamsters (*Cricetulus barabensis*, Rodentia, Cricetidae). Zool. Zh. 87: 361–374 [in Russian with Eng. summary].

Lebedev V.S. & Potapova E.G. (2008). The zygomasseteric structure in Palearctic hamsters (Cricetinae, Rodentia) and the taxonomic status of *Cricetulus kozlovi* Satunin 1902. Zool. Zh. 87 (1): 1–14 [in Russian with Eng. summary].

Lebedev V., Likhnova O., Bulat S. & Pavlinov I. (1998). The two forms of *Cricetulus migratorius* (Rodentia) from the southeast of Europe. In: *Euro-American Mammal Congress, Santiago de Compostela, Spain, July 19–24 1998*, p. 355.

Lebedev V.S., Likhnova O.P. & Bulat S.A. (2000). [Two forms of the grey hamster *Cricetulus migratorius* (Rodentia) from South Russia and West Kazakhstan]. In: Agadjianian A.K. & Orlov V.N. (2000), pp. 82–84 [In Russian].

Lebedev V.S., Ivanova N.V., Pavlova N.K. & Poltoraus A.B. (2003). Molecular phylogeny of the Palaearctic hamsters. In: Averianov A. & Abramson N. (2003), pp. 114–118 [in Russian with Eng. abstract].

Lebedev V.S., Bannikova A.A., Neumann K., Ushakova M.V., Ivanova N.V. & Surov A.V. (2018a). Molecular phylogenetics and taxonomy of dwarf hamsters *Cricetulus* Milne-Edwards, 1867 (Cricetidae, Rodentia): description of a new genus and reinstatement of another. Zootaxa 4387 (2): 331–349.

Lebedev V., Poplavskaya N., Bannikova A., Ryurikov G. & Surov A. (2018b). Genetic differentiation in *Cricetulus migratorius* Pallas, 1773 (Rodentia, Cricetidae). Mamm. Bio. 92: 115–119.

Lee J.-B., Kim Y.-K. & Bae Y.-S. (2014). Historical review and notes on small mammals (Mammalia: Erinaceomorpha, Soricomorpha, Rodentia) in Korea. Anim. Syst. Evol. Divers. 30 (3): 159–175.

Lehmann E.v. (1969). Eine neue Säugetieraufsammlung aus der Türkei im Museum Koenig (Kumerloeve-Reise 1968). Zool. Beitr., N. F. 15: 299-327.

Lemyanchik V.T. (2006). [Common Hamster *Cricetus cricetus* (Linnaeus, 1758)]. In Khoruzhik L.I. (Ed.): [*Red Book of Belarus Republic. Animals.*] [Belarus Encyclopaedia], Minsk, pp. 40–41 [in Russian].

Lenders A. & Pelzers E. (1985). Distribution of the common hamster (*Cricetus cricetus* L.) in The Netherlands. Z. Säugetierkunde 52: 90–96.

Lepekhin I.I. (1771). [*Diary of travels of Doctor and Secretary of the Academy of Sciences through different provinces of the Russian State in 1768 and 1769.*] [Imperial Academy of Sciences], St. Peterburg [in Russian].

Leske, N. G. 1779. *Anfangsgründe der Naturgeschichte. Erster Theil. 10. Algemeine Natur- und Tiergeschichte mit 10 Kupfertafeln.* Siegfried Lebrecht Crusius, Leipzig, Germany.

Lesson R.P. (1827). *Manuel de mammalogie, ou histoire naturelle des mammifères.* Roret, Paris.

Lesson R.P. (1842). *Nouveau tableau du règne animal. Mammifères.* Arthus-Bertrand, Paris.

Levenkova E.S. (2003). Hybrid meiosis abnormalities in some rodent species. In: Averianov A. & Abramson N. (2003), pp. 121–124 [in Russian with Eng. abstract].

Li X. & Wang T. (1996). An analysis of relationship between ecological factors and number of species of rodents in Shaanxi District. Acta Theriol. Sin. 16 (2): 29–135 [in Chinese with Eng. abstract].

Li Y., Lu H., Tian J. & Hu J. (1990). Assessment of age indices of greater long-tailed hamster by use of principal component analysis. Acta Theriol. Sin. 19 (2): 121.–127 [in Chinese with Eng. abstract].

Liao J., Xiao Z., Dong Y., Zhang Z., Liu N. & Li J. (2007). Taxonomic status of *Cansumys canus* (Allen, 1928). Acta Zool. Sin. 53: 44–53.

Libois F. & Rosoux R. (1982). Le hamster commun *Cricetus cricetus* (L.) en Belgique: status actuel et ancient des populations. Belg. J. Zool. 112 (2): 227–236.

Likhovid A.A. (2002). [Radde's Golden Hamster *Mesocricetus raddei* Nehring, 1894.] In: Sigida S.I. (Ed.): [*Red Book of Stavropol' Krai. Vol. 2. Animals.*] OLO Poligrafservis, Stavropol', p. 201 [in Russian].

Lim B.K. & Ross P.D. (1992). Taxonomic status of *Alticola* and new record of *Cricetulus* from Nepal. Mammalia 56 (2): 300–302.

Lindsay E.H. (1994). The fossil record of Asian Cricetidae with emphasis on Siwalik cricetids. In: Tomida Y., Li C.K. & Setoguchi T. (Eds.): *Rodent and lagomorph families of Asian origins and diversification.* Nat. Sci. Mus. Monographs 8, Tokyo.

Linnaeus C. (1758). *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus 1. Editio decima, reformata.* Laurentii Salvii, Holmiae [Stockholm], Sweden.

Lipkow J. (1954). Über das seitenorgan des goldhamsters (*Mesocricetus auratus auratus* Waterh.). Z. Morph. Ökol. Tiere 42: 333–372.

Lissovsky A.A., Sheftel B.I., Saveljev A.P., Ermakov O.A., Kozlov Yu.A., Smirnov D.G., Stakheev V.V. & Glazov D.M. (2019). *Mammals of Russia. Species list and applied issues.* KMK Sci. Press, Moscow.

Liu S., Liu Y., Meng G., Zhou C., Liu Y. & Liao R. (2020). A new record of mammal in China and new provincial records in Xizang, Hubei and Sichuan. Acta Theriol. Sinica 40: 261–270.

Louarn Le H. & Saint Girons M.-C. (1977). *Les rongeurs de France.* INTA, Paris.

Loukashkin A.S. (1937). The Mammals of North Manchuria. J. Mammalogy 18 (3): 327–332.

Lozan M.N. (1971) [*Rodents of Moldova. History of fauna formation and the ecology of recent species.*] Shtiintsa, Kishinev, 186 pp. [in Russian].

Lu J. & Wang T. (1996). Studies on the Glires (Rodentia and Lagomorpha) fauna and its division of Henan Province. Acta Theriol. Sinica 16 (2): 119–128 [in Chinese with Eng. summary].

Luk'yanchenko A.A. (1954). [On the changes of the northern distributional border of Radde's golden hamster (*Mesocricetus raddei nigriculus* Nehr., 1898]. Zool. Zh. 33: 218–220 [in Russian].

Luo Z., Chen W. & Gao W. (2000). *Fauna Sinica. Mammalia, Vol. 6, Rodentia, Part III: Cricetidae.* Science Press, Beijing [in Chinese with Eng. summary].

Lv X., Xia L., Ge D., Wen Z., Qu Y., Lu L. & Yang Q. (2016). Continental refugium in the Mongolian plateau during quaternary glacial oscillations: phylogeography and niche modelling of the endemic desert hamster, *Phodopus roborovskii.* PLoS One 11:e0148182.

Lydekker R. (1909). Mammalia. Zool. Record (for 1907) 44: 1–74.

Lyman, C.P. & O'Brien R.C. (1977). A laboratory study of the Turkish hamster *Mesocricetus brandti.* Breviora 442: 1–27.

Ma Y., Yang Q. & Zhou L. (1987). Taxonomy and geographic distribution of Glires in China. In: Zheng Z. & Chen Z.K. (Eds): Conspectus of Glires. Shangai Jia Tong Univ. Press, Shangai, pp. 35–116 [in Chinese].

Magalhaes H. (1968). Gross anatomy. In: Hoffman et al. (1968), pp. 91–109.

Major C. I. Forsyth. (1897). On the Malagasy rodent genus *Brachyuromys*; and on the mutual relations of some groups of the Muridae (Hesperomyinae, Microtinae, Murinae, and "Spalacidae") with each other and with the Malagasy Nesomyinae. Proc. Zool. Soc. Lond. 1897: 695–720.

Makino S. (1951). Karyotype of *Tscherkia triton* (Muridae-Cricetinae). Kromosomo 8: 311–312.

Malygin V.M., Startsev N.V. & Zima J. (1992). [Karyotypes and distribution of dwarf hamsters from the "*barabensis*" group (Rodentia, Cricetidae).] Moscow Univ. Biol. Sci. Bull. 2: 32–39 [in Russian].

Malykova M.G., Vakhrushev A.V. & Korsakov N.G. (2005). [Siberian hairy-footed hamster *Phodopus sungorus* (Pallas, 1773)]. In: Sidorov G.N. & Rusakov V.N. (Eds) [*Red book of Omsk Oblast*]. Omsk State Pedagogical University, Omsk, p. 230–231 [in Russian].

Marches G. (1964). Contributions a l'etude taxonomique, biologique, écologique et de la croissance en captivité du hamster de Dobroudja (*Mesocricetus newtoni*). Studii și cercetări de igienă și sănătate publică, București.

Marinina L.S. (2005). [Migratory hamster (*Cricetulus migratorius* Pallas, 1773)]. In: Kucheruk V.V. & Khlyap L.A. (Eds): *Lagomorpha and rodents of the Middle Asia's deserts.* Geos, Moscow, pp. 152–161 [in Russian; book abstract in Eng.].

Markov G. (1960). [A contribution to the study of hamsters (Cricetinae) in Bulgaria.] Izv. Zool. inst. BAN 9: 293–303 [in Bulgarian].

Martino V. & Martino E. (1916). Contributions à la classification et à la distribution géographique des mammifères de la Steppe des Kirgiuises (1-er partie). Ann. Musée Zool. Acad. Sci. 21: 269–301 [in Russian with French title].

Matschie P. (1901). Ueber rumänische Säugetiere. Sitzungsber. Gesell. Naturforschen. Freunde Berlin 9: 220–238.

Matschie P. (1918). Eine neue Form des Zwergamsters, *Cricetulus falzfeini.* Sitzungsber. Gesell. Naturforschen. Freunde Berlin 1919: 298–300.

Matthey R. (1952). Chromosomes de Muridae (Microtinae et Cricetinae). Chromosoma 5: 115–138.

Matthey R. (1959). Formules chromosomiques de Muridae et de Spalacidae. La question du polymorphisme chromosomique chez les mammifères. Rev. suisse Zool. 66: 175–209.

Matthey R. (1960). Chromosomes, heterochromosomes et cytologie comparee des Cricetinae paleartiques (Rodentia). Caryologia 13: 199–223.

Matthey R. (1961). Cytologie comparée des Cricetinae paléartiques et américains. Les chromosomes *de Calomyscus bailwardi* Thomas et la position du genre *Calomyscus* dans la systématique des Cricetinae. Rev. suisse zool. 68 (2): 41–61.

Matveevsky S.N., Malygin V.M., Lebedev V.S., Poplavskaya N.S., Surov A.V. & Kolomiets O.L. (2014). Sporadic disorders in the meiotic prophase I in *Cricetulus barabensis* hybrids (Cricetidae, Rodentia) do not lead to reproductive isolation between karyomorphs. Caryologia, 67 (2): 149–154.

Maul L. (1990). Überblick über die unterpleistozän Kleinsäugerfaunen Europas. Quartärpaläont. (Berlin) 8: 153–191.

McKenna M.C. & Bell S.K. (1997). *Classification of mammals above the species level*. Columbia Univ. Press, New York.

Meinig H., Buschmann A., Reiners T.E., Neukirchen M., Balzer S, & Petermann R. (2014). Der Status des Feldhamsters (*Cricetus cricetus*) in Deutschland. Nat. Landsch. 89 (8): 338–343.

Mendelssohn H. & Yom-Tov Y. (1999). *Fauna Palestina. Mammals of Israel*. Isr. Acad. Sci. Human., Jerusalem.

Ménétries E. (1832). *Catalogue raisenné des objets de zoologie recueillies dans une voyage au Caucase et jusqu'aux frontières actuelles de la Perse entrepris par ordre de S[a] M[ajeste] l'Empereur*. L'Impremerie de l'Académie l'Impériale des sciences, St. Pétersbourg.

Meshchersky I.G. & Feoktisova N.Y. (2009). Intraspecific organization of dwarf hamsters *Phodopus campbelli* and *Phodopus sungorus* (Rodentia: Cricetinae) basing on *mt*DNA analysis. Dokl. Biol. Sci. 424: 35–38.

Meschersky I.G. & Feoktisova N.Y. (2011). Analysis of genetic diversity of the desert hamster (*Phodopus roborovskii*) in the northern part of its range. Biol. Bull. 37 (1): 82–86.

Meschersky, I.G., Feoktistova, N.Y., Gureeva, A.V. & Surov A.V. (2004). Allele Diversity of the DRB1 Gene of the Major Histocompatibility Complex in Two Species of Hamsters of the Genus *Allocricetulus* Argyropulo 1932. Biol. Bull. Russ. Acad. Sci. 51: 2317–2326.

Meulen van den A. J. & Kolfschoten van T. (1986). Review of the Late Thurolian to Early Biharian mammal faunas from Greece and Tureky. Mem. Soc. Geol. It. 31: 201–211.

Meyer M.N. & Skholl' E.D. (1977). [On some biological peculiarities of long-tailed hamster (*Cricetulus longicaudatus*) (Rodentia, Cricetidae).] Zool. Zh. 56 (3): 484 [in Russian].

Mezzherin S.V. (2001). [About the taxonomic status of the grey hamster *Cricetulus migratorius isabellinus* from the Kopetdag: analysis of the allozyme diversity]. Vestn. Zool. 35 (6): 91–94 [in Russian].

Mezhzherin S.V. & Lashkova O.I. (2013). [*Mammals of Ukraine (Determination key)*.] Naukova Dumka, Kiev [in Ukrainian with Eng. abstract].

Migulin O.O. (1938). *Mammals of the Ukr[ainian] SSR*. Acad. Sci. Press, Kiev [in Ukrainian with Eng. title].

Miljutin A. (2011). Trends of specialisation in rodents: the hamsters, subfamily Cricetinae (Cricetidae, Rodentia, Mammalia). Acta Zool. Lith. 21 (3): 192–206.

Miller G.S. (1910). Two new genera of murine rodents. Smithson. Misc. Coll. 52 (5): 497–498.

Miller G.S. (1912). *Catalogue of the Mammals of Western Europe (Europe exclusive of Russia) in the Collection of the British Museum*. Brit. Mus., London.

Miller G.S. & Gidley J.W. (1918). Synopsis of the supergeneric groups of rodents. J. Washington Acad. Sci. 8: 431–448.

Milne-Edwards H. (1834). *Élémens de zoologie, ou, Leçons sur l'anatomie, la classification et les moeurs des animaux*. Crochar, Paris.

Milne Edwards A. (1867). Observations sur quelques mammifères du nord de la Chine. Ann. Sci. naturelles 5 (7): 375–377.

Milne Edwards A. (1871). Études pour servir a l'histoire de la faune mammologique de la Chine. In: Milne Edwards H. & Milne Edwards A. (1868–1867), pp. 67–229.

Milne Edwards H. & Milne Edwards A. (1868–1874). *Recherches pour servir à l'histoire naturelle des mammifères comprenants des considéation sur la classification de ces animax. Tom second – Atlas*. Librariae de l'Academie de médicine, Paris.

Minoransky V.A., Sibel'nikov V.V. & Usik N.N. (1997). [Mammal fauna of Rostov oblast]. Izv. Vysshikh Uchenykh Zavedeniy. Sev-Kavkaz. Reg. Est. Nauki 1: 79–87 [in Russian].

Missone X. (1959). *Analyse zoogéographique des mammifères de l'Iran*. Mem. Inst. Roy. Sci. Nat. Belgique, 12me ser., fasc. 59, 81 pp.

Mitina I.P. (1959). Geographical variability of the hamster *Cricetulus eversmanni* Br[andt] (Mammalia, Glires). Zool. Zh. 38 (12): 1869–1875 [in Russian with Eng. summary].

Modorov M.V. & Polyakov V.E. (2021). [Eversmann's Hamster *Allocricetulus eversmanni* Brandt, 1859.] In: [*Red Book of Kurgan Oblast. 2nd ed.*] Kurgan State University, Kurgan, p. 26 [in Russian].

Mori T. (1930). On four new small mammals from Manchuria. Ann. zool. japonenses 12: 417–420.

Mori T. (1939). Mammalia of Jehol and district north of it. In: *Report of the first scientific expedition to Manchuokuo*. Sect. 5, Div. 11, Part 4: 1–92 + 16 Plates [in Japanese and Eng.].

Moskvitina N.S., Ravkin Yu.S., Nemolkova O.V., Kokhonov E.V., Bogomolova I.N., Panov V.V., Kislyi A.A. & Zhigalin A.V. (2022). The common hamster *Cricetus cricetus* L., 1758 in Western Siberia: the species' past, present and future. South of Russia: Ecology, Development 17 (2): 6–18 [in Russian with Eng. summary].

Mukhamedkulov M. (1964). [Rodents.] In: Bogdanov O.P. (Ed.): [*Ecology and economic significance of vertebrates in southern Uzbekistan (Bassin Surkhandary)*.] FAN Uz SSR, Tashkent, pp. 58–72 [in Russian].

Müller D., Hauer J., Schöttner K., Fritzsche P. & Weinert D. (2015). Seasonal adaptation of dwarf hamsters (genus *Phodopus*): differences between species and their geographic origin. J. Comp. Physiol. B 185: 917–930.

Murariu D. (1998). About the hamster (*Cricetus cricetus* L., 1758 – Cricetidae, Rodentia) in Romania. In: Stubbe & Stubbe (Eds.), pp. 91–99.

Murariu D. & Stanciu C.R. (2009). Data on the presence of the species *Mesocricetus newtoni* (Nehring, 1898) (Mammalia: Muridae: Cricetinae) in Dobrogea (Romania). Trav. Mus. Nat. d'Hist. Nat. "Grigore Antipa" 52: 363–369.

Murray A. (1866). *The Geographical distribution of Mammals*. Day and Son Ltd., London.

Musser G.G. & Carleton M.D. (1993). Family Muridae. In: Wilson D.E. & Reeder DA.M. (1998.): *Mammal Species of the World. 2nd ed*. Smithsonian Institution Press, Washington, pp. 501–755.

Musser G.G. & Carleton M.D. (2005). Superfamily Muroidae. In: Wilson D.E. & Reeder DA.M. (2005): *Mammal species of the World. 3rd ed., Vol. 2*. John Hopkins Univ. Press, Baltimore, pp. 894–1531.

Nechay G. (2000). *Status of hamsters*: *Cricetus cricetus, Cricetus migratorius, Mesocricetus newtoni and other hamster species in Europe*. Nature and environment No. 106. Council of Europe Publ., Strasbourg.

Nechay G., Hamar M. & Grulich I. (2000). The common hamster (*Cricetus cricetus* [L.]): a review. EPPO Bull. 7 (2): 255–276.

Nedyalkov N. (2016). Distribution and current status of *Cricetulus migratorius* (Mammalia: Cricetidae) in Bulgaria, with comments on its status in the Balkans. Turk. J. Zool. 40: 925–932.

Nedyalkov N., Raykov I., Koshev Y., Atanasova I., Dekov O., Kolev I., Raykova V. & Stanewa A. (2015). Current status, distribution and conservation of *Mesocricetus newtoni* and *Cricetus cricetus* (Mammalia: Cricetinae) in Bulgaria. *Poster presentation, 7th In. Zool. Congress "Grigore Antipa" Museum, 18–21 Nov. 2015*, Bucharest, Programme, p. 18.

Nehring A. (1894a) Die Verbreitung des hamsters (*Cricetus vulgaris*) in Deutschland. Arch. Naturgeschichte 60 (1): 15–31.

Nehring A. (1894b). *Cricetus nigricans* Brdt. in Ost-Bulgarien und Dagestan. Zool. Anz. 17 (445): 147–150.

Nehring A. (1898a). Über *Cricetus Raddei* n. sp. Zool. Anz. 21 (553): 182–183.

Nehring A. (1898b). Über *Cricetus Newtoni* n. sp. aus Ostbulgarien. Zool. Anz. 21 (559): 329–332.

Nehring A. (1898c). Über *Cricetus, Cricetulus* und *Mesocricetus* (n. subg.). Zool. Anz. 21 (566): 493–495.

Nehring A. (1898d). Die Gruppe der *Mesocricetus*-Arten. Arch. f. Naturgescht. 64 (1): 373–392 + 1 plate.

Nehring A. (1899a). Der ostbulgarische Hamster (*Mesocricetus Newtoni* Nhrg.). Natuwissenscahft. Wochenschrift 14 (1): 1–2.

Nehring A. (1899b). Über einige Varietäten des gemainen Hamster (*Cricetus vulgaris* Desm.). Sitz.-Ber. Gessell. Naturforsch. Freunde Berlin 1: 1–3.

Nehring A. (1902). Über einige griechische Nager: *Mus epimelas* n. sp., *Cricetulus atticus* n. sp., und *Myoxus nitedula Wingei* n. subsp. Sitz.-Ber. Gessell. Naturforsch. Freunde Berlin 1902: 1–7.

Nehring A. (1903). Über das Vorkommen einer Abart des gemainen Hamsters (*Cricetus vulgaris babylonius* n. subsp.) südöstlich von Bagdad. Sitz-Ber. Gessell. Naturforsch. Freunde Berlin 8: 360–361.

Neuhäuser G. (1936). Die Muriden von Kleinasien. Z. Säugetierkunde 11: 161–236.

Neumann K. (2007). Untersuchungen zur Systematik der Hamster (Cricetinae) sowie zur genetischen Populationsstruktur und Phylogeografie des Feldhamsters *Cricetus cricetus* (Linneaus, 1758) und des Goldhamsters *Mesocricetus auratus* (Waterhouse, 1839). Unpubl. habilitation Thesis, Martin Luther University Halle Wittenberg, Halle (Saale), Germany.

Neumann K. (2013). A genetic tale of two species. In: *20th meeting of the International Hamster Workgroup. The European hamster – new problems and prospects of their solutions*. Adam Mieckiewicz University, Poznań, Poland, p. 13.

Neumann K., Michaux J.R., Maak S., Jansman A.H., Kayser A., Mundt G. & Gattermann R. (2005). Genetic spatial structure of European common hamsters (*Cricetus cricetus*) – a result of repeated range expansion and demographic bottlenecks. Mol. Ecol. 14: 1473–1483.

Neumann K., Michaux J., Lebedev V., Yigit N., Colak E., Ivanova N., Poltoraus A., Surov A., Markov G., Maak S., Naumann S. & Gattermann R. (2006). Molecular phylogeny of the Cricetinae subfamily based on the mitochondrial cytochrome b and 12S rRNA genes and the nuclear vWF gene. Mol. Phyl. Evol. 39: 135–148.

Newton A. (1870). On *Cricetus nigricans* as a European species. Proc. Zool. Soc. Lond. 1870: 331–332.

Niethammer J. (1982). Familie Cricetidae Rochebrune, 1883 – Hamster. In: Niethammer J. & Krapp F. (Eds.): *Handbuch der Säugetiere Europas. Band 2/I, Rodentia II (Cricetidae, Arvicolidae, Zapodidae, Spalacidae, Hystricidae, Capromyidae)*. Akademische Verlagsgesellschaft, Wiesbaden, pp. 1–50.

Novikov K.L. (1935). Systematic peculiarities of the hamster (*Cricetus cricetus* L.). Bul. Soc. Nat. Moscou, Sec. Biol. 45 (6): 302–313 [in Russian with Eng. summary].

Nurgel'dyev P.N. (1969). [Ecology of mammals in flat-land of Turkemia.] Ylym, Ashabad [in Russian].

O'Brien S.J., Menninger J.C. & Nash W.G. (Eds.) (2006). *Atlas of mammalian chromosomes*. Wiley & Sons, Hoboken, NJ.

Obuch J. (2018). On the diet of owls (Strigiformes) in Jordan. Slovak Raptor J. 12: 9–40.

Ogneff [Ognev] S.I. (1925). Mammiferes du dnt. de Samara et de la province de l'Oural. Bul. Soc. Nat. Moscou, Sec. Biol. 33: 1–47 [in Russian with French summary].

Ognev S.I. (1914). Die Säugetiere aus dem Südlichen Ussuri-Gebiete. Dnevnik Zoologicheskogo Otd'lenya Imperatorskago Obshchestva Ljyubiteley Estestvoznaniya, Antropologii i Etnografii N.S. 2 (3): 101–128 + 3 plates [in Russian with German summary].

Ognev S.I. (1916). [Mammals of the Taurida Governorate, mainly from the Crimean Peninsula. Part I. Rodents]. Bull. Soc. Natural. Amis Nature Crimée 5: 51–111 [in Russian].

Ognev S.I. (1922). [Materials for the systematics of Russian mammals]. Biologicheskiya Izvestja 1: 102–116 [In Russian].

Ognev S.I. (1923). [New and little studied species of Russian rodents]. Trans. Moscow Soc. nat. 31:67–98 [In Russian].

Ognev S.I. (1924). *Rodents of the North Caucasus*. [No publisher], Rostov-na-Donu [in Russian with Eng. title].

Ognev S.I. & Heptner V.G. (1927). A new subspecies of hamster from Daghestan (*Mesocricetus raddei*, Nehr.) and some remarks on the Russian species of *Mesocricetus* (with a key to them). Ann. Mag. Nat. Hist. 9, 19: 142–150.

Omarov K.Z. & Chunkov M.M. (2020). [Brandt's hamster *Mesocricetus brandti* (Nehring, 1898).] In: Mogamedov M.-R.D. (Ed.): [*Red Book of the Republic of Dagestan.*] Typography IP Dzhamaludinov, Makhachkala, pp. 700–701 [in Russian].

Omarov K.Z. & Yarovenko Yu.A. (2011). [Current situation in Brandt's hamster (*Mesocricetus brandti* Nehring, 1898) in Daghestan]. In: [*Teriofauna of Russia and adjacent territories. International Meeting. 9th Congress of Theriological Society at RAS, 1–4 February 2011*]. Tovarischestvo nauchnich izdaniy KMK, Moskva, p. 346 [in Russian].

Ondrias J.C. (1966). The taxonomy and geographical distribution of the rodents of Greece. Säugetirkundl. Mitt. 14: 1–136.

Oparin M.L. (2005). Changes in rodent population of typical and dry steppe of Volga Region in XX century. Proc. Zool. Inst. St. Petersburg 306: 82–101 [in Russian with Eng. abstract].

Orlov V.N., & Iskhakova E.N. (1975). Taxonomy of a superspecies of *Cricetulus barabensis* (Rodentia, Cricetidae). Zool. Zh. 54 (4): 597–604 [in Russian with Eng. abstract].

Orlov V.N. & Malygin V.M. (1988). A new species of hamsters — *Cricetulus sokolovi* sp. n. (Rodentia, Cricetidae) from the Mongolian People's Republic. Zool. Zh. 67 (2): 304–308 [In Russian with Eng. summary].

Orlov V.N., Radzhabli S.I., Malygin V.M., Khotolkhu N., Koval'skaya Y.M., Bulatova N.S. & Baskevich M.I. (1978). [Karyotypes of Mongolian Mammals]. In: Bannikova I.A. & Medvedev L.N. (Eds.): [*Geography and dynamics of the flora of the Mongolian People's Republic*]. Nauka, Moscow, pp. 149–164 [in Russian].

Osborn D.J. **(**1965). Rodents of the subfamilies Murinae, Gerbillinae, and Cricetinae from Turkey. J. Egypt. Public Health Assoc. 40: 401–424.

Pallas P.S. (1773). *Reise durch verschiedene Theile des Rußischen Reichs im 1771sten Jahr*. Keiserlichen Academie der Wießenschaften, St. Petersburg, Russia.

Pallas P.S. (1779). *Novæ species quatrupedum e glirum ordine cum illustrationibus variis complurium ex hoc ordine animalium*. Academia Petropolitana, Erlangae [Erlangen], Germany.

Pallas P.S. (1811). *Zoographia Rosso-Asiatica, sistens omnium animalium in extenso Imperio Rossico et adjacentibus maribus observatorum recensionem domicilia, mores et descriptiones, anatomen atque icones plurimorum. Tomus primus.* Officina Caes. Academiae Scientarium impress, Petropoli [St. Petersburg], Russia.

Pallas P.S. (1831). *Zoographia Rosso-Asiatica, sistens omnium animalium in extensor Imperio Rossico […].* Tomus primus. Off. Caes. Acad. Sci. Impress, Petropoli [Sankt Petersburg], Russia.

Palmer T.S. (1897). A list of generic and family names of rodents. Proc. Biol. Soc. Washington 11: 241–270.

Palmer T.S. (1899). Scientific books. Catalogus mammalium tam viventium quam fossilium. By Dr. E. L. Trouessart, Berlin, R. Friedländer & Sohn. New ed., fasciculus VI., Appendix and Index, 1899. 8º, pp. 1265–1469. Price of complete work 66 Marks. Science, N.S., 10 (249): 491–495.

Palmer T.S. (1904). Index generum mammalium. A list of the genera and families of mammals. North American Fauna 23: 1–984.

Pan X., Wang X., Liu Y., Li Y., Liao R., Chen Z., Peng B., Zhu X., Li J. & Liu S. (2024). Phylogenomic analyses of hamsters (Cricetinae) inferred from GBS data and mitochondrial genomes. Mol. Phylogen. Evol. (early online) doi: https://doi.org/10.1016/j.ympev.2024.108241

Panteleyev P.A. (1998). *The Rodents of the Palaearctic: composition and areas.* RAS, Moscow.

Pardiñas U.F.J., Myers P., Léon-Paniagua L., Ordóñez Garza N., Cook J.A., Kryštufek B., Haslauer R., Bradley R.D., Shenbrot G.I. & Patton J.L. (2017). Family Cricetidae (True hamsters, voles, lemmings and New World rats and mice). In: Wilson D.E., Lacher T.E. & Mittermeier R.A. (Eds.): *Handbook of the Mammals of the World. Vol. 7. Rodents II.* Lynx Ediciones, Barcelona, pp. 204–535.

Park J-H. & Oh H-S. (2017). External and cranial characters of the *Tscherskia triton* in Jeju Island, Korea. Korean J. Environ. Biol. 35 (3): 389–397.

Pavlenko T.A. & Allabergenov K. (1974). [Rodents - Rodentia]. In: Sultanov G.S. (Ed.): [*Vertebrates of Fergana Valley.*] FAN Uz SSR, Tashkent, pp. 142 –182 [in Russian].

Pavlinov I.Ya. (2003). Systematics of recent mammals. Arch. Zool. Mus. Moscow State Univ. 46: 1–287.

Pavlinov I.Ya. (2006). Systematics of recent mammals. Arch. Zool. Mus. Moscow State Univ. 47: 1–287.

Pavlinov I.Ya. & Rossolimo O.L. (1987). [Systematics of the mammals of the USSR]. Arch. Zool. Mus. Moscow State Univ. 25: 1–284 [In Russian].

Pavlinov I.Ya., Yahontov E.L. & Agadzhanyan A.K. (1995). [Mammals of Eurasia. I. Rodentia. Systematic and geographic manual]. Arch. Zool. Mus. Moscow State Univ. 32: 1–239 [In Russian].

Pavlov D.S. & Shishkin V.S. (1998). Vladimir E. Sokolov: 1928-98. Oryx 32: 249–249.

Peng J. & Zhong X. (2005). *A guide to identification and conservation of wild mammals in Ganzi Tibetan Autonomous Prefecture of Sichuan Province.* Huayu Nat. Books [no place; in Chinese and Eng.].

Peshev Ts.H., Peshev D.Ts. & Popov V. (2004). *Fauna Bulgarica 27. Mammalia.* Edition Academica "Marin Drinov", Sofia [in Bulgarian with title page in Eng.].

Petrov BM. (1954). [Studies of rodents in Dobrogea, their economic significance and means of control]. Spisanie na nauchno-izsledovatelskito instituti pri M-vo na zemledelnito (Sofia), 2: 81–97 [in Bulgarian with Russian summary].

Petzsch H. & Petzsch H. (1956). Zum Problem des Vererbungsmodus für Melanismus bei dem gemeinen Hamster (*Cricetus cncetus* L.) in Hinsicht auf die Evolution. D. Zool. Garten (N.F.) 22: 119–154.

Petzsch H. (1936a). Bemerkungen zur Melanismus- und Farbspielfrage beim Hamster. Z. Säugetierkunde 11: 343–344.

Petzsch H. (1936b). Beiträge zur Biologie, inbesondere Fortpflanzungsbiologie des Hamsters (*Cricetus cricetus* L.). Ergebnisse und Probleme. Z. f. Kleintierkunde und Pelztierkd. Monograph. 12 (1): 11–83.

Petzsch H. (1941). Vererbungsuntersuchungen an Farbspielen des Hamsters (*Cricetus cricetus* L.). J. Anim. Breeding Genet. 48 (1): 67–83.

Petzsch H. (1952). *Der Hamster.* Die Neue Brehm-Bücherei, Akad. Verlagsgesellschaft, Leipzig, Germany.

Pidoplitshka I. (1928). Hamster der Art *Cricetulus migratorius.* Acad. Sci. de l'Ukraïne. Mém. Classe Sci. Phys. Math. 8 (3): 413–457 [in Ukrainian with title in German].

Pieper H. (1984). Eine neue *Mesocricetus*-Art (Mammalia: Cricetidae) von der griechischen Insel Armathia. Stuttgarter Beitr. Naturkund, Ser. B (Geol., Paläont.) 107: 1–9.

Popescu N.C. & DiPaolo J.A. (1980). Chromosomal interrelationship of hamster species of the genus *Mesocricetus.* Cytogenet. Cell Genet. 28: 10–23.

Poplavskaya N.S., Lebedev V.S., Malygin V.M. & Surov A.V. (2012). New data on the distribution of chromosomal races in the supraspecies complex *Cricetulus barabensis sensu lato* (Rodentia, Cricetidae) and analysis of reproductive barriers among them. Biol. Bull. 39: 759–767.

Poplavskaya N.S., Kropotkina M.V., Feoktisova N.Yu., Kuznetsova E.V., Surov A.V. & Toplinets N.N. (2016). [Dramatic decline of a commodity species – the common hamster (*Cricetus cricetus*) in XX–XXI centuries.] Izv. Orenburg. State Agric. Univ. 5 (55): 223–255 [in Russian].

Poplavskaya N.S., Romanenko S.A., Serdyukova N.A., Trifonov V.A., Yang F., Nie W., Wang J., Bannikova A.A., Surov A.V. & Lebedev V.S. (2017a). Karyotype evolution and phylogenetic relationships of *Cricetulus sokolovi* Orlov et Malygin 1988 (Cricetidae, Rodentia) inferred from chromosomal painting and molecular data. Cytogenet. Genome Res. 152 (2): 65–72.

Poplavskaya N.S., Lebedev V.S., Bannikova A.A., Belokon M.M., Belokon Y.S., Pavlenko M.V., Korablev V.P., Kartavtseva I.V., Bazhenov Yu.A. & Surov A.V. (2017b). Microsatellite loci variation and investigation of gene flow between two karyoforms of *Cricetulus barabensis sensu lato* (Rodentia, Cricetidae). Russ. J. Gen. 53 (1): 76–90.

Poplavskaya N.S., Bannikova A.A., Neumann K., Pavlenko M. Kartavtseva I., Bazhenov Y., Bogomolov P., Abramov A., Surov A & Lebedev V.S. (2018a). Phylogeographic structure in the chromosomally polymorphic rodent *Cricetulus barabensis sensu lato* (Mammalia, Cricetidae). J. Zool. Syst. Evol. Res. 57: 679–694.

Poplavskaya N.S., Bannikova A.A., Fang Y., Sheftel B.I., Ushakova M.V., Surov A.S. & Lebedev V.S. (2018b). Is the center of origin of long-tailed hamster *Cricetulus longicaudatus* Milne-Edwards 1867 (Rodentia, Cricetidae) located in Tibet? Dokl. Biol. Sci. 479: 70–73 [Eng. translation of Russian text in Dokl. Biol. Nauk 479 (6): 716–719].

Popov V.I. (1955). [Rodent pests and their control.] Zemizdat, Sofia [in Bulgarian].

Popov V.A. (1960). [*Mammals of the Volga-Kama region: Insectivora, Chiroptera, Rodentia*]. Izdatel'stvo AN SSSR, Kazan [in Russian].

Popov V. (2007). [Class Rodents (Rodentia).] In: Popov V., Spasov N., Ivanova T., Mikhova B. & Georgiev K. (Eds.): [*Mammals of conservation concern in Bulgaria*]. Dutch Mamm. Soc. VVZ, Arnhem, NL, pp. 163–215 [in Bulgarian].

Potapova E.G. (2005). Phylogenetic relationships of Palaearctic hamsters Cricetinae (Rodentia, Muroidea), based on the structure of auditory bullae. Proc. Zool. Inst. St. Petersburg 306: 116–141 [in Russian with Eng. abstract].

Pradel A. (1985). Morphology of the hamster *Cricetus cricetus* (Linnaeus, 1758) from Poland with some remarks on the evolution of this species. Acta Zool. Cracov. 29 (3): 29 – 52.

Priddy R.B. & Broddie A.F. (1948). Facial musculature, nerves and blood vessels of the hamster in relations to the cheek pouch. J. Morphol. 33 (2): 149–180.

Qumsiyeh M.B. (1996). *Mammals of the Holly Land*. Texas Tech Univ. Press, Lubbock.

Raicu P. & Bratosin S. (1966). Le Caryotype chez le *Mesocricetus newtoni* (Nehring, 1898). Z. Säugetierkunde 31: 251–255.

Raicu P. & Bratosin S. (1968). Interspecific reciprocal hybrids between *Mesocricetus auratus* and *M. newtoni*. Genet. Res. Camb. 11: 113–114.

Raicu P., Ionescu-Varo M., Nicolaescu M. & Kirillova M. (1972). Interspecific hybrids between Romanian and Kurdistan hamsters. Genetica 43: 223–230.

Ramachandran V., Joshi M., Ambekar M., Charoo S.A. & Ramakrishnan U. (2020). The desert hamster *Phodopus roborovskii* (Satunin, 1903) (Rodentia, Cricetidae) from north-western Tibetan plateau, Ladakh, India: an addition to the mammalian fauna of the Indian Subcontinent. Mammalia 84 (3): 253–258.

Ray [Rajus] J. (1693). *Synopſis methodica animalium quadrupedum et serpenti generis*. Impenſis S. Smith & B. Walford, Londini [London].

Rey-Rodríguez I., Lopez-García J-M., Blain H-A, Stoetzel E., Denys C., Fernández-García M., Tumung L., Olle A. & Bazgir B. (2020). Exploring the landscape and climatic conditions of Neanderthals and anatomically modern humans in the Middle East: the rodent assemblage from the late Pleistocene of Kaldar Cave (Khorramabad Valley, Iran). Quat. Sci. Rev. 236: 1–14.

Reznik-Schüller, H., G. Reznik, and U. Mohr. (1974). The European hamster (*Cricetus cricetus* L.) as an experimental animal: breeding methods and observations of their behavior in the laboratory. Z. Versuchstierkunde 16: 48–58.

Reznik G, Reznik-Schüller H. & Mohr U. (1979). *Clinical anatomy of the European hamster Cricetus cricetus, L.* Franklin Inst., Philadelphia. (https://digital.library.unt.edu/ark:/67531/metadc28308/m1/67/: accessed September 23, 2022).

Richmond N.D. & Roslund H.R. (1952). A mid-ventral dermal gland in *Peromyscus maniculatus*. J. Mammalogy 33 (1): 103–104.

Rinker G.C. (1954). The comparative myology of the mammalian genera *Sigmodon, Oryzomys, Neotoma* and *Peromyscus* (Cricetinae), with remarks on their intergeneric relationships. Misc. Publ. Mus. Zool., Univ. Michigan 83: 1–126.

Roberts T.J. (1977). *The mammals of Pakistan*. Ernest Benn Ltd., London.

Robinson, R. (1968). Genetics and karyology. In: Hoffman et al. (1968), pp. 41–72.

Rochebrune A.T. de (1883). Faune de la Sénégambie. Mammifères. Actes Soc. Linn. Bordeaux 37: 49–203.

Rode P. 1945. Catalogue des types de mammifères du Muséum nationale d'histoire naturelle. Bull. Mus. Natl. Hist. Nat (Paris) 2ᵉ Sér. 17 (1): 24–29.

Romanenko S.A., Volobouev V.T., Perelman P.L., Lebedev V.S., Serdukova N.A., Trifonov V.A., Biltueva L.S., Nie W., O'Brien P.C.M., Bulatova N.Sh., Ferguson-Smith M.A., Yang F. & Graphodatsky A.S. (2007). Karyotype evolution and phylogenetic relationships of hamsters (Cricetidae, Muroidea, Rodentia) inferred from chromosomal painting and banding comparison. Chromosome Res. 15: 283–297.

Romanenko S.A., Perelman P.L., Trifonov V.A. & Graphodatsky A.S. (2012). Chromosomal evolution in Rodentia. Heredity 108: 4–16.

Romanenko S.A., Lebedev V.S., Serdukova N.A., Feoktistova N.Y., Surov A.V. & Graphodatsky A.S. (2013). Comparative cytogenetics of hamsters of the genus *Allocricetulus* Argyropulo 1932 (Cricetidae, Rodentia). Cytogen. Gen. Res. 139 (4): 258–266.

Romanenko S.A., Lebedev V.S., Bannikova A.A., Pavlova S.V., Serdyukova N.A., Feoktistova N.Yu., Qu J., Sun Y., Surov A.V. & Graphodatsky A.S. (2021). Karyotypic and molecular evidence supports the endemic Tibetan hamsters as a separate divergent lineage of Cricetinae. Sci. Rep. 11, 10557 (2021) https://doi.org/10.1038/s41598-021-89890-1.

Ross P.D. & Cameron D.M. (1989). A comparison of the physical development and ontogeny of behaviour in the Djungarian hamster and the desert hamster. Acta Theriol. 34 (18): 253–268.

Ross P.D. (1988). The taxonomic status of *Cansumys canus* (Rodentia, Cricetinae). In: *Proc. Symp. Asian-Pacific Mamm.*, Beijing, not paginated.

Ross P.D. (1992). *Morphological variation and phylogeny of Palaearctic hamsters (Rodentia, Cricetinae)*. Vol. I. Ph. D. Thesis, Toronto, University of Toronto, 381 pp.

Ross P.D. (1994). *Phodopus roborovskii*. Mammalian Species 459: 1–4.

Ross P.D. (1995). *Phodopus campbelli*. Mammalian Species 503: 1–7.

Ross P.D. (1998). *Phodopus sungorus*. Mammalian Species 595: 1–9.

Rumyantsev V.Yu., Khitrov D.A. & Golubinsky A.A. (2018). Distribution of mammals in the southern part of European Russia: historical and ecological analysis based on material from General Land Survey. Arid Ecosyst. 8 (3): 173–173 [Eng. translation of Russian text in Aridnye Ecosist. 24 (3/76): 29–40].

Rusinov A.A. 2004. [Common hamster *Cricetus cricetus* (Linnaeus, 1758).] In: Voronin L.V. (Ed.): [*Red Book of Yaroslavl′ Oblast*]. A. Rutman Press, Yaroslavl′, Russia, pp. 343–344 [in Russian].

Ružić A. (1978). Distribution and abundance of the common hamster (*Cricetus cricetus* Linnaeus, 1758, Mammalia) in Yugoslavia. Biosistematika [Belgrade] 4 (1): 203–208 [in Serbian with Eng. abstract].

Ryabitseva V.K. (2020). [Siberian hairy-footed hamster *Phodopus sungorus* (Pallas, 1773)]. In: Petrova O.A. (Ed.): [*Red book of Tyumen Oblast*], 2nd ed. FGBUN of Uralsk Dept., RAS, Kemerovo, p. 29 [in Russian].

Ryan J.M. (1986) Comparative morphology and evolution of cheek pouches in rodents. J. Morphol. 190: 27–42.

Sachs L. (1952). Polyploid evolution and mammalian chromosomes. Heredity 6 (3): 357–362.

Safronova L.L., Malygin V.M., Levenkova E.S. & Orlov V.N. (1992). [Cytogenetic consequences of hybridization of hamsters *Phodopus sungorus* and *Phodopus campbelli*]. Dokl. Akad. Nauk 327 (2): 266–271 [in Russian].

Saint Girons M.-C. (1973). *Les mammifères de France et de Benelux*. Doin, Paris.

Samosh V.M. (1969). Response of two colour forms (black and red) of *Cricetus cricetus* L. to the temperature gradient. Vestn. Zool. 3 (5): 22–25 [in Russian with Eng abstract].

Sandzhiev V.B.-H., Bukreeva O.M. & Sangadzhieva G.V. (2013). [141. Ciscaucasian hamster (Radde's hamster).] In: Ochirov N.L. (Ed.): [*Red Book of the Republic of Kalmykia. Vol. 1. Animals.*] Ministry for Natural Resources […], Elista, Russia, p. 175 [in Russian].

Santel W. & Koenigswald W.v. (1998). Preliminary report on the middle Pleistocene small mammal fauna from Yarimburgaz Cave in Turkish Thrace. Eiszeitalter u. Gegenwart 48: 162–169.

Satunin K. (1900). Die kaukasichen *Mesocricetus*-Arten nebst Bescreibung einer neue Art: *Mesocricetus Koenigi* nov. spec. Zool. Anz. 23 (616): 301–305.

Satunin K.A. (1901). Ueber die Säugethiere der Steppen des nordöstlichen Kaukasus. Mitt. Kaukas. Museums 1 (4): i–ii, 1–154 [in Russian with German summary].

Satunin K. (1902). Neue Nagetiere aus Centralasien. Ezh. Zool. mus. Imp. Akad. Nauk 7 (4): 547–589.

Satunin K. (1903). [A review of mammal research of the Caucasian Kray.] Zap. Kavk. otd. Imperat. Russ. Geograph. Obsch. 24 (2): 3–63 [in Russian].

Satunin K.A. (1905). [A review of mammals of the Trans-Caspian Region.]. Mitt. Kaukas. Mus. 25 (3): 1–56 [in Russian].

Satunin K.A. (1906). Die Säugetiere des Talyschgebietes und der Mughansteppe. Mitt. Kaukas. Mus. 2: 87–394.

Satunin K.A. (1907). Die Säugetiere des Nordöstlichen Ciscaucasien. Mitt. Kaukas. Mus. 3: 1–82 [in Russian with German summary].

Satunin K. (1908). [Essay on geographical distribution of mammals in Russian Empire.]. In: Kozhevnikov G. (Ed.): [*Game Encyclopaedia*] [in Russian].

Schaub S. (1930). Quartäre und jungtertiäre Hamster. Abh. Scweiz. Palaeont. Gessel. 2: 1–49 + 2 plates.

Schegolev V.N. (1925). [*Fauna, biology and economic significance of mammals of Cherepovetskoy Guvernorate.*] Komunist, Gor. Cherepovets [in Russian].

Schley L. & Herr J. (2018). *Säugetiere Luxemburgs*. Minist. nachhaltige Entwickl. Infrastr. & Naturverwaltung, Luxemburg.

Schlott M. (1924). Albinotische Hamster. Pallasia 1: 138.

Schmidt M., Haaf T., Weis H. & Schempp W. (1986). Chromosomal homologies in hamster species of the genus *Phodopus* (Rodentia, Cricetinae). Cytogen. Cell. Genet. 43: 168–173.

Schreber J.C.D. von (1792). *Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen. Vierter Theil*. Wolfgang Walther, Erlangen.

Schröder O., Astrin J. & Hutterer R. (2013). White chest in the west: pelage colour and mitochondrial variation in the common hamster (*Cricetus cricetus*) across Europe. Acta Theriol. 59: 211–221.

Selewin A.M. (1934). Neue Formen der Nagetiere aus Kasakhstan. Bull. Central-Asiatic State Univ. 13: 75–78 [In Russian and German].

Sélys Longchams de E. (1842). *Faune Belge*. Dessain, Liège.

Serebrennikov M.K. (1929). Contribution à la classification et à l'oecologie des rongeurs (Mammalia, Rodentia) de la Transouralie méridionale. Ann. Zool. Mus. AN USSR 30: 251–284.

Serzhanin I.N. (1961). [*Mammals of Belarus. 2nd ed.*]. AN Beloruskoy SSR, Minsk [in Russian].

Severtsov N.A. (1873). [Vertical and horizontal distribution of the animals of Turkestan]. Izvestya Imperatorskago Obschestva lyubiteley estestvoznaniya, antropologii i etnografii [Moscow] 8 (2): 1–157 [In Russian].

Severtsov N.A. (1879). [Notes on vertebrate fauna of Pamir]. Zapiski Turkestanskago otdyala Imperatorskago Obschestva lyubiteley estestvoznaniya, antropologii i etnografii [Tashkent] 1 (1): 58–89 [In Russian].

Severtzoff [Severtsov] N. (1876). The mammals of Turkestan. Ann. Mag. Nat. Hist. 4, 18: 40–57.

Shehab A., Daoud A., Kock D. & Amr Z. (2004). Small mammals recovered from owl pellets from Syria (Mammalia: Chiroptera, Rodentia). Zool. Middle East 33: 27–42.

Shenbrot G.I. (2017a). 1. Roborovski's desert hamster *Phodopus roborovskii*. In: Pardiñas et al. (2017), pp. 281.

Shenbrot G.I. (2017b). 2. Campbell's desert hamster *Phodopus campbelli*. In: Pardiñas et al. (2017), pp. 281.

Shenbrot G.I. (2017c). 3. Stripped desert hamster *Phodopus sungorus*. In: Pardiñas et al. (2017), pp. 281.

Shenbrot G.I. (2017d). 14. Gansu hamster *Cansumys canus*. In: Pardiñas et al. (2017), pp. 285.

Shenbrot G.I. (2017e). 15. Greater long-tailed hamster *Tscherskia triton*. In: Pardiñas et al. (2017), pp. 285–286.

Shenbrot G.I. (2017f). 17. Eversmann's hamster *Allocricetulus eversmanni*. In: Pardiñas et al. (2017), pp. 286.

Shenbrot G.I. (2017g). 16. Mongolian hamster *Allocricetulus curtatus*. In: Pardiñas et al. (2017), pp. 286.

Sheremetyeva I.N., Kartavtseva I.V., Pavlenko M.V., Vasiljeva T.V. & Korablev V.P. (2017). Genetic variability of the peripheral population of the greater long-tailed hamster *Tscherskia triton* (De Winton 1899) in the northeastern part of the distribution range based on sequencing data of the control region of mitochondrial DNA. Biol. Bull. 44 (4): 391–400.

Shevchyk L.O. & Lechachenko S.A. (2020). The European hamster (*Cricetus cricetus*) in Podilia: Description of a new settlement and the finding of a melanistic form. Nov. Theriol. 11: 125–130 [in Ukrainian with Eng. abstract].

Shidlovskiy M.V. (1962). [*Key to Mammals of the Caucasus.*] AN Gruzinskoy SSR, Tbilisi [in Russian].

Shlyakhtin G.V., Il'in V.Yu., Oparin M.L., Belyachenko A.V., Bystrakova N.B., Ermakov O.A., Zav'yalov E.V., Zakharov K.S., Kaybeleva E.I., Koshkin V.A., Kumaeva N.M., Luk'yanov S.B., Mosoleva E.Yu., Oparina O.S., Semikhatova S.N., Smirnov D.G., Sonin K.A., Tabachishin V.G., Timov S.V., Filin'echev A.O., Khucraev S.O. & Yakushev N.N. (2009). *Mammals of the northern Lower-Volga region. Vol. I*. Saratov University Press, Saratov [in Russian with Eng. summary].

Shnitnikov V.N. (1936). [*Mammals of Semirechye*]. AN URSS, Moscow [in Russian].

Shubin I.G. & Alimbaev P.A. (1977). Striped Desert hamster – *Phodopous sungorus* Pallas, 1770. In: Sludskiy (1977a), pp. 457–466 [in Russian].

Shubin I.G. (1977a). [Family hamsters – Cricetidae.] In: Sludskiy (1977a), pp. 454–456 [in Russian].

Shubin I.G. (1977b). [Grey hamster – *Cricetulus migratorius* Pallas (1770).] In: Sludskiy (1977a), pp. 482–491 [in Russian].

Shubin I.G. (1977c). [Genus Common hamsters – *Cricetus* Leske (1779).] In: Sludskiy (1977a): pp. 491–505 [in Russian].

Shubin I.G. (1977d). [Genus Eversmann's hamsters – *Allocricetulus* Argyropulo (1933).] In: Sludskiy (1977a), pp. 505–513 [in Russian].

Sickenberg O. (1971). Über das Vorkommen des Goldhamsters (*Mesocricetus auratus brandti* Nehring, 1898) in Centralanatolien. Säugetierkdl. Mitt. 19: 362–363.

Siddiqi M.S.U. (1969). *Fauna of Pakistan*. Agric. Res. Council, Karachi, Pakistan.

Sidorov G.N., Kassal B.Yu., Frolov K.V. & Goncharova O.V. (2009). [*Furbearers of the Middle Irtysh region (Theriofauna of the Omsk Oblast).*] Nauka, Omsk [in Russian].

Simak S.V. 2009. [Migratory hamster *Cricetulus migratorius* (Pallas, 1773).] In: Azarov D.I. (Ed.): [*Red Book of Samara Oblast. Vol. 2. Rare animal species.*] [Ecological Institute of the Volga Basin RAN], Samara, p. 300 [in Russian].

Simionescu V. (1966). Donnees sur la présence et la propagation de *Cricetulus migratorius* Pall. dans la faune de la Roumanie. Anal. Ştiinţ. Univ. "Al I. Cuza" Iaşi 12 (2/1): 109–113 + 4 plates [in Romanian with French summary].

Simpson G.G. (1945). The principles of classification and a classification of mammals. Bull. Am. Mus. Nat. Hist. 85: i–xbi + 1–350.

Simroth H. (1906). Über den schwarzen Hamster als typische Mutation. Biol. Zentralblatt 26: 334–340.

Skirrow M.H. & Ryšan M. (1976). Observations on the social behaviour of the Chinese hamster, *Cricetulus griseus*. Can. J. Zool. 54: 361–368.

Sludskiy A.A. (Ed.) (1977a). M*ammals of Kazakhstan. Vol. 1, part 2. Rodents (Ex[c]ept the marmots, susliks, longc[l]awded ground squirrels, gerbils and voles*. Nauka, Kazakh SSR, Alma-Ata [in Russian with Eng. abstract].

Sludskiy A.A. (1977b) [Desert hamster – *Phodopus przhewalskii* Vorontzov, Krjukova (1969)]. In: Sludskiy (1977a), pp. 467–474 [in Russian].

Smirnov N.G. & Popov B.V. (1979). [Historical ecological analysis of the secular and geographic variability of the common hamster in the Urals]. Trudy Instit. Ekol. Rastenii i Zhivotnykh (Sverdlovsk) 122: 21–47 [in Russian].

Smith A.T. & Hoffmann R.S. (2008). Subfamily Cricetinae – Hamsters. In: Smith A.T. & Xie Y. (Eds.): *A guide to the mammals of China*. Princeton University Press, Princeton, pp. 239–247.

Snit'ko V.P. (2017). [Siberian hairy-footed hamster *Phodopus sungorus* (Pallas, 1773)]. In: Bol'shakov V.N., Bogdanov V.D., Knyazev M.S. & Lagunov A.V. (Eds.): [*Red book of Chelyabinsk Oblast*]. Ministry of Ecology of Chelyabinsk Oblast, Moscow, p 24. [in Russian].

Sokolov V.E. & Orlov V.N. (1980). [*Key to the mammals of Mongolian People's Republic*]. Nauka, Moscow [In Russian].

Sokolov V.E. & Vasil'eva N.Yu. (1994). Hybridological analysis confirms species independence of *Phodopus sungorus* (Pallas, 1773) and *Phodopus campbelli* (Thomas, 1905). Dokl. Biol. Sci. 332: 327–330.

Soldatović B., Tolksdorf M. & Reichstein H. (1971). The karyotype of the Djungarian dwarf hamster *Phodopus sungorus* Pallas 1773. Arch. Biol. Sci. (Belgrade) 23 (3–4): 121–128.

Song Sh. (1985). A new subspecies of *Cricetulus triton* from Shaanxi, China. Acta Theriol. Sinica 5 (2): 137–139 [in Chinese with Eng. summary].

Sonntag C.F. (1924). The comparative anatomy of the tongues of the Mammalia. X. Rodentia. Proc. Zool. Soc. Lond. 1924: 725–741.

Sowerby A. de C. (1923). *The naturalist in Manchuria. The mammals and birds of Manchuria*. Tientsin Press Ltd., Tientsin (China).

Spitzenberger F. & Bauer K. (2001). Hamster *Cricetus cricetus* (Linnaeus, 1758). In: Spitzenberger F. (Ed.): *Die Säugetierfauna Österreichs*. Bundesministeriums für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Vienna, pp. 406–415.

Spyropoulos B., Ross P.D., Moens P.B. & Camerom D.M. (1982). The synaptonemal complex karyotypes of the Palearctic hamsters, *Phodopus roborovskii* Satunin and *Phodopus sungorus* Pallas. Chromosoma (Berlin) 86: 397–408.

Stadler H. (1920). Tractatus secundus de quadrupedibus, Book 12 (2/1). In: Albertus Magnus, *de animalibus libri XXVI*. [According to the Cologne original. Books XIII–XVI]. Arschendorffschen Verlagsbuchhandlung, Münster, pp. 1355–1429.

Stakheev V.V. (2008). Fauna transformation on rodents of Western Ciscaucasia steppes. Vestnik Juzhnogo Nauchnogo Centra RAN 4 (2): 87–92 [in Russian].

Stefen C. (2013). Variability and differences in the skulls of the common hamster (*Cricetus cricetus*) from several areas in Central Europe and from different time periods. Folia Zool. 62: 155–164.

Steppan S.J. & Schenk J.J. (2017). Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. PLoS ONE 12(8):e0183070. doi.org/10.1371/journal.pone.0183070

Stogov I.I. (1951). [A review of fauna and ecology of mammals along the upper River Tekes.] Trudy Sredne-Aziatskogo nauchno-issledovatel'skogo protivchumnogo instituta 1: 45–59 [in Russian].

Storch G. (1974). Neue Zwerghamster aus dem Holozän von Aserbaidschan, Iran (Rodentia: Cricetinae). Senckenberg. biol. 55: 21–28.

Storch G. (1975). Eine mittelpleistozäne Nager-Fauna von der Insel Chios, Ägäis. Senckenberg. biol. 56: 165–189.

Stroganova A.S. (1954). [Mammals in the steppes and semideserts of Trans-Volga region.] Trudy ZIN 16: 30–116 [in Russian].

Stuart A.J. (1991). Mammalian extinctions in the Late Pleistocene of northern Eurasia and North America. Biol. Rev. 66: 453–562.

Stubbe M. & Chotolchu N. (1968). Zur Säugetiere der Mongolei. Ergebnisse der Mongolisch-Deutschen Biologischen Expeditionen seit 1962, Nr. 30. Mitt. Zool. Mus. Berlin 44 (1): 5–121.

Stubbe M. & Stubbe A. (Eds.) (1998). *Ecology and Protection of the Common Hamster*. Wissenschaftliche Beiträge Martin-Luther-Universität, Halle-Wittenberg.

Sudeikin V.A., Liapunova K.L. & Tikhomirov S.I. (1972). Cases of mass reproduction of *Cricetus cricetus* in Moscow. Zool. Zh. 51 (8): 1258–1259 [in Russian with Eng. abstract].

Sulzer F.G. (1774). Versuch einer Naturgeschichte des Hamsters. Johann Christian Dieterich, Göttingen & Gotha.

Surdacki S. (1983). 0041 *Cricetus cricetus* (Linnaeus, 1758). In: Pucek Z. & Raczyński J. (Eds.): *Atlas of Polish mammals. Maps*. Polish Sci. Publ., Warszawa, p. 85.

Surov A.V. & Feoktisova N.Yu. (2023). *The common hamster*. RAS, Moscow [in Russian with Eng. abstract].

Surov A., Banaszek A., Bogomolov P., Feoktistova N. & Monecke S. (2016). Dramatic global decrease in the range and reproduction rate of the European hamster *Cricetus cricetus*. Endangered Spec. Res. 31: 119–145.

Sutcliffe A.J. & Kowalski K. (1976). Pleistocene rodents of the British Isles. Bull. Brit. Mus. (Nat. Hist.) Geology 27: 31–147.

Sviridenko P.A. 1936. [Rodents of the Northern Caucasus and the Cis-Caucasian steppe]. Byuletin Nauchno-issledovatelnogo instituta zoologii Moskovskogo universiteta 3: 86–89 [in Russian].

Sviridenko P.A. 1940. [Rodents of the Rostov Oblast.] In: [*Nature of the Rostov Oblast*], Rostov-on-Don, pp. 86–89 [in Russian].

Tatarinov K.A. (1973). *Fauna of vertebrates of the western Ukraine: ecology, significance, preservation*. Izd-vo L'vovskogo un-ta, L'vov [in Ukrainian with Eng. title page].

Tate G.H. (1947). *Mammals of Eastern Asia*. Macmillan Comp., New York.

Tchernov E. (1975). Rodent faunas and environmental changes in the Pleistocene of Israel. In: Prakash I. & Ghosh P.K. (Eds.): *Rodents in desert environments*. Dr. W. Junk, The Hague, pp. 331–361.

Tembotov A.K. (1960). [*Mammals of Kabardino-Balkariya ASSR*]. Kabardino-Balkariya Book Publishing, Nal'chik [In Russian].

Tembotov A.K. (1965). [Key to *mammals of Northern Caucasus*]. Kabardino-Balkariya Dept. All-Russian Soc. Conservation Nat., Nal'chik [In Russian].

Tembotov A.K. (1972). [*Geography of mammals in the Northern Caucasus*.] El'brus, Nal'chik [In Russian].

Tembotova F.A. (2015). [*Mammals of the Caucasus and adjacent seas. A key*.] KMK, Moscow [In Russian].

Thomas O. (1888). On a new and interesting annectant genus of the Muridae with remarks on the relation of the Old- and New-World members of the family. Proc. Zool. Soc. Lond. 1888: 130–135.

Thomas O. (1905) A new *Cricetulus* from Mongolia. Ann. Mag. Nat. Hist. 7, 15 (87): 322–323.

Thomas O. (1907). The Duke of Bedford's zoological exploration in Eastern Asia. – Second list of mammals from Korea. Proc. Zool. Soc. Lond. 1907: 462–466.

Thomas O. (1908a). [On mammals collected in the Provinces of Shan-si and Shen-si, Northern China, by Mr. M. P. Anderson, for the Duke of Bedford's zoological exploration of eastern Asia]. Proc. Zool. Soc. Lond. [Abstracts 15 Dec] 63: 44–45.

Thomas O. (1908b) The Duke of Bedford's Zoological Exploration in Eastern Asia. - VI. List of mammals from the Shangtung Peninsula, Northern China. Proc. Zool. Soc. Lond. 1908: 5–10.

Thomas O. (1908c) The Duke of Bedford's Zoological Exploration in Eastern Asia. - X. List of mammals from the Provinces of Chih-li and Shan-si, N. China. Proc. Zool. Soc. Lond. 1908: 635–646.

Thomas O. (1908d). The Duke of Bedford's zoological exploration in eastern Asia. – XI. On mammals from the provinces of Shan-si and Shen-si, northern China. Proc. Zool. Soc. Lond. 1908: 963–983.

Thomas O. (1908e). The Duke of Bedford's Zoological Exploration in Eastern Asia. - IX. List of mammals from the Mongolian Plateau. Proc. Zool. Soc. Lond. 1908: 104–110.

Thomas O. (1909). A collection of mammals from northern and central Mantchuria. Ann. Mag. Nat. Hist. 8 (4): 500–503.

Thomas O. (1911). The mammals of the tenth edition of Linnaeus; an exempt to fix the types of the genera and the exact bases and localities of the species. Proc. Zool. Soc. Lond. 1911: 143–149.

Thomas O. (1917). On the small hamsters that have been referred to *Cricetulus phaeus* and *campbelli*. Ann. Mag. Nat. Hist. 8, 19 (114): 452–456.

Thomas E. (1963). Melanistische hamster, *Cricetus cricetus* L., Rheinhessen. Z. Säugetierkunde 28: 43–47.

Thomas O. & Hinton M.A.C. (1922). Mount Everest expedition. Ann. Mag. Nat. Hist. 9, 9: 178–186.

Tikhomirov A.A. & Korchagin A.N. (1889). [List and description of objects in the Zoological Museum of the Imperial Moscow University. Part 4. List and description of mammal collection in the Museum. No.1]. Izvestya Imperatorskago obschestva ljubiteley estestvoznaniya, antropologii i etnografii 56 (4): 1–31 [In Russian].

Tobias P.V. 1953. Trends in the evolution of mammalian chromosomes. S. Afr. J. Sci. 50: 134–140.

Todd N.B., Nixon C.W., Mulvaney D.A. & Conelly M.E. (1972). Karyotypes of *Mesocricetus brandti* and hybridization within the genus. J. Hered. 63: 73–77.

Tohmé G. & Tohmé H. (1985). *Les mammifères suavages du Lebanon*. Univ. Libanaise, Sec. Sci. Nat., Beyrouth.

Toktosunov A. (1958). [*Rodents of Kyrgysia*.] AN Kyrg SSR, Frunze [Bishkek] [in Russian].

Tokuda M. (1941). A revised monograph of the Japanese and Manchouk-Korean Muridae. Biogeographica 4: 1–155 + 9 plates.

Topachevskiy V.A. & Skorik A.F. 1992. [*Pliocene and Pleistocene lower hamsters of South-Eastern Europe*]. Naukova Dumka, Kiev [in Russian].

Topsel [Topsell] E. (1658). *The history of four-footed beasts and serpents*. Sawbridge, London.

Trapp M. (1979). Die Haarstruktur einiger Muriden und Cricetiden. Z. Säugetierkunde 45: 337–348.

Trouessart E.-L. (1897). *Catalogus mammalium tam viventium quam fossilium. Nove edition (Prima complete). Fasciculus III. Rodentia II. (Myomorpha, Hystricomorpha, Lagomorpha.).* R. Friedländer & Sohn, Berolini [Berlin].

Trouessart E.-L. (1904). *Catalogus mammalium tam viventium quam fossilium. Quinquennale Supplementum Anno 1904*. R. Friedländer & Sohn, Berolini [Berlin].

Trouessart E.-L. (1910). *Conspectus mammalium Europae. Faune des Mammifères d'Europe*. R. Friedländer & Sohn, Berlin.

Tsapko N.V., Achibokov U.M., Korzhov P.N. & Vetoshkin A.A. (2022). Fauna and distribution of mammals of the Stavropol region. Nauki o zemle 4: 53–96 [in Russian with Eng. summary].

Tsuchiya K. & Won P.H. (1976). Karyotype of *Cricetulus triton nestor* (Rodentia, Cricetidae). J. Mamm. Soc. Jap. 6 (5–6): 218–223 [in Japanese with Eng. abstract].

Tullberg T. (1899). *Ueber das System der Nagethiere. Eine Phylogenetische Studie*. Königl. Gesellschaft der Wissenschaften zu Upsala, Upsala.

Turnbull P.F. (1975). Prehistoric rodents of the Middle East. In: Prakash I. & Ghosh P.K. (Eds.): *Rodents in desert environments*. Dr. W. Junk, The Hague, pp. 363–378.

Vakhrushev A.V. & Sidorov G.N. (2011). [New records of the common Eversmann's hamster along the Irtysh near Omsk]. In: [*Teriofauna of Russia and adjacent territories. International Meeting. 9th Congress of Theriological Society at RAS, 1–4 February 2011*]. Tovarischestvo nauchnich izdaniy KMK, Moskva, p. 93 [in Russian].

Vakurin A.A., Kartavtseva I.V., Korablev V.P. & Pavlenko M.V. (2014). Features of cytogenetic differentiation of hamsters *Cricetulus barabensis* and *Cricetulus pseudogriseus* (Rodentia, Cricetidae). Zool. Zh. 93: 877–886.

Vasileiadou K. & Sylvestrou I. (2022). The fossil records of rodents (Mammalia: Rodentia) in Greece. In Vlachos E. (Ed.): *Fossil vertebrates of Greece. Vol. 1. Basal vertebrates, amphibians, reptiles, afrotherians, Glires and primates*. Springer, Cham (Switzerland), pp. 407–610.

Vasilenko N.F., Prislegina D.A., Tsapko N.V., Volynkina A.S., Semenko O.V., Ashibokov U.M., Tokhov Yu.M., Maletskaya O.V. & Kulichenko A.N. (2021). The current state of the vertebrate animal populations and their role in the persistence of natural zoonoses foci in the Stavropol territory. Problems of Particularly Dangerous Infections 4: 54–61 [in Russian with Eng. summary].

Vereshchagin N.K. (1959). *The Mammals of the Caucasus. A History of the Evolution of the Fauna*. AN USSR, Leningrad [St. Petersburg] [in Russian; translated into English in 1967 and published by the Israel Program for Scientific Translations, Jerusalem].

Veselovský Z. & Grundová S. (1965). Beitrag zur Kenntnis des Dsungarischen Hamsters, *Phodopus sungorus* (Pallas, 1773). Z. Säugetierkunde 80: 305 –311.

Viktorov L.V. & Istomin A.V. (2002). [Mammals – Mammalia.] In: Sorokin A.S. (Ed.): [*Red Book of Tver' Oblast.*] [Ministry for Natural Resources], Tver', p. 153–161 [in Russian].

Vinogradov B.S. (1927). Small mammals from Minussinsk district and Urjankhai. Jahrbuch des Martjanov'schen Staatsmuseums in Minussinsk 5 (1): 33–50 [in Russian with Eng. title].

Vinogradov B.S. (1931). Mammalia. In: Lindgol'm V.A. (Ed.): *Pamir-Expedition 1928. Abhandlungen der Expedition, Lieferung VIII, Zoologie*. AN SSSR, Leningrad, pp. 1–22 [in Russian with German summary].

Vinogradov B.S. (1933). *Tableaux analytiques de la faune de l'URSS […]. Les mammifères de l'URSS. Les rongeurs*. AN USSR, Leningrad [St. Petersburg].

Vinogradov B.S. (1935). [Order Rodentia – Rodents.] In: Vinogradov B.S., Pavlovsky E.N. & Flerov K.K. (Eds.): [*Mammals of Tajikistan, their life and impact on man.*] AN SSSR, Moscow, pp. 201–255 [in Russian].

Vinogradov B.S. & Argyropulo A.I. (1941). *Faune de l'URSS. Mammifères. Tableaux analytique des rongeurs*. AS URSS, Moscow [Eng. translation of Russian original published in 1968 as *Fauna of the U.S.S.R. Mammals. Key to rodents*.' Israel Program for Scientific Translations, Jerusalem].

Vinogradov B.S. & Gromov I.M. (1952). [*Rodents in the fauna of the USSR*]. AN USSR, Moscow [In Russian].

Vinogradov B.S. & Gromov I.M. (1956). [*A short key to the rodent fauna of the USSR*]. AN USSR, Moscow [In Russian].

Vinogradov B.S. & Gromov I.M. (1984). [*A short key to the rodent fauna of the USSR*]. AN USSR, Leningrad [St. Petersburg] [In Russian].

Vinogradov B.S., Argyropulo A.I. & Geptner [Heptner] V.G. (1936). *Rodents of Central Asia*. Izdatel'stvo AN SSSR, Moscow [in Russian with title page in Eng.].

Vistorin G., Gamperl R. & Rosenkranz W. (1976). Analysis of mitotic and meiotic chromosomes in the European hamster, *Cricetus cricetus* (L.). Z. Säugetierkunde 41 (6): 342–348.

Volf J. & Volf P. (1993). Breeding of the migratory hamster, *Cricetulus migratorius* (Pallas, 1770) under laboratory conditions. Gazella 20: 102–108.

Vorontsov N.N. (1957). The structure of the stomach and the relative development of the different segments of the intestine in Cricetinae Rodentia, Mammalia from the Palaearctic region and the New World. C.R. Acad. Sci. URSS 117: 524–529.

Vorontsov N.N. (1958). The structure of the tongue of Palaearctic hamsters (Cricetinae). Trudy ZIN AN SSSR 25: 321–335 [in Russian with Eng. title].

Vorontsov N.N. (1960). [Species and genera of Palaearctic hamsters *in statu nascendi*]. Dokl. AN SSSR 132 (6): 1450–1451 [in Russian].

Vorontsov N.N. (1962). The ways of food specialization and evolution of the alimentary system in Muroidea. In: Kratochvíl J. & Pelikán J. (Eds.): *Symposium Theriologicum*. CS Acad. Sci., Prague, pp. 360–377.

Vorontsov N.N. (1967). *Evolution of the alimentary system [of] myomorph rodents*. Nauka, Siberian branch, Novosibirsk [in Russian with Eng. front page].

Vorontsov N.N. (Ed.) (1969). *The Mammals. Evolution, Karyology, Taxonomy, Fauna*. AN USSR, Novosibirsk.

Vorontsov N.N. (1982). [*Primitive cricetids (Cricetidae) of teh World fauna. Part I. Morphology and ecology. Fauna of the USSR, N.S. No. 125, Mammals III/6*] Nauka, Leningrad [= Sant Petersburg] [in Russian].

Vorontsov N.N. & Gurtovoi N.N. (1959). Structure of the midabdominal gland of the true hamster (Cricetini, Cricetinae, Rodentia, Mammalia). Doklady, Biol. Sci. Sects. Akad. Nauk, SSSR, 125: 385–388 [in Russian with Eng. title].

Vorontsov N.N. & Krjukova E.P. (1969a). Chromosomes and taxonomical position of the hamsters (genus *Allocricetulus*) from Zaissan Basin, with description of a new natio. In: Vorontsov N.N. (1969), pp. 98–100 [in Russian with Eng. title].

Vorontsov N.N. & Krjukova E.P. (1969b). *Phodopus przhewalskii* species nova, a new species of desert hamsters (Cricetinae, Cricetidae, Rodentia) from the Zaissan Basin. In: Vorontsov N.N. (1969), pp. 102–104 (in Russian with Eng. Title).

Vorontsov N.N. & Krjukova E.P. (1969c). The karyotypical differentiation of *Mesocricetus raddei* and taxonomical relationships of members of the genus *Mesocricetus*. In: Vorontsov N.N. (1969), pp. 107–109 [in Russian].

Vorontsov N.N. & Radjabli S.I. (1969). Chromosomes and specific independence of Primorye ratlike hamster *Tscherskia albipes* Ognev (Rodentia, Cricetinae). In: Vorontsov N.N. (1969), pp. 96–97 [in Russian with Eng. title].

Vorontzov [Vorontsov] N.N. (1958). Importance de l'etude des composition chromosomes pour la systématique des mammifères. Trans. Moscow Soc. nat. 63 (2): 5–36 [in Russian with French title].

Vorontzov [Vorontsov] N.N. (1959a). The system of hamster (Cricetinae) in the sphere of the World fauna and their phylogenetic relations. Trans. Moscow Soc. nat. 64 (5): 134–137 [in Russian with Eng. title].

Vorontzov [Vorontsov] N.N. (1959b). The geographical distribution of hamsters (Cricetinae) and some problems concerned with the zoogeography of New World. Trans. Moscow Soc. nat. 64 (5): 137–139 [in Russian with Eng. title].

Vrtiš V. (1932). The cutaneous umbilical glandular organ of the hamster *Cricetus cricetus* (L). Publ. Biol. l'Ecole des Hautes Etudes Veterin. Brno 11 (13): 199–214 [in Czech with Eng. summary].

Wagner A. (1848). Beschreibung einiger kleine Säugethiere aus Syrien und Afrika. Arch. Naturgesch. 14 (1): 180–187.

Wahlert J. (1984). Relations of the extinct rodent *Cricetops* to *Lophiomys* and the Cricetinae (Rodentia, Cricetidae). Am. Mus. Nov. 2784: 1–15.

Walton H.J. (1905). Appendix A. Notes on the natural history of southern Tibet. In: Landon P. (Ed.): *The opening of Tibet*. Doubleday, Page & Co., New York, pp. 419–432.

Wang F.-g. (1980). Subspecific classification of the black stripe hamsters (*Cricetulus barabensis*) in China, with description of a new subspecies. Acta zootax. sin. 5: 315–319 [in Chinese with Eng. summary].

Wang Y. (2003). *A complete checklist of mammal species and subspecies in China. A taxonomic and geographic reference*. China Forestry Publ. House, Beijing.

Wang S., Cheng C.-L. (1973). Notes on Chinese hamsters (Cricetinae). Acta zool. Sinica 19 (1): 61–68 [in Chinese with Eng. summary].

Wang J., Zhao X., Deng Y., Qi H., Liu Y., Zhang Z., Koh H.S. & Shan X. (1999). Karyotypes and B chromosomes of greater long-tailed hamster (*Cricetulus triton*). Acta Theriol. Sin. 19 (3): 197–203.

Wang Y., Wang C., Cheng Z., Miao J., Xue X. et al. (2024). Genomic-transcriptomic analysis reveals Syrian hamster as a superior human disease animal model. BMC Genomics (under revision); accessed on August 23, 2024.

Waterhouse [G.R.] (1837). Characters of new species of the genus *Mus*, from the collection of Mr. Darwin. Proc. Zool. Soc. 1837: 15–21.

Waterhouse G.R. (1839a). Description of a new species of hamster (*Cricetus auratus*). Proc. Zool. Soc. Lond. 1839 (7): 57–58.

Waterhouse G.R. (1839b). Observations on the Rodentia, with a view to point out the groups as indicated by the structure of the crania, in this order of mammals. Mag. Nat. Hist. 1839: 274–279.

Weiner J. & Heldmeir G. (1987). Metabolism and thermoregulation in two races of Djunagrian hamsters: *Phodopus sungorus sungorus* and *P. s. campbelli*. Comp. Biochem. Physiol. 86A (4): 639–642.

Weissenborn Dr. (1839). On the natural history of the German marmot (hamster). Mag. Nat. Hist. ser. 2, 3: 473–483, 533–536, 577–584.

Wepner A. (1934). Was ist *Cricetus babylonicus* Nehring? Z. Säugetierkunde 9: 437–438.

Wepner A. (1936). Zur Frage der subspezifischen Abtrennung des Westhamsters. Z. Säugetierkunde 11: 254–256.

Werth E. (1934). Der gegenwärtige Stand der Hamsterfrage in Deutschland. Arb. Biol. Reuichs. F. Land-orstwirtschaft 21 (2): 201–253.

White M.J.D. (1959). Speciation in animals. Austr. J. Sci. 22: 32–39.

Wineski, L. E. (2009). Movements of the cranial vibrissae in the Golden hamster (*Mesocricetus auratus*). J. Zool. Lond. 200 (2): 261–280.

Winge H. (1887). [*Extant terrestrial rodents (Rodentia) from Lagos Santa, Minas Geraes, Brasilia] with a note on relationships among rodent genera*]. E. Museo Lundii, Copenhagen [in Danish].

Winton de W.E. (1899). On Chinese mammals, principally from Western Sechuen. Proc. Zool. Soc. Lond. 1899: 572–578 + 2 Plates.

Witte G.R. (1971). Jungentransport in den Backentaschen beim Syrischen Goldhamster (*Mesocricetus auratus* Waterhouse, 1839). Z. Säugetierkunde 36: 216—219.

Won P.-O. (1961). Studies of the avi-mammalian fauna of Korea from the viewpoint of the forestry protection. In: *Avi-Mammalian fauna of Korea*. Suwon, Korea, Pp. 31–139.

Won H. K. (1968). [*Animals of Korea*]. Academy of Sciences, Pyongyang [In Korean].

Wu X-D. & Fu H-P. (2005). Rodent communities in desert and semi-desert regions in Inner Mongolia. Acta Zool. Sinica 51 (6): 961–972 [in Chinese with Eng. abstract].

Wu X., Fu H., Yuan S., Gao Q. & Yue X. (2015). Study on the classification and diversity of zonal rodent community in semi-desert and desert areas of China. Open J. Ecol. 5: 39–54.

Wynne-Edwards K.E. (1995). Biparental care in Djungarian but not Siberian dwarf hamsters (*Phodopus*). Anim. Behav. 50: 1571–1585.

Wynne-Edwards K.E. & Lisk R.D. (1987). Behavioral interactions differentiate Djungarian (*Phodopus campbelli*) and Siberian (*Phodopus sungorus*) hamsters. Can. J. Zool. 65: 2229–2235.

Wynne-Edwards K.E., Surov A.V. & Telitzina A.Y. (1992). Field studies of chemical signalling: direct observations of dwarf hamsters (*Phodopus*) in Soviet Asia. In: Doty R.L. & Muller-Schwarze D. (Eds.): *Chemical Signals in Vertebrates VI*. Plenum Press, New York, pp. 485–491.

Wynne-Edwards K.E., Surov A.V. & Telitzina A.Y. (1999). Differences in endogenous activity within the genus *Phodopus*. J. Mammal. 80: 855–865.

Xie J. & Zhang Z. (2005a). Genetic variations of the greater long-tailed hamster among several local populations in North China. Acta Theriol. Sin. 26 (1): 64–67 [in Chinese with Eng. abstract].

Xie J. & Zhang Z. (2005b). Mitochondrial DNA phylogeography of populations of *Cricetulus triton* in the North China Plain. J. Mammalogy 86 (4): 833–840.

Xu R. (2016). [*Fauna of Inner Mongolia, Vol. 5. Mammals (Rodentia and Lagomorpha)*.] [in Chinese].

Yakovlev M.G. & Kolesnikov I.M. (1954). [Some new data on distribution and ecology of the Ciscaucasian golden hamster in Rostov Oblast.] Zool. Zh. 33 (3): 693–700 [in Russian].

Yang L., Chen X., Zhao X., Wang J. (2003). Karyotype and classification status of *Cansumys canus* (Cricetidea, Rodentia). Acta Theriol. Sinica 23 (3): 235–238.

Yerganian G. (1972). History and cytogenetics of hamsters. Progr. exp. Tumor Res. 16: 2–41.

Yerganian G. & Papoyan S. (1965). Isomorphic sex chromosomes, autosomal heteromorphism, and telomeric associations in the grey hamster of Armenia, *Cricetulus migratorius*, Pall. Hereditas 52 (3): 307–319.

Yiğit N., Çolak E., Sözen M., Özkurt Ş. & Verimli R. (2000). The distribution, morphology, and karyology of the genus *Mesocricetus* (Mammalia: Rodentia) in Turkey. Folia Zool. 49: 167–174.

Yiğit N., Çolak E., Sözen M. & Özkurt Ş. (2003). A study on the geographical distribution along with habitat aspects of rodent species in Turkey. Bonn. zool. Beitr. 50: 355–368.

Yiğit N., Çolak E., Gattermann R., Neumann K., Özkurt Ş., Gharkheloo M.M., Fritzsche P. & Çolak R. (2006a). Morphological and biometrical comparisons of *Mesocricetus* Nehring, 1898 (Mammalia: Rodentia) species distributed in the Palaearctic Region. Turk. J. Zool. 30: 291–299.

Yiğit N., Gharkheloo M.M., Çolak E., Özkurt Ş., Bulut Ş., Kankılıç T. & Çolak R. (2006b). The karyotypes of some rodent species (Mammalia: Rodentia) from eastern Turkey and northern Iran with a new record, *Microtus schidlovskii* Argyropulo, 1933, from eastern Turkey. Turk. J. Zool. 30: 459–464.

Yudin B.S., Galkina L.I. & Potapkina A.F. (1979). [*Mammals of the Altai-Sayan mountains*]. Nauka, Novosibirsk [In Russian].

Yusefi G.H., Faizolahi K., Darvish J., Kamran S. & Brito J.C. (2019). The species diversity, distribution and conservation status of the terrestrial mammals of Iran. J. Mammal. 100 (1): 55–71 + Suppl. info.

Zdansky O. (1928). Die Säugetiere der Quartärfauna von Chou-K'ou-Tien. Palaeontol. Sinica, C, 5 (4): 1–146.

Zhang X. & Yu Y. (1995). Study on the fauna and the zoogeographical division of mammals in Ningxia. Acta Theriol. Sin. 15 (2): 128–136 [in Chiense with Eng. summary].

Zhang Y.Z., Jin S.K., Quan G.Q., Li S.H., Ye Z.Y., Wang F.G. & Zhang M.L. (1997). *Distribution of Mammalian Species in China*. China Forestry Publ. House, Beijing.

Zheng S. (1984). A revision of the fossil cricetines (Rodentia, Mammalia) from Zhoukoudian, the Peking Man site. Vert. PalAsiat. 22: 179–197.

Zheng C.-l. (1986). Cricetidae. In Feng Z.-j., Cai G.-q. & Zheng C.-l. (Eds.) *The mammals of Tibet. The comprehensive scientific expedition to the Qinghai-Xizan Plateau*. Science Press, Beijing, pp. 368–396 [in Chinese with Eng. abstract].

Zil'fyan V.N., Fichidzhyan B.S., Saakyan M.S. & Kumkumadzhyan V. A. (1969). [On a systematic position of the Transcaucasian and the golden hamsters (*Mesocricetus*; Mammalia; Rodentia).] Biol. Zh. Armenii 22 (7): 98–101 [in Russian with Armenian summary].

Zima J. & Král B. (1984). Karyotypes of European mammals II. Acta Sc. Nat. Brno 18 (8): 1–62.

Zimmermann E.A.W. von (1777). *Specimen Zoologiae Geographicae, Quadrupedum domicilia et migrationis sistens. Dedit, tabulamque mundi zoographicam adjunxit*. Lugduni Batavorum, apud Theodorum Haak et socios, Leiden, The Netherlands.

Zimmermann K. (1964). Zur Säugetier-Fauna Chinas. Mitt. Zool. Mus. Berlin 40 (2): 87-140.

Zimmermann W. (1969). Die gegenwärtige Verbreitung melanistischer Hamster (*Cricetus c. cricetus* L.) in Thüringen und Bemerkungen zu deren Morphologie. Hercynia N.F. 6: 80–89.

Zimmermann W. & Handike K. (1968). Atypischer melanismus beim Gemainen Hamster *Cricetus c. cricetus* L. im Nördlichen Harzvorland und in der Magdeburger Börde. Hercynia 5 (1): 1–6.

Zlatanov S. (1961). Beobachtung der wanderungen einiger Feldmausarten in Aghängigkeit von der Grundelementen des Landwirtschaftlichen Betriebstyps in der Dobrudzha und verbesserung der entsprechenden Bekämpfungmassnahmen. Izv. Dobr. Selskostop. Inst. Tolbukhin 1: 151–165 [in Bulgarian with Russian and German summaries].

Zolotarev N.T. (1936). Mammals of the Iman River Basin (Ussuri Land). Acad. Sci. Press, Moscow [in Russian with Eng. title page].

Zoltán B. (2007). [Common hamster *Cricetus cricetus* (Linnaeus, 1758)]. In: Zoltán B., Csorba G. & Miklós H. (Eds.) [*Atlas of Hungarian mammals*.] Kossuth Kiadó, Budapest, pp. 176–178 [in Hungarian].

Zykov A.E. (1991). [*Systematic-faunsitic and zoogeographical analysis of small mammals (Insectivora, Rodentia, Lagomorpha) of Kopet Dag*]. Ph.D. Thesis, Kiev, AN USSR, Institut zoologii im. I. I. Shmal'gauzena, 295 pp. [in Russian].

Index to the technical names

Each species group name is entered only once, under the genus in which it is recognized in this book. Names of extant Palaearctic arvicolines printed in bold face are those which are given full status. Family group names are in small capitals. Bold face figures refer to the pages of the detailed description.

True Hamsters (Cricetinae) of the Palaearctic Region

Boris Kryštufek,[1,2] Georgy Isidorovich Shenbrot[3]

[1] Slovenian Museum of Natural History, Vertebrate Department, Ljubljana, Slovenia
bkrystufek@pms-lj.si
[2] Science and Research Centre Koper, Mediterranean Institute for Environmental Studies,
Koper, Slovenia
boris.krystufek@zrs-kp.si
[3] Ben-Gurion University of the Negev, Jacob Blaustein Institutes for Desert Research, Mitrani Department of Desert Ecology,
Beer-Sheva, Israel
shenbrot@bgu.ac.il

True hamsters are a small subfamily (Cricetinae) containing only 19 species which are endemic to the Palaearctic region. Despite such low species richness, general public is well familiar with hamsters, primarily knowing them as pets, experimental laboratory animals and species of conservation concern. The present work is a compilation integrating achievements of the genomic era with the traditional taxonomy. The aim was to provide an authoritative and up-to-date taxonomic guide to the animal group, which is of great interest to experts engaged in medical zoology, epidemiology, biostratigraphy, zooarchaeology, evolutionary research, population ecology, animal systematics, biodiversity conservation, museum collection management and many more biological subdisciplines. The most significant original contribution is perhaps revision of the family-group taxa with naming 2 new subtribes and 2 new tribes. The text is supplemented by 120 illustrations and over 700 references. Morphological details of skull and dentition of each of the 19 species are depicted, and their distributions are mapped in detail. The book will allow the user to interpret intelligently the taxonomic system of Cricetinae and to follow taxonomic progress with a critical eye.

University of Maribor Press

I foretell for this book to be used as standard text for true hamsters in decades to follow.

Professor Dr. **Ivan Horáček**
Charles University, Prague, Czechia

A welcome update of the most recent review of rodents in the *Handbook of the Mammals of the World* (2017)

Dr. **Jan Decher**, Curator
Leibniz-Institute for the Analysis of Biodiversity Change, Bonn, Germany

University of Maribor

Faculty of Natural Sciences
and Mathematics