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Taxonomic revision of the Palaearctic rodents (Rodentia). Part 2. Sciuridae: *Urocitellus*, *Marmota* and *Sciurotamias*

Taxonomická revise palearktických hlodavců (Rodentia). Část 2.
Sciuridae: *Urocitellus*, *Marmota* a *Sciurotamias*

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Abstract. A revision of family group names for squirrels (Rodentia: Sciuridae) uncovered a neglected name Arctomyinae Gray, 1821 which predates Marmotinae Pocock, 1923. We propose a new subtribe Ammospermophilina, to encompass the Nearctic *Ammospermophilus* and *Notocitellus* and holds a basal position in a lineage of ground squirrels and marmots. Furthermore, we reviewed the Palaearctic Arctomyinae from the genera *Urocitellus*, *Marmota* and *Sciurotamias*. On the basis of published data and our own examination of 926 museum specimens we recognize 12 species and 15 subspecies: *Urocitellus undulatus* (two subspecies: *undulatus* and *eversmanni*), *U. parryii* (the only Palaearctic subspecies is *leucosticus*), *Marmota marmota* (*marmota* and *latirostris*), *M. bobak*, *M. baibacina*, *M. kastschenkoi*, *M. sibirica*, *M. himalayana*, *M. camtschatica* (*camtschatica*, *bungei*, *doppelmayeri*), *M. caudata* (*caudata*, *aurea*, *dichrous*), *M. menzbieri* (*menzbieri* and *zachidovi*), and *Sciurotamias davidianus* (*davidianus* and *consobrinus*). All species names (69 in total) are reviewed and linked to senior synonyms. We showed that *Arctomys marmota tigrina* Bechstein, 1801 is a junior synonym of *M. bobak* and not of *M. marmota*. Descriptions are provided for valid taxa, together with photographs of skins or living animals, and drawings of skulls. Geographic ranges are mapped for all species and subspecies.

Key words. Species delimitation, taxonomic characters, geographic distribution, identification keys, zoological nomenclature, Ammospermophilina new subtribe.

INTRODUCTION

With a revision of the Palaearctic *Urocitellus*, *Marmota* and *Sciurotamias*, we continue our compilation of the Palaearctic rodents, initiated in the previous year (Kryštufek & Vohralík 2012). The geographic setting and taxonomic scope remain as defined in this publication.

MATERIAL AND METHODS

This paper is a compilation based on a study of literature, examination of museum material and our own research of the Palaearctic rodents. We studied museum vouchers for character states, dimensions and colouration; 926 museum specimens representing all 12 species recognized subsequently, were examined in 15 collections. These collections are listed subsequently (abc):

BMNH – Natural History Museum, London (formerly British Museum Natural History), UK;
DZCU – Department of Zoology, Charles University, Prague, Czech Republic;
IVB – Institute of Vertebrate Biology, Academy of Sciences of the CR, Brno, Czech Republic;
LBT – Laboratory for Biomonitoring, Academy of Sciencies of Tatarstan Republic, Kazan, Russia;
MNM – Hungarian Natural History Museum, Budapest, Hungary;
NMP – National Museum, Prague, Czech Republic;
NMW – Natural History Museum, Vienna, Austria;
PMBg – Natural History Museum Belgrade, Belgrade, Serbia;
PMS – Natural History Museum of Slovenia, Ljubljana, Slovenia;
SMF – Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt am Main, Germany;
SMG – Senckenberg Museum für Naturkunde Görlitz, Germany;
SZM – Siberian Zoological Museum, Institute for Systematics and Ecology of Animals, Russian Academy of Sciences, Siberian Branch, Novosibirsk, Russia;
ZFMK – Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany;
ZMB – Zoologisches Museum, Humboldt Universität, Berlin, Germany;
ZSM – Zoologische Staatssammlung München, Munich, Germany.

Thanks to the courtesy of Jan Matějů we had at disposal measurements and photographs of ground squirrels' vouchers which he gathered in the collections of the National Museum of Natural History, Washington D. C., USA (NMNH), American Museum of Natural History, New York, USA (AMNH), and Zoological Institute of the Academy of Sciences in Sankt-Peterburg, Russia (ZISP).

The following morphometric variables are used throughout the text: HbL – length of head and body; TL – length of tail; HF – length of hind foot; E – length of ear; W – weight (body mass); CbL – condylobasal length of skull, ZgB – breadth across zygomatic arches, MxT – length of maxillary tooth-row (alveolar); occasionally we refer also to PL – profile (or greatest) length of the skull. We should like to remind the reader that metric data of adult animals are given as descriptive statistics (mean with a range parenthesized); sample sizes are indicated by numbers in subscript to character abbreviations. Types of teeth are designated by letters; capitals indicate the maxillary teeth and lower-case letters the mandibular teeth; the position in the tooth-row (anterior → posterior) is indicated by the relevant number; e.g.: M1 and m3 denote the first upper and the third lower molar, respectively. Abbreviations are as follows: I/i – upper/lower incisors; P/p – upper/lower premolars; M/m – upper/lower molars.

TAXONOMY OF SCIURIDAE

Family: Sciuridae Fischer, 1817

In a recent compilation of squirrels Thorington et al. (2012) continue to credit Fisher de Waldheim for the family name Sciuridae. As shown by Hutterer (2003), Fisher attained his noble title after the publication of 1817 paper (Fischer 1817) therefore the quotation in Thorington et al. (l. c.) is not correct.

Phylogenetic reconstruction inferred from a molecular supermatrix (Fabre et al. 2012) chellanges the established taxonomic division of the family and forces a revision of several groups of squirrels. Modifications and adjustments are addressed subsequently (Fig. 1).

1. Subfamily: Ratufinae Moore, 1959

Giant squirrels are basal in the family Sciuridae; the subfamily contains a single Oriental genus *Ratufa* with 4 species. The group name was proposed as a tribe Ratufini, but changed to a subfamily by Steppan et al. (2004). In compliance with the Principle of Coordination (Article 36.1

of the International Code for Zoological Nomenclature the authority for the name Ratufinae is Moore (1959).

2. Subfamily: Sciurillinae Moore, 1959

Contains a single monotypical genus from the Neotropics. Proposed as a tribe Sciurillini, changed to a subfamily by Steppan et al. (2004). In compliance with the Principle of Coordination (Article 36.1 of the International Code for Zoological Nomenclature) the authority for the name Sciurillinae is Moore (1959).

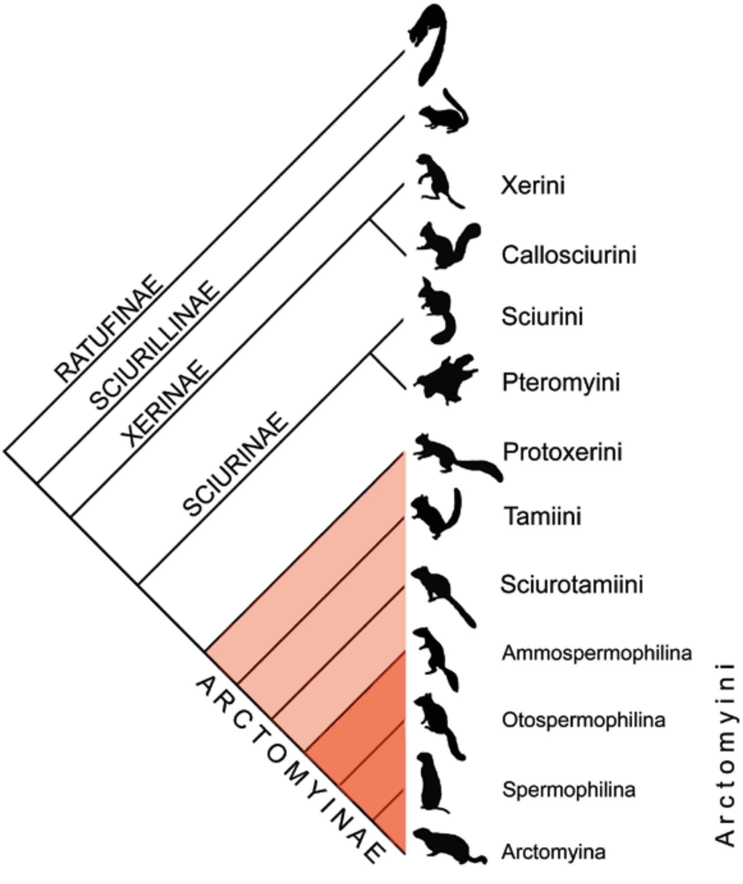

Fig. 1. Taxonomic relations and hierarchy of subfamilies (capitalized), tribes and subtribes (lower case letters) in the squirrel family Sciuridae. The radiation of Arctomyinae is highlighted red. Based primarily on Fabre et al. (2012).
Obr. 1. Taxonomické vztahy a hierarchie podčeledí (velké písmo), tribů a subtribů (malé písmo) v čeledi veverkovitých (Sciuridae). Radiace podč. Arctomyinae je zvýrazněna červeně. Založeno především na práci Fabre et al. (2012).

3. Subfamily: Xerinae Murray, 1866

Xerinae (or Xerini) were earlier defined to include African genera *Xerus* and *Atlantoxerus*, and the Asiatic *Spermophilopsis* (Osborn 1910, Pocock 1923, Moore 1959). Steppan et al. (2004) redefined the scope of Xerinae to include genera which are here in Xerini and in Arctomyinae. By including Callosciurini into Xerinae we follow Fabre et al. (2012).

3.1. Tribe: Xerini Murray, 1866

The tribe contains *Xerus*, *Atlantoxerus* and *Spermophilopsis*. In the results by Fabre et al. (2012) *Xerus* is paraphyletic with respect to *Atlantoxerus*.

3.2. Tribe: Callosciurini Simpson, 1945

The scope is identical to the content of the subfamily Callosciurinae (with Callosciurini and Funambulini) of Steppan et al. (2004). The tribe contains 14 Oriental genera of which only *Funambulus* and *Tamiops* are marginally Palaearctic.

4. Subfamily: Sciurinae Fischer, 1817

Rank and scope are identical to those in Thorington & Hoffmann (2005).

4.1. Tribe: Sciurini Fischer, 1817

The tribe contains 5 genera, of which only *Sciurus* is Palaearctic (with 3 species of a total 28).

4.2. Tribe: Pteromyini Brandt, 1855

Ranked in Hoffman et al. (1993) as a subfamily Petauristinae Miller, 1912; Miller (1912: 940) proposed this as a family name Petauristidae (still accepted as such by Pavlinov & Rossolimo 1987); rank of subfamily proposed by Simpson (1945). Ranked as a tribe Pteromyini by Steppan et al. (2004). See Jackson & Thorington (2012) for thorough discussion on the history of the group name.

5. Subfamily: Arctomyinae Gray, 1821

1821 Arctomydae Gray (p. 303). The correct name is Arctomyinae. Type genus is *Arctomys* (= *Marmota* Blumenbach, 1779; see p. 304 in Gray 1821).

1844 Arctomydina Brandt (p. 362). The type genus is *Arctomys* (by tautonomy).

1891 Arctomyinae Blanford. Blanford (1891: 388) included three genera: *Arctomys*, *Spermophilus*, and *Cynomys*. The type genus is *Arctomys* Schreber, 1780 (= *Marmota* Blumenbach, 1779).

1891 Arctomyinae Flower et Lydekker. Flower & Lydekker (1891) made no reference on Gray (1821). Their Arctomyinae was defined to include “burrowing forms which may be collectively known as Marmots”, i.e. *Arctomys*, *Cynomys* and *Spermophilus*. The type genus is *Arctomys* Schreber, 1780 (= *Marmota* Blumenbach, 1779).

1923 Marmotinae Pocock. Type genus is *Marmota* (by tautonomy). Defined to include *Marmota*, *Marmotops* (see synonymy under *Marmota*), *Cynomys*, “*Citellus* with many subgenera” (= *Spermophilus* sensu lato), *Tamias*, and *Eutamias* (Pocock 1923: 240). Gromov et al. (1965) applied Marmotinae in similar way as Pocock (c. l.) but included also *Sciurotamias*.

Although Marmotinae Pocock, 1923 is a widely used name for marmots and relatives, the oldest available name for the subfamily is by Gray (1821). The subfamily name Arctomyinae, still used by Osborn (1910), was neglected afterwards.

5.1. Tribe: Protoxerini Moore, 1959

MOORE (1959) classified into Protoxerini only *Protoxerus*, *Epixerus* and *Heliosciurus*, placing the remaining sun squirrels into Funambulini. Protoxerines were traditionally included into the subfamily Xerinae (e.g. STEPPAN et al. 2004), and earlier on even into the genus *Xerus* (e.g. FORSYTH MAJOR 1893). In the results of FABRE et al. (2012) the sun squirrels form a sister group to the Tamiini + Sciurotamiini + Arctomyini combined. Protoxerini are difficult to be defined on cranial traits (MOORE 1959). They notably differ from the remaining Arctomyinae in lacking cheek-pouches. Protoxerini could be equally well ranked as a subfamily on its own. The group is entirely Ethiopian.

5.2. Tribe: Tamiini Moore, 1959

1959 Tamiina Moore. Type genus: *Tamias* Illiger, 1811.
1963 Tamiini Black.

The results of FABRE et al. (2012) retrieved a supported sister position of *Eutamias* against all the Nearctic chipmunks. Therefore, *Eutamias* merits a generic status, rather than being kept as a subgenus of *Tamias*. In a traditional taxonomy, "this is based mainly on the presences in *Eutamias* of a rudimentary P^3 that is absent in [the Nearctic] *Tamias* s.s. This is not quite constant in *Eutamias* (e.g., JONES & JOHNSON 1965 found these teeth lacking in 2 out of 41 skulls of *T. sibiricus* from Korea) ..." (CORBET 1978: 84). To get an insight on the frequency of oligodonty of a peg-like third upper premolar (P3), we scored 460 skulls of *Eutamias sibiricus sibiricus* (SZM) and found this tooth present in all individuals.

Distribution map for *Eutamias sibiricus* in KRYŠTUFEK & VOHRALÍK (2012: Fig. 5 in pp. 28–29) reqires ammendments. During second half of the 20th century burunduks expanded soutward along the western coast of Kamchatka and reached the settlement of Palana. There were actualy two introductions of burunduks from the Far East to the western Moscow region: (i) near the Lake Glubokoe, and (ii) the region of Porečû (BOBROV et al. 2008).

5.3. Tribe: Sciurotamiini Kryštufek et Vohralík, 2012

The tribe contains two species, of which one is entirely Oriental; reviewed below.

5.4. Tribe: Arctomyini Gray, 1821

1821 Arctomydae Gray (p. 303). See comments under the subfamily Arctomyinae.
1945 Marmotini Simpson. Type genus: *Marmota* Blumenbach, 1779.

Arctomydae of GRAY (1821) predate Marmotini Simpson, 1945. In compliance with the Principle of Coordination (Article 36.1 of the International Code for Zoological Nomenclature) the proper name for the tribe is Arctomyini Gray, 1821.

5.4.1. Subtribe: Ammospermophilina new subtribe

The type genus is *Ammospermophilus* Merriam, 1893 with 4–5 species. Another genus in the subtribe is *Notocitellus* Howell, 1938, with 2 species (BEST 1995a, b).

All phylogenetic reconstructions of ground squirrels which were based on molecular markers (HARRISON et al. 2003, HERRON et al. 2004, FABRE et al. 2012) retrieved a monophyly of *Notocitellus* + *Ammospremophilus* combined; this clade holds a supported basal position in Arctomyini. Multivariate analysis of cranial dimensions conform molecular results and placed both, *Notocitellus* and *Ammospermophilus*, well outside the range of variation in all ground squirrels traditionally referred to *Spermophilus* sensu lato (see Fig. 3 in HELGEN et al. 2009:

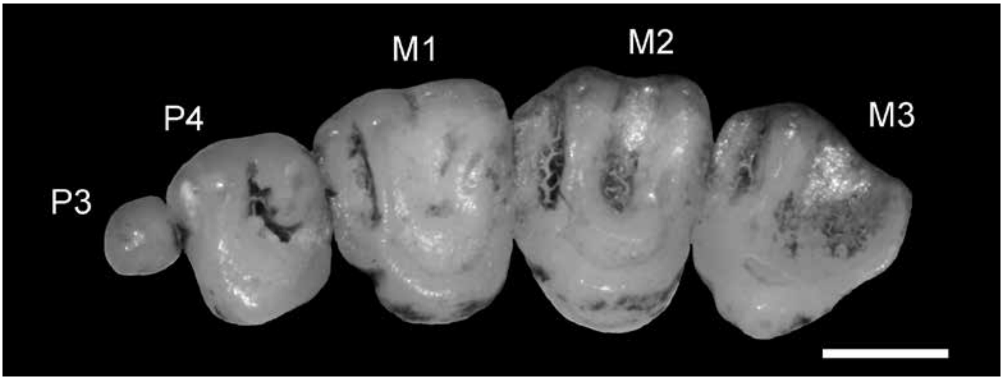

Fig. 2. Maxillary cheek-teeth in *Ammospermophilus leucurus* (California, San Bernardo County; SMF 52244). Note a peg-like 3rd premolar P3. Scale bar = 5 mm. Photo by Boris Kryštufek.
Obr. 2. Horní řada zubů u *Ammospermophilus leucurus* (California, San Bernardo County; SMF 52244). Zajímavý je kolíčkovitý 3. horní premolár P3. Měřítko vpravo dole = 5 mm. Foto Boris Kryštufek.

275). Morphologically, Ammospermophilina new subtribe is characterized by short nasals, wide interorbital region, small and slender postorbital processes, stout and recurved upper incisors, and a reduced third upper premolar P3 (Fig. 2). *Notocitellus* is unique among the tribe Arctomyini in having only three pairs of nipples; *Ammospermophilus* has 5–6 pairs of mammae (Moore 1961). Diploid number of chromosomes (2n = 32) is at the lowest end of variation range in Arctomyini (from 2n = 30 to 2n = 46; Lâpunova & Voroncov 1969, Helgen et al. 2009). Both genera have large cheek pouches and similar structure of baculum. The baculum consists of a shaft with thickened base and nearly symmetrical expanded concave distal disc with crenulate edges; the disc is bent abruptly to the shaft in *Ammospermophilus*, but is set at lesser angle to the axis of the shaft in *Notocitellus* (Howell 1938, Best 1995b).

Notocitellus and *Ammospermophilus* differ clearly in external appearance. The new subtribe provides a noteworthy parallel in this respect with the two genera of Otospermophilina. Namely, in both subtribes the smaller genus is striped and relatively short-tailed (*Ammospermophilus* in Ammospermophilina new subtribe, and *Callospermophilus* in Otospermophilina) while the larger genus (*Notocitellus* in Ammospermophilina new subtribe, and *Otospermophilus* in Otospermophilina) is long-tailed and grizzled.

The range of the subtribe is restricted to xeric shrublands of western North America, from Oregon and Idaho to Sierra Madre del Sur in Mexico. Majority of species have small ranges.

5.4.2. Subtribe: Otospermophilina Gromov, 1965

1965 Otospermophilini Gromov. Type genus: *Otospermophilus*.

Originally described as a tribe (Gromov et al. 1965: 138) to include genera *Ammospermophilus*, *Otospermophilus*, *Callospermophilus* (as a subgenus of *Otospermophilus*), *Ictidomys*, *Poliocitellus*, and *Xerospermophilus*. Of these genera, only *Otospermophilus* + *Callospermophilus* combined are monophyletic against Spermophilina + Arctomyina combined. Of the remaining genera which Gromov et al. (1965) classified into their tribe Otospermophilini, *Ammospermo-*

philus is here in a new subtribe Ammospermophilina; *Ictidomys*, *Poliocitellus*, and *Xerospermophilus* are in the subtribe Spermophilina.

5.4.3. Subtribe: Arctomyina Gray, 1821

1821 Arctomydae Gray (p. 303). See comments under the subfamily Arctomyinae.
1945 Marmotini Simpson. Type genus: *Marmota*.
1959 Marmotina Moore. Type genus: *Marmota* Frisch, 1775 (= *Marmota* Blumenbach, 1779); *Marmota* Frisch, 1775 is unavailable name (see below under that genus).

Arctomydae of Gray (1821) predates Marmotini Simpson, 1945. In compliance with the Principle of Coordination (Article 36.1 of the International Code for Zoological Nomenclature) the proper name for the subtribe is Arctomyina Gray, 1821. The subtribe contains *Marmota* as the only genus.

5.4.4. Subtribe: Spermophilina Moore, 1959

1959 Spermophilina Moore. Type genus: *Spermophilus* Cuvier, 1825.
1965 Citellini Gromov. Type genus: *Citellus* (= *Spermophilus*).
1965 Cynomyini Gromov. Type genus: *Cynomys* (by tautonomy).

A Holarctic group which contains 4 genera and about 31–34 species: *Spermophilus* (14 species in Helgen et al. 2009, 11 species in Kryštufek & Vohralík 2012), *Urocitellus* (12), *Ictidomys* (3), *Poliocitellus* (1), and *Xerospermophilus* (4) (Helgen et al. 2009).

Subtribe: Spermophilina Moore, 1959

Genus: *Urocitellus* Obolenskij, 1927 – Long-tailed Sousliks

1817 *Anisonyx* Rafinesque. Type species: *Anisonyx brachiura* Rafinesque, 1817: 45 (= *Urocitellus columbianus*; Nearctic). A junior homonym of *Anisonyx* Latreille, 1807 (Coleoptera; Thorington & Hoffmann 2005).
1927 *Urocitellus* Obolenskij. Type species: *Spermophilus eversmanni* Brandt, 1842. Correct spelling of the authority is Obolenskij (cf. Ognev 1947, Pavlinov & Rossolimo 1987, Hoffmann & Thorington 2005, Helgen et al. 2005), not Obolensky as occasionally quoted (e.g. Ellerman & Morrison-Scott 1951, Gromov et al. 1965, Pavlinov & Lissovsky 2012). The entire paper of Obolenskij (1927) is in Latin script although the title and the author's name appear also in Cyrillic (Russian) script.

Originally described as a subgenus of the genus *Citellus* (= *Spermophilus*; Obolenskij 1927) and treated such way by majority of authors (Ognev 1947, 1963, Gromov et al. 1965, Corbet 1978, Thorington & Hoffmann 2005); elevated to generic rank by Helgen et al. (2009). Despite their external and cranial similarity, *Urocitellus* and *Spermophilus* are unlikely to be sister genera (Harrison et al. 2003, Herron et al. 2003). *Urocitellus* is most probably of North American origin and diversified during the Pleistocene glacial-interglacial cycles in the subarctic Beringia. During the late Pliocene (Villanyian) and throughout the Pleistocene several species of *Urocitellus* were identified even in Europe (Kowalski 2001): *U. nogaicus* (Topačevskij, 1957), *U. polonicus* (Gromov, 1965), *U. primigenius* (Kormos, 1934), and *U. superciliosus* (Kaup, 1839). In the Palaearctic, the genus *Urocitellus* occupies north-central and north-eastern Asia and is largely allopatric with respect to *Spermophilus*. In western Siberia, where *U. undulatus*

Fig. 3. Skins in dorsal (above) and ventral views (below) of Palaearctic long-tailed sousliks *Urocitellus*. a – *U. undulatus undulatus* (adult male from the Ulunga River, Amur Region, Russia; SZM 13247); b – *U. undulatus eversmanni* (adult female from the south-eastern Altai Mts., Russia; SZM 33967); c – *U. parryii* (adult male from Anadyr', Chukotka, Russia; SZM 6523). Photo by Boris Kryštufek.
Obr. 3. Balky z hřbetní (nahoře) a břišní strany (dole) palearktických syslů rodu *Urocitellus*. a – *U. undulatus undulatus* (adultní samec od řeky Ulunga, Amurská oblast, Rusko; SZM 13247); b – *U. undulatus eversmanni* (adultní samice z jihovýchodního Altaje, Rusko; SZM 33967); c – *U. parryii* (adultní samec z Anadyru, Čukotka, Rusko; SZM 6523). Foto Boris Kryštufek.

lives in sympatry with *Spermophilus erythrogenys*, the former inhabits slopes and mountainous regions, and the latter flat steppes (Ûdin et al. 1979).

Of 12 species recognized by Helgen et al. (2009), 10 are Nearctic (central and western North America), one is trans-Beringian (*U. parryii*), and only *U. undulatus* is endemic to the Palaearctic. Gromov et al. (1965) and Gromov & Erbaeva (1995) classified *Spermophilus relictus* as a putative member of *Urocitellus*, but this opinion was not accepted (cf. Pavlinov & Rossolimo 1987, Kryštufek & Vohralík 2012). Further division of *Urocitellus* is into two species groups: the *columbianus* species-group (large and long-tailed sousliks with big ears), which encompasses both Palaearctic species, and the *townsendi* species group (small and short-tailed sousliks with small ears; Helgen et al. 2009).

Species taxonomy of the *undulatus-parryii* tandem is confusing and the scope of both varied in time. At one time long-tailed sousliks on both sides of Beringia were clumped under *U. undulatus*; at another time *U. undulatus* was restricted to Asia and *U. parryii* to North America (for reviews see Rausch 1953, Vorontsov et al. 1980, and MacDonald & Cook 2009). Gromov (in Gromov et al. 1963) is credited to be the first to distinguish two Palaearctic species in their present taxonomic scope, and set the Lena River as a boundary between them.

Definition. Both Palaearctic species are large and long-tailed (TL ≈ 30–50% HbL) ground squirrels. Pelage is usually flecked or spotted, and longer and less sleek than in *Spermophilus*. Membranous internal cheek pouches are present. The skull is of similar appearance as in *Spermophilus*, except for wider *processus nasalis ossis premaxillae* and wider interpterygoid fossa in *Urocitellus*. Post-incisive pits are deep and marked. Cheek-teeth are proportionally less massive but P3 is relatively heavier. Females have 8–12 nipples; baculum is essentially as in *Spermophilus*. Dental formula: 1/1, 0/0, 2/1, 3/3 = 22; number of cheek-teeth roots (Palaearctic species): 1/0, 3/2, 3/4, 3/4, 3/3-4. Diploid number in the genus: 2n = 30–46 (Liapunova & Vorontsov 1970, Nadler 1966, Nadler et al. 1984); the karyotype of *U. undulatus* is rearranged compared to *Spermophilus* (Beklemisheva et al. 2011). Alarm call consists of several harmonic tones (only fundamental frequency in *Spermophilus*; Nikol'skij 1979).

Various external and cranial traits are reported in the literature to distinguish between *U. undulatus* and *U. parryii* (Gromov et al. 1963, 1965, Krivošeev 1984, Gromov & Erbaeva 1995). We checked variability of these characteristics on more than five hundred long-tailed sousliks belonging to both species and covering the majority of their ranges. Both species show extraordinary among-population variability in colour, relative length of tail, and size. In our conclusion, the colour is the most reliable morphological trait to distinguish the two species (Fig. 3). There are also differences in vocalization between these two species; calls have 2–6 kHz in *U. undulatus* and 1.5–1.8 kHz in *U. parryii* (Nikol'skij 1979).

Key to Species

1 Dorsal pelage with bold white spots, a brightly rufous head contrasts greyish back (Fig. 3c); 2n = 34; occurring east of the Lena R. .... *U. parryii*

1* Dorsal pelage with fine white speckles or plain, head usually of same colour as back, never brightly rufous and sharply distinct (Fig. 3a, b); 2n = 32; occurring west of the Lena R. .... *U. undulatus*

Urocitellus undulatus (Pallas, 1778) – Long-tailed souslik

1779 *Mus citellus undulata* Pallas. Type locality: "quae in frigidiore & alpestri Sibiria albidior evasit, passim magis minusve *guttata* apparet, ad Selengam autem maxime longitudine caudae eminet." (= in regions of Siberia which are colder and of higher elevation [sousliks are] whitish, elsewhere spotted, along [the river] Selenga [they] are outstanding for their long tail) (Pallas 1779: 127). Ognev (1947: 185) restricted the type locality to "dolin[a] r. Selangi v Zabajkal'e" (= valley of the river Selenga, in Buryatia, central Siberia); 1778 is quoted as the year of publication.

1842 *Spermophilus eversmanni* Brandt. Type locality: "Habitat in montibus Altaicis (Gebler), prope Kokatan (Schrenk)" (= Lives in the Altai mountains (Gebler), close to Kokatan (Schrenk)). We could not identify the locality Kokatan, which is not mentioned in Ognev (1947) and Pavlinov & Rossolimo (1987). A lectotype, deposited in the Zoological Institute of the Russian Academy of Sciences, Sankt Peterburg, is from "[Džungarskij] Alatau" (Baranova & Gromov 2003) (= Džungarian Alatau Mts. on the Kazakhstan-China border). Year of publication also given as 1841 (Ognev 1947, Baranova & Gromov 2003).

1842 *Arctomys altaicus* Eversmann. Type locality: "Loca montium altaicorum herbida" (Ognev 1947), (= grassy hills in the Altai Mts.). Ognev (l.c.) quotes 1841 as the year of publication.

1844 *Spermophilus jacutensis* Brandt. Type locality: "... quae Jacutia mittuntur observare licet" (= observed in Yakutia). Ognev (1947: 210) restricted the type locality to "okresnost Âkutska" (= vicinity of Yakutsk) in eastern Siberia, Russia. This was translated in the 1963 edition as "Yakutsk area" (Ognev 1963: 179). Ognev (l.c.) quotes 1843 as the year of publication.

1927 *Citellus eversmanni stramineus* Obolenskij. Type locality: "N. W. Mongolia ... Laman – Gégén". (= Monastery Laman-Gègèn [known also as Lamaiin Gegeenii Hüryee], near Bayankhongor, north-western Mongolia). For proper spelling of the authority see remark under the generic name.

1927 *Citellus eversmanni transbaicalicus* Obolenskij. Type locality: "Transbaicalia … Lake Ivan, 48 km NW from Tshita" (= Čita [in Russian] or Chita, Trans-Baikal territory, Russia). For proper spelling of the authority see remark under the generic name.

1937 *Citellus* (*Urocitellus*) *eversmanni intercedens* Ognev. Type locality: "Zabajkale, Sretenskij okrug, Nerčinskij rajon" (Ognev 1947), (= Trans-Baikal territory, Sretensk Region, Nerčinsk District), Russia.

1937 *Citellus* (*Urocitellus*) *eversmanni menzbieri* Ognev. Type locality: "Okrestnosti Ignatevki, v 23 km ot g. Blagoveŝenska, na r. Amure" (Ognev, 1947) (= vicinity of Ignatevka, 23 km from the town Blagoveŝensk, on the river Amur). The region is in Russian Far East, not in "Eastern Siberia" (Ellerman & Morrison-Scott 1951).

1979 *Citellus* (*Urocitellus*) *eversmanni incertedens* Rossolimo et Pavlinov. Lapsus calami of *Citellus* (*Urocitellus*) *eversmanni intercedens* Ognev, 1937 (Pavlinov & Rossolimo 1987).

Remarks. In the past frequently reported as *Citellus eversmanni* (Allen 1940, Švecov et al. 1984). The oldest fossil remnants of *U. undulatus* are from the Middle Pleistocene layers in western Siberia (Ûdin et al. 1979).

Description (Figs. 3a, b, 4). Medium-sized to large souslik with relatively long tail (in majority of animals ≈ 42–48% HbL, range = 34–52%; Fig. 3a,b); hairy area on soles restricted to heel or

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Fig. 4. Long-tailed sousliks *Urocitellus undulatus*. a – Koš Agač, Altai Republic, Russia; b – Kanskaâ steppe, Central Altai Mts., Russia; c – lactating female emitting alarm call; Republic Tuva, Russia; d – Jaruusum, Mongolia. Photo courtesy Alenka Kryštufek (a), Igor Karyakin (b and c), and Hermann Ansorge (d). e – "*Spermophilus eversmanni* Brandt" as depicted in Plate II ("Table II") in Méhely (1901); based on a specimen from "bei Minusinsk" (on R. Enisej, south of Krasnoârsk, Russia). Specimen (d) is of the nominotypical subspecies; specimens (a – c), and (e) belong to subspecies *eversmanni*.

Obr. 4. Sysel dlouhoocasý *Urocitellus undulatus*. a – Koš Agač, Republika Altaj, Rusko; b – Kanská step, pohoří Střední Altaj, Rusko; c – kojící samice vydávající varovný hlas z Tuvinské republiky, Rusko; d – Jaruusum, Mongolsko. Foto Alenka Kryštufek (a), Igor Karyakin (b, c), Hermann Ansorge (d). e – "*Spermophilus eversmanni* Brandt" jak byl zobrazen na Tab. II v Méhelym (1901); podle exempláře "od Minusinska" (na řece Jenisej, jižně od Krasnojarska, Rusko). Exemplář (d) patří k nominotypickému poddruhu, exempláře (a – c) a (e) patří k poddruhu *eversmanni*.


a
b
c
d
e

reaching the pads. Summer pelage is yellow-buff on the head, neck and shoulders and a mixture of black and grey on mid-back and rump. There is great deal of individual variation in colour and one can find in the same population long-tailed sousliks with bright rufous shoulders and blackish rump, or individuals with grey and black hairs extending till the neck and forehead. Dorsal pelage is frequently speckled or spotted (diameter of spots ~2 mm) because dark hairs with black tips have light subterminal bands which tend to concentrate or overlap. Pattern varies and spots are frequently restricted to the posterior back, more rarely expanded up to shoulders; some animals are only indistinctly speckled. Forehead is either of same colour as shoulders or is darker, grey or grey brown; sides are lighter, buff, whitish or cream. Eye ring is whitish and

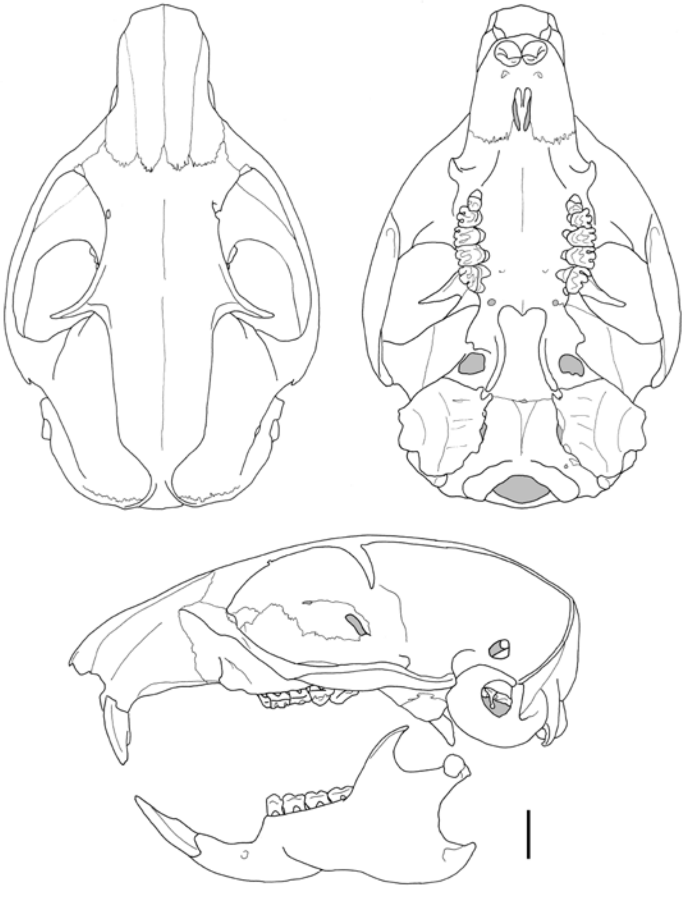


Fig. 5. Skull and mandible of *Urocitellus undulatus eversmanni* (adult female from Bayan-Ölgiy, Mongolia; SMG M6948). Scale bar = 5 mm.
Obr. 5. Lebka a mandibula *Urocitellus undulatus eversmanni* (adultní samice z Bayan- Ölgiy, Mongolsko; SMG M6948). Měřítko = 5 mm.

light stripe expands in some animals towards the ears. Lips, chin and throat are white, rarely buff. Belly is lighter than flanks, rarely whitish-grey, normally washed buff and frequently with rusty chests; bases of hair are slate. Long hairs on the tail are tawny ochraceous for basal two-thirds, than black, tipped white or cream; in general appearance the tail is greyish buff above, brightly ochraceous to rusty ventrally and fringed white with sub-terminal black stripe of various width. Feet are whitish, greyish or ochraceous. Winter pelage tends to be lighter and greyer; juveniles are duller. Females have 5–6 pairs of nipples (Ognev 1947). Skull shows no peculiarities (Fig. 5). It is convex in profile, with moderately expanded zygomatic arches (ZgB accounts for 66–69% of CbL in majority of individuals; range = 63.2–77.6%). Dentition as for the genus; enamel on the upper incisors light yellow to nearly white (Allen 1925, 1940, Ognev 1947). Ranges for external and cranial dimensions (in mm, weight in grams): HbL = 204–350, TL = 80–144, HF = 38.0–57.0, E = 7.0–17.0, W = 251–1009, CbL =42.6–60.1, ZgB = 29.2–43.0, MxT = 10.0–14.0. Males are slightly larger. Karyotype 2n = 32 (Lâpunova 1969, Voroncov & Lyapunova 1969); this number, which is reduced if compared to other Palaearctic sousliks, is a consequence of chromosomal fusions (Beklemisheva et al. 2011).

Geographical range (Fig. 6) is in several fragments in Western and central Siberia between the Tian Shan Mts. and the Lena River; an isolated population occupies the left bank of the Amur in Russian Far East. The major fragment extends from the Kuznecky Alatau Mts. and the Altai Mts. in Russia and Mongolia as east as Buryatia and the upper reaches of the Onon River in north-eastern Mongolia. The northernmost populations are isolates along the upper flow of the Enisej (reaching Krasnoârsk in the north) and in the Kuznecky Alatau Mts. Further east the northern border crosses the central part of Lake Baikal. In the south, long-tailed sousliks occupy Mongolian Altai, Hangaj and Hentaj (Bannikov 1954, Bobrinskij et al. 1965, Sludskij et al. 1969, Sokolov & Orlov 1980, Švecov et al. 1984). Two isolates are to the southwest of the main fragment, in north-eastern Kazakhstan and northern China (northern Xinjang and northern Heilongjiang; Zhang 1997) where the species is of very marginal occurrence. The smaller of these fragments is in the Tarnagataj Mts., and the larger fragment is in the eastern Tian Shan Mts. and Džungarian Alatau (Sludskij et al. 1969, Zhang 1997). The SZM is in possession of two vouchers (catalogue numbers 6528 and 6529) which were collected in April 1956 in Pokrovka on the south-eastern margin of Lake Issyk-Kul, Kyrgyzstan. Originally identified as *Spermophilus relictus* they actually represent *U. undulatus* (identified by B.K. in October 2013), a species which is not reported for the area of Issyk-Kul (Zimina 1964), or for Kyrgyzstan (Ajzin 1979). Long-tailed sousliks occupy the Island Olhon in the Baikal Lake (Švecov et al. 1984); this population shows a remarkable genetic diversity combined with high level of endemic alleles (Titov et al. 2009).

Two large isolates of long-tailed sousliks are (i) in the plains of the upper reaches of rivers Zeâ and Bureâ which are left tributaries of the central Amur (Krivošeev 1984), and (ii) in the central Yakutsk plain with the rivers Lena and Vilûj setting the northern border (Tavrovskij et al. 1971). Shar & Lkhagvasuren (2008) mapped further two fragments, one of them to the north of the Vilûj River, and another one on the left bank of the Amur at about the latitude of Skovorodino. We were unable to identify any of them in Russian sources and therefore did not plot any of these on Fig. 6.

Long-tailed souslik inhabits dry steppes in river valleys, well drained riverine terraces, intermountain valleys of grasses and sagebrush vegetation, alpine meadows, forest clearings and occasionally open taiga and other types of sparse forest. Preferred habitats are low-grass steppes on a thin layer of chernozem <100–300 m away from water sources. Strong preference

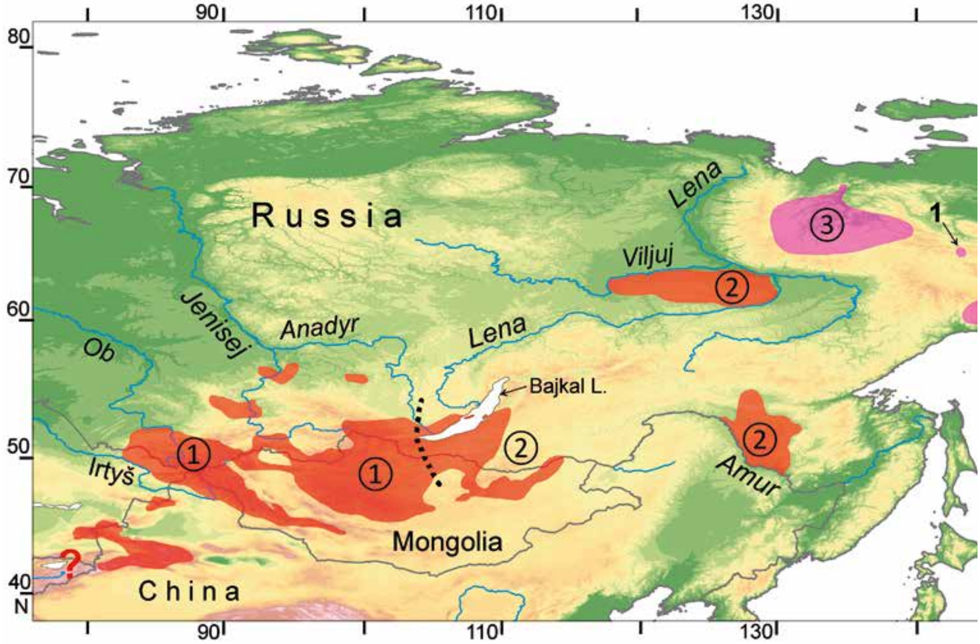
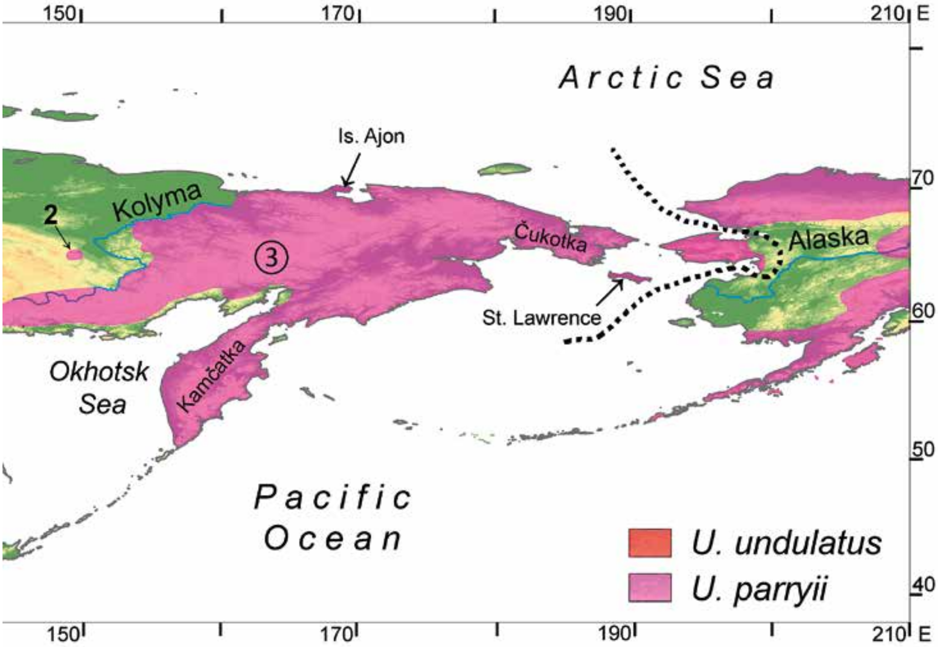


Fig. 6. Ranges of *Urocitellus undulatus* and *U. parryii*. Distribution of *U. parryii* is based on: Yakutsk region – Tavrovskij et al. (1971); Kolyma, Okhotsk, Chukotka and Kamchatka – Ûdin et al. (1976), Krivošeev (1984). Arrows point on two small population isolates : 1 – on R. Indigirka; 2 – in the Momske Mts. Range of *U. undulatus* was compiled from the following sources: overall range – Vorontsov et al. (1980); Yakutsk region – Tavrovskij et al. (1971); Far East – Krivošeev (1984); Baikal region – Švecov (1977), Švecov et al. (1984); Altai Mts., Regions of Tuva, Buryatia, Čita and Hakasia – ZMS specimen tags; Kazakhstan – Sludskij et al. (1969); Mongolia – Bannikov (1954), Sokolov & Orlov (1980); China – Zhang (1997). Question mark in eastern Kyrgyzstan is commented in the text. Subspecies (circled digits): 1 – *Urocitellus undulatus eversmanni*; 2 – *U. u. undulatus*; 3 – *U. parryii leucostictus*. Geographic delimitation between *eversmanni* and the nominotypical subspecies *undulatus* is tentative.

for proximity of water possibly prevents long-tailed sousliks from spreading deeper into steppes (Ricankova et al. 2006). This souslik locally prefers “areas in and around rocky outcroppings as opposed to open steppe” (Tinnin et al. 2002). Long-tailed sousliks are locally common to abundant. Elevational range is 1800–3000 m a. s. l. in Tuva, Russia (Ûdin et al. 1979), and the upper limit is at 2900 m in Mongolia (Bannikov 1954), 3400 m in Kazakhstan and 3500 m in the Altai Mts. (Ognev 1947), but abundance normally declines with increasing elevation (Sludskij et al. 1969). Low-lying flatland is inhabited along the Amur; sousliks aggregate around arable land and penetrate into secondary oak and birch forests (Krivošeev 1984). Tavrovskij et al. (1971) report these animals to be eurytopic in Yakutia, where they live on dry grasslands in river valleys, clearings inside the taiga and along the forest edges where they penetrate 100–200 m inside the forest. They live around human settlements and within them, and even dig burrows beneath



Obr. 6. Areály rozšíření *Urocitellus undulatus* a *U. parryii*. Rozšíření *U. parryii* je založeno na: Jakutská oblast – Tavrovskij et al. (1971); Kolyma, Ochotsk, Čukotka a Kamčatka – Ûdin et al. (1976), Krivošeev (1984). Šipky označují dva malé isoláty: 1 – na řece Indigirka; 2 – v Momském pohoří. Rozšíření *U. undulatus* bylo zkompilováno podle následujících pramenů: celkový areál – Voroncov et al. (1980); Jakutská oblast – Tavrovskij et al. (1971); Dálný Východ – Krivošeev (1984); oblast Bajkalu – Švecov (1977), Švecov et al. (1984); pohoří Altaj, oblasti Tuva, Burjatská, Čitinská and Chakasijská – lokalitní lístky exemplářů v ZMS; Kazachstán – Sludskij et al. (1969); Mongolsko – Bannikov (1954), Sokolov & Orlov (1980); Čína – Zhang (1997). Otazník ve východní Kyrgizii je komentován v textu. Poddruhy (čísla v kroužku): 1 – *Urocitellus undulatus eversmanni*; 2 – *U. u. undulatus*; 3 – *U. parryii leucostictus*. Geografická hranice mezi *eversmanni* a nominotypickým poddruhem *undulatus* je stanovena jen přibližně.

the houses. Long-tailed sousliks hibernate from mid-October to end of March in Kazakhstan (Sludskij et al. 1969), from late September to early April in Mongolia (Bannikov 1954), from late October to April in Amur Region (Krivošeev 1984), and between end of September – early October and mid-April in Yakutia (Tavrovskij et al. 1971).

Subspecies. Interpopulation variability in colouration and size is outstanding in *U. undulatus* (Fig. 7). In terms of cranial differentiation, the two eastern isolates on the Amur and the Lena, respectively, “reach the level of a species difference” (Vorontsov et al. 1980). The overall pattern of size variability was assessed by Vorontsov et al. (1980) who found the smallest sousliks around Tuva (ssp. *eversmanni* as defined below), and the largest along the Lena and the Amur. Our reanalysis of their data suggests a longitudinal cline with a weak albeit significant west-to-east increase in size within the main segment (length of skull = 38.445 + 0.0937 longi-

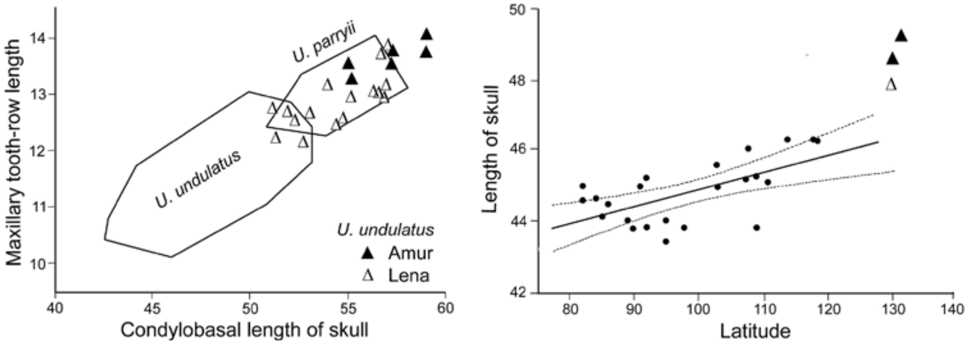


Fig. 7. Left: Bi-variate plot of maxillary tooth-row length against condylobasal length (in mm) for the two Palaearctic long-tailed sousliks, *Urocitellus undulatus* and *U. parryii*. Polygons enclose extremes for all *U. parryii* and the small-sized *U. undulatus*, respectively; big eastern samples of *U. undulatus* are shown by triangles. Note that the eastern populations of *U. undulatus* overlap in size with *U. parryii.* Based on 470 skulls measured in BMNH, SMF, SMG and SZM. Right: Plot of mean skull length in 26 geographic samples of *Urocitellus undulatus* against longitude. Based on data in Vorontsov et al. (1980); reference points at which the skull length was scored, are not specified. Dots represent small and medium-sized populations, while large-sized eastern isolates are shown as triangles. Dotted line is 95% confidence interval of the regression curve.

Obr. 7. Vlevo: Korelační diagram délky horní řady zubů vynesené proti kondylobasální délce (v mm) pro palearktické sysly *Urocitellus undulatus* a *U. parryii*. Polygony ohraničují extremní hodnoty všech *U. parryii* a drobných *U. undulatus*; vzorky velkých východních *U. undulatus* jsou zobrazeny trojúhelníky. Všimněte si, že velcí východní *U. undulatus* se velikostně překrývají s *U. parryii.* Založeno na vzorku 470 lebek z BMNH, SMF, SMG a SZM. Vpravo: Průměrná délka lebky 26 geografických vzorků *Urocitellus undulatus* vynesená proti zeměpisné délce. Založeno na údajích Voroncova et al. (1980); jednotlivé geografické vzorky nejsou specifikovány. Tečky zobrazují populace syslů drobného a středního vzrůstu, kdežto populace velkých syslů z východních isolátů jsou zobrazeny trojúhelníky. Přerušované linky ukazují 95% konfidenční interval regresní křivky.

tude; $R^2 = 0.39$, $p = 0.0014$). Size of the eastern isolates is outside the confidence band for the regression curve and is therefore unlikely due to a simple extension of longitudinal trend (Fig. 7).

Gromov & Erbaeva (1995) recognized six subspecies as being valid (*undulatus*, *eversmanni*, *stramineus*, *intercedens*, *jacutensis*, *menzbieri*); these taxa are described and diagnosed in Ognev (1947, 1963). Results from allozyme polymorphism assessments (Vorontsov et al. 1980, Frisman & Korablev 2007, Frisman 2008) and from randomly amplified polymorphic DNA (RAPD) fragments (Tsvirka & Korablev 2012), however, cut across the above subspecific arrangement. Genetic analyses invariably retrieved two deeply divergent lineages (the Western and the Eastern) which hybridize in the area of the Lake Baikal. The hybrid zone is presumably due to a secondary contact and may be a consequence of habitat transformations which facilitated spreading of long-tailed sousliks across previously unoccupied territories (Frisman 2008). These lineages are classified as distinct (semi)subspecies by Pavlinov & Lissovsky (2012), but we keep them as well divergent subspecies. The two taxa cannot be separated on ground of traditional morphological traits. Although they tend to differ in size, even means for length of skull widely overlap.

Urocitelus undulatus undulatus (Pallas, 1778)

Synonyms. *jacutensis*, *leucositicus*, *transbaikalicus*, *intercedens*, *menzbieri.*

Remarks. The type locality of *U. undulatus* is within the hybrid zone with ssp. *eversmanni* (Frisman 2008) which makes the present nomenclatural arrangement uncertain. More sampling is required along the Baikal Lake and west of it to understand the nature of the hybrid zone and to link topotypes with phylogenetic lineages. If the oldest name is not applicable due to its putative hybrid origin, than *jacutensis* is available for this subspecies.

Description (Fig. 4c, d, Fig. 8). Included are medium-sized and large sousliks which are monomorphic for a specific transferrin allele *Tf-11* (Vorontsov et al. 1980, Frisman 2008). Populations from the main fragment (Baikal and eastward) are of medium size. Dimensions (in mm, weight in grams); subspecific names are from Gromov & Erbaeva (1995). Baikal Lake region, Russia (*undulatus* and possibly *intercedens*), males: HbL$_2$ = 230, 240, TL$_2$ = 115,120, HF$_2$ = 40, 42, E$_2$ = 7, 8, W$_2$ = 350, 365, CbL$_7$ = 50.2 (45.1–53.2), ZgB$_7$ = 34.1 (29.7–37.2), MxT$_7$ = 12.1 (11.3–12.8); females: HbL$_4$ = 234.3 (224–241), TL$_3$ = 104.3 (80–117), HfL$_4$ = 43.0 (40.0–46.0), E$_4$ = 13.5 (7–17), W$_2$ = 284, 305, CbL$_{18}$ = 48.6 (44.8–50.9), ZgB$_{17}$ = 32.8 (30.6–35.5), MxT$_{18}$ = 11.6 (10.0–12.3) (Unžakov & Vasil'čenko 1980, and specimens in SZM).

Animals from the regions of the Amur and the Lena are outside the size range for the remaining long-tailed sousliks (Fig. 7). Population from the Lena (*jacutensis*) is readily distinguished by

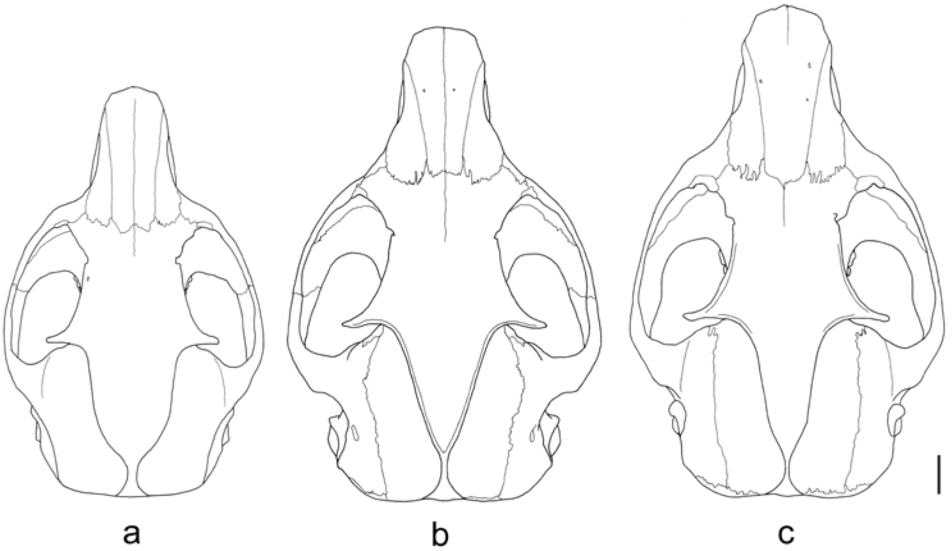


Fig. 8. Skulls (dorsal view) in different populations of *Urocitellus undulatus undulatus*: a – adult male from Džidinskij District, Buryatia, Russia (SZM 18455); b – adult male from Yakutsk, Russia (BMNH 28.6.19.1); c – adult male from the Ulunga River, Amur Region, Russia; SZM 13248). Scale bar = 5 mm.
Obr 8. Lebky (dorsální pohled) z různých populací *Urocitellus undulatus undulatus*: a – adultní samec z Džidinského okresu, Burjatsko, Rusko (SZM 18455); b – adultní samec z Jakutska, Rusko (BMNH 28.6.19.1); c – adultní samec od řeky Ulungy, Amurská oblast, Rusko; SZM 13248). Měřítko = 5 mm.

a combination of its large size, relatively wide zygomatic arches (ZgB = 65.9–69.0% CbL; Fig. 8b) and less bright pelage; back lacks rufous tints, sides are whitish and lightly tinted buff in some animals; white belly is washed by slate grey undercolour and can be buff in its anterior in some individuals. Dimensions (vicinity of Yakutsk), males: HbL_{27} = 277.7 (254–330), TL_{28} = 123.8 (110–141), HF_{3} = 51.0 (50.0–53.0), W_{25} = 613.5 (335–1009), CbL_{28} = 56.6 (54.0–59.0), ZgB_{27} = 38.7 (36.0–43.0), MxT_{29} = 12.9 (12.0–13.1); females: HbL_{34} = 260.0 (236–285), TL_{34} = 110.7 (90–125), HF_{9} = 47.2 (40.0–52.0), W_{25} = 443.5 (249–615), CbL_{33} = 56.9 (51.2–58.3), ZgB_{33} = 35.8 (33.0–39.0), MxT_{34} = 12.7 (12.0–13.1) (Tavrovskij et al. 1971, and specimens in BMNH and SZM). Obolenskij (1927) treated *jacutensis* as a species on its own right.

The left bank of the Amur River is inhabited by long-tailed sousliks (*menzbieri*) which are even bigger than those along the Lena (Figs. 7, 8c). Pelage is bright and does not differ from the remaining conspecifics (Fig. 3a), except those from Lena; the skull is relatively narrower (ZgB = 63.2–66.4% CbL; Fig. 8c). Dimensions, males: HbL_{80} = 278.9 (250–350), TL_{80} = 104.2 (75–144), HF_{82} = 52.5 (44.0–57.0), E_{80} = 13.5 (10.0–14.0), W_{74} = 607.3 (385–950), CbL_{89} = 57.7 (50.2–60.1), ZgB_{89} = 37.0 (34.1–40.7), MxT_{90} = 12.9 (11.3–14.0) (Krivošeev 1984, and specimens in SZM).

Geographic range. It encompass the eastern part of the main segment in the Baikal region and eastward (in Buryatia, very marginally in the Čita Region, and in adjacent Mongolia), as well as the isolates on Lena and Amur (Fig. 6). The western border is insufficiently resolved.

Urocitelus undulatus eversmanni (Brandt, 1841)

Synonym. *stramineus.*

Description (Figs. 3b, 4a, b, e, 5). Small to medium-sized long-tailed sousliks with exclusive transferrin alleles *Tf-DZ*, *Tf-Sh*, and *Tf-10* (Vorontsov et al. 1980, Frisman 2008). Ognev (1947) claims that typical *eversmanni* from Altai is the most brightly coloured of all long-tailed sousliks; after examination of large series of skins (SZM collection) we cannot concur with this view. The population isolated in Džungarian Alatau is monomorphic for specific transferrin allele *Tf-Dz* (Vorontsov et al. 1980). Dimensions (in mm, weight in grams); subspecific names (in parentheses) are from Bannikov (1954) and Gromov & Erbaeva (1995). The Altai Mts. in Russia (*eversmanni*), males: HbL_{41} = 224.9 (204–255), TL_{40} = 101.7 (81–142), HF_{44} = 43.0 (38.0–51.0), E_{37} = 10.1 (7.7–14.0), W_{27} = 391.5 (280–600), CbL_{30} = 46.5 (44.0–48.4), ZgB_{26} = 31.7 (30.3–33.2), MxT_{30} = 11.4 (10.6–13.8); females: HbL_{25} = 229.8 (205–270), TL_{20} = 103.8 (81–116), HfL_{25} = 42.5 (38.8–49.0), E_{20} = 10.0 (8.7–12.0), W_{15} = 350.0 (251–500), CbL_{27} = 45.6 (42.6–50.8), ZgB_{25} = 30.9 (29.2–34.7), MxT_{27} = 11.0 (10.4–11.6) (specimens in SZM). Džungarskij Alatau, Mongolia (*stramineus*), sexes pooled: HbL_{346} = 245 (210–280), TL_{346} = 106 (70–135), HfL_{346} = 45 (40–51), CbL_{346} = 48.1 (44.0–51.1), ZgB_{346} = 32.3 (30.0–35.4), MxT_{346} = 11.5 (10.9–11.9) (Sludskij et al. 1969).

Geographic range. The western portion of the main range to the west of Baikal Lake (Fig. 6). The eastern border is insufficiently resolved.

Urocitellus parryii (Richardson, 1825) – Arctic souslik

1825 *Arctomys parryii* Richardson. Type locality: “Five Hawser Bay” (p. 319) in “Lyon Inlet, Melville Peninsula, Hudson Bay, Canada” (Howell 1938). Richardson (1825) mentioned further two localities: "Point Lake in lat. 65°" (on pp. 318 and 319), and "Churchill" (p. 318). Type locality was restricted to Five Hawser Bay already by Preble (1902).

1844 *Spermophilus leucosticus* Brandt. Type locality (p. 379): "... regionibus versus Ochotam et Uth fluvium valde aestimatae" (= highly prized in regions towards Okhotsk and along the Uth River). "Habarovskij kraj, Ohotskij rajon, reka Ohota" (Pavlinov & Rossolimo 1987) (= Khabarovsk Region, Okhotsk District, Ohota River), Eastern Siberia, Russia.

1858 *Spermophilus brunniceps* Kittlitz. Type locality: "Kamchatka". von Kittlitz (1858: p. 337) wrote: "Die Art unterscheidet sich von ähnlichen bei Pallas beschrieben haupsächlich durch geringere Zahl der Mammelen, deren nur acht sind. Das Exemplar ward in Petersburg unter der Namen *Spermophilus brunniceps*, Brandt, aufgestellt und von mir im Jahr 1835 beschreiben und angebilden" (= This species differs from a similar [species] described by Pallas primarily by lower number of nipples, which are only eight. The specimen was deposited in Petersburg [= ZISP in Sankt Peterburg] under the name *Spermophilus brunniceps* Brandt, and described and illustrated by myself in 1835). According to Allen (1903) *brunniceps* is *nomen nudum* because the species was never properly described, and this was accepted by Pavlinov & Rossolimo (1987), Thorington et al. (2005), and Pavlinov & Lissovsky (2012). Omitted from the list of types in ZISP (Baranova & Gromov 2003).

1903 *Citellus buxtoni* Allen. Type locality: "Gichiga, west coast of Okhotsk Sea, Siberia" (= Gižiga, Kamchatka Region, Russia).

1903 *Citellus stejnegeri* Allen. Type locality: "Near Petropaulski, southeastern Kamchatka" (= near Petropavlovsk, south-eastern Kamchatka, Russia).

1937 *Citellus* (*Urocitellus*) *eversmanni janensis* Ognev. Type locality: "Mestnost' Kenûrâh, v verhovâh r. Âny, dolina reki, Verhoânskij okrug" (Ognev 1947) (= locality Kenûrâh [also Ken-Ûrâh], upper reaches of the river Âna, valley of the river, Verhoânsk District), Eastern Siberia, Russia.

1963 *Citellus undulatus coriakorum* Portenko. Type locality: "Kamčatskaâ oblast', Korâkskij AO, r. Ačajvaâm" (Pavlinov & Rossolimo 1987) (= Russia, Kamchatka Region, Korâkskij Autonomous District, Ačajvaâm River).

1972 *Citellus parryi* (sic) *tschuktschorum* Černâvskij. Type locality: "sred. teč. r. Amguèma, Vost. Čukotka" (Baranova & Gromov 2003) (= middle reaches of the Amguema River, eastern Chukotka Peninsula, Russia).

Names available for Nearctic populations are not listed; for these cf. Miller & Kellog (1955).

Remarks. *U. parryii* diverged from the *U. richardsonii-elegans* lineage relatively recently (1.3 mya; Harrison et al. 2003); its considerable dental size and shape peculiarities are attributed to rapid morphological evolution (Goodwin 2009).

Description (Figs. 3c, 9 and 10). A large souslik with relatively long tail (~36–41% of HbL); sole is hairy at the heel. Head is tawny or cinnamon, upper parts reddish brown, cinnamon or fuscous and more or less flecked with whitish spots. Eye ring white, cream or buff, under parts, flanks and legs are tawny or cinnamon buff during summer, buff or greyish white in winter. Tail ochraceous tawny or cinnamon buff, mixed with fuscous black, below russet or tawny (Fig. 3c). Baculum (length ~4 mm) is essentially as in *Sermophilus*: distal spatula is moderately expanded and edged along its anterior margin with a continuous row of 7 tooth-like projections; there is a ventral median knob on the distal end. The proximal base is expanded and nearly circular in cross section (Burt 1960). Females have 4–6 pairs of nipples (Torre not dated). Skull is essentially as in *U. undulatus*; zygomatic width accounts for 65.1–70.8% of CbL (Fig. 10). Dimensions (in mm, weight in grams), males: HbL_{174} = 284.8 (266–320), TL_{173} = 103.1 (89–122), HF_{127} = 52.8 (51.7–55.0), E_{127} = 13.6 (12.7–16.0), W_{173} = 741.6 (545–950), CbL_{260} = 55.1 (50.2–60.1), ZgB_{257} = 37.3 (34.1–42.0), MxT_{258} = 12.7 (11.3–14.4); females: HbL_{43} = 279.3 (258–303), TL_{37} = 101.1 (90–113), W_{43} = 620.8 (405–765), CbL_{117} = 52.9

Fig. 9. Arctic souslik *Urocitellus parryii* (Kamchatka, Russia). Photo courtesy Vít Tejrovský.
Obr. 9. Sysel Parryův *Urocitellus parryii* (Kamčatka, Rusko). Foto Vít Tejrovský.

(50.0–56.0), ZgB$_{117}$ = 36.3 (32.6–39.0), MxT$_{117}$ = 13.0 (11.5–14.0) (Tavrovskij et al. 1971, Černâvskij 1984, Krivošeev 1984, and specimens in SMF and SZM). Body mass up to 1675 grams in Asia (Gromov et al. 1965), up to 1500 g in America (Torre not dated). Females are on average smaller than males. Karyotype 2n = 34 (Nadler 1966, Lâpunova 1969, Voroncov & Lâpunova 1969).

Geographic range (Fig. 6). *Urocitellus parryii* is the only Holarctic squirrel. Range in North America covers Alaska and northwestern Canada (MacDonald & Cook 2009). Asiatic range is in several fragments in northeastern Siberia as west as the Lena River. The largest fragment is in Chukotka, Kamchatka, and the Kolyma Mts. reaching in the west the Kolyma River and the city of Okhotsk (Krivošeev 1984); the Kolyma River is posing a hard border between its delta and Srednekolymsk (Tavrovskij et al. 1971). Next in size is a fragment along the Âna River, with radius of ~300–400 km around the city of Verhoânsk. Two small isolates are (i) between the Âna and the Kolyma on the Indigirka River between Predporožnyj and Tebûlâh (at about 69° of northern latitude; pt. 1 in Fig. 6) where sousliks expanded range during the 20th century (Tavrovskij et al. 1971); and (ii) in the Momske Mts. between the rivers Indigirka and Kolyma (pt. 2 in Fig. 6; Tavrovskij et al. 1971).

Of the Siberian islands *U. parryii* inhabits only Ajon (Ûdin et al. 1984) but is widespread in the islands offshore southwestern Alaska. Cook et al. (2010) list 37 such islands in six island groups: Kodiak Archipelago (6 islands populated by *U. parryii*), Barren Islands (1), Semidi Islands (11), Shumagin Islands (13), Sandman Reefs (1), and Aleutian Islands (5). Island occurrences are mainly the result of human-mediated introductions since 1895. The Arctic souslik is known to be indigenous on 3 islands and introduced on 4 islands; it was probably/possibly introduced on further 10 islands while it is possibly indigenous on two islands (Cook et al. 2010). *U. parryii* is native to St. Lawrence Island (MacDonald & Cook 2009).

Arctic sousliks occupy well drained steppe in river valleys and on riverine terraces, mountain tundra, tree-less Alpine belt, sparse taiga, and screes on mountain slopes. Broadleaf woodland is avoided, as are also wet and dump places (Tavrovskij et al. 1971, Krivošeev 1984). Well drained sites (which are also permafrost-free) are required in river valleys but mesic habitats are populated in high-elevation tundra (Kišinskij 1972). Habitat selection is similar in North America: tundra, Alpine meadows and boreal forests with short (6–10 weeks) growing season (Torre not dated). While this species is common to abundant in meadows, boreal forests are

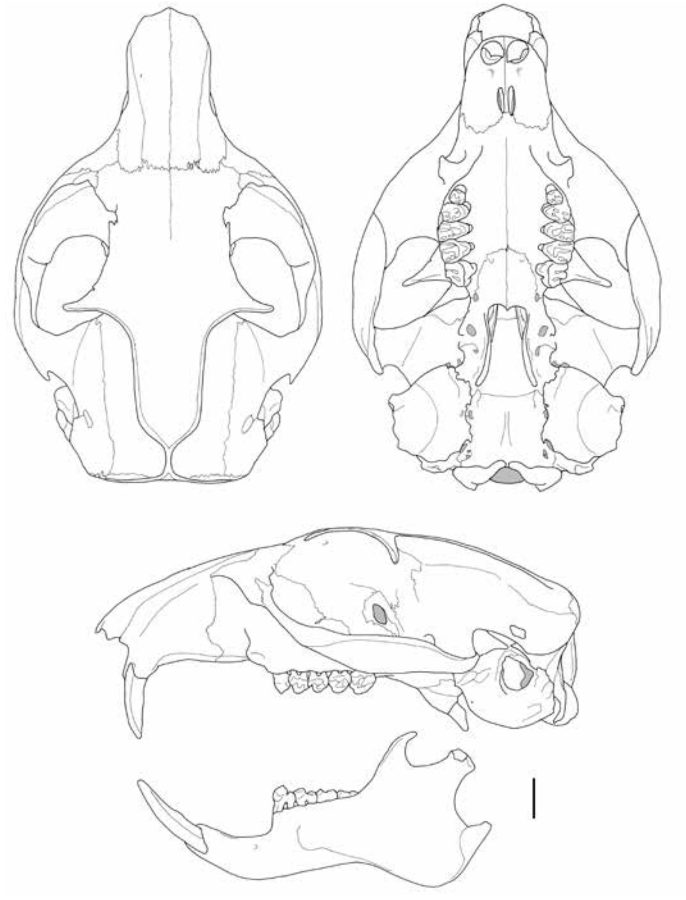


Fig. 10. Skull and mandible of *Urocitellus parryii leucosticus* (adult male from Lavrentiâ Gulf, Chukotka, Russia; SMF 47903). Scale bar = 5 mm.
Obr. 10. Lebka a mandibula *Urocitellus parryii leucosticus* (adultní samec z Lavrentijského zálivu, Čukotka, Rusko; SMF 47903). Měřítko = 5 mm.

population sinks for Arctic sousliks (Donker & Krebs 2011). Elevational range is from sea level to upper margin of tundra in Siberia (Krivošeev 1984), up to 1300 m a. s. l. in the Kolyma highlands (Kišinskij 1972), up to 1400–1500 m elsewhere (Gromov et al. 1965); from "sea level to well above tree line" (Mac Donald & Cook 2009) in Alaska.

Arctic sousliks are the northernmost hibernating terrestrial mammal. Their survival in extreme latitudes is facilitated by their low critical body temperature (–18° C), the lowest known metabolic rate in any endothermic hibernator (0.012 ml O_2 g $hour^{-1}$ during torpor at 4° C), and the capacity to recover even if their body temperature drops down to –2.9° C during hibernation (Sheriff et al. 2011, Torre not dated). Arctic sousliks hibernate from mid-October to second half of April in Yakutia (Tavrovskij et al. 1971) and from September–October and mid-April further northeast (Krivošeev 1984). In North America hibernation lasts for 215–240 days and sousliks emerge around mid-April (Torre not dated); phenology varies even over a small spatial scale (Sheriff et al. 2011).

Subspecies. Ten subspecies are reported from the entire range (Thorington et al. 2012) and up to four subspecies were recognized from Siberia (Gromov & Erbaeva 1995). Vorontsov et al. (1980) found no significant cranial variability among Siberian populations. Phylogeographic assessment retrieved a single Beringian phylogeographic lineage which occupies also St. Lawrence Island and Seward Peninsula in western Alaska (Galbreath et al. 2011). Evidently, *U. parryii* diversified in North America and colonized Siberia fairly recently. We classify all Siberian populations as a single subspecies.

Urocitellus parryii leucosticus (Brandt, 1844)

Synonyms. *brunniceps*, *buxtoni*, *stejnegeri*, *janensis*, *coriakorum*, *tschuktschorum*; also *Citellus lyratus* Hall et Gilmore, 1932, with the type locality on St. Lawrence Island ("Iviktook Lagoon, about 35 miles NW Notheast Cape"; MacDonald & Cook 2009).

Description. See above under species.

Geographic range. The entire Siberian range, St. Lawrence Island, and Seward Peninsula in western Alaska (Fig. 6). Morphological uniqueness of the Seward population among the Alaskan Arctic sousliks was noted already by Rausch (1953).

Subtribe: Arctomyina Gray, 1821

Since the subtribe contains a single genus *Marmota*, the description of the genus serves for the subtribe.

Genus: *Marmota* Blumenbach, 1779 – Marmots

1775 *Marmota* Frisch. Genus includes *Mus alpinus*, *Marmota polonica*, *Cricetus* ("der Hamster") and *Gerbus* ("das barbarische hüpfende Murmelthier" from Africa) (Frisch 1775: 9). The entire publication is rejected for nomenclatorial purposes and *Marmota* Frisch is unavailable name (ICZN 1954).

1777 *Glis* Erxleben. This name contains various rodents, incl. marmots (*marmota*, *monax*, *canadensis* = *monax*). Antedated by *Glis* Brisson, 1762, which is undoubtedly a member of Gliridae.

1779 *Marmota* Blumenbach. Type species: *Marmota alpina* Blumenbach, 1779 (= *Mus marmota* Linnaeus, 1758).

1780 *Arctomys* Schreber. Included are species now in *Marmota* (*marmota*, *monax*, *bobac = bobak*, *empetra=monax*; Plates CCVII–CCX), *Poliocitellus* (*franklinii*; Plate CCX.A), *Urocitellus* (*richarsonii* in Plate CCX.B, and *parryi* (sic) in Plate CCX.D), *Ictidomys* (*hoodi =tridecemlineatus*; Plate CCX.C), *Otospermophilus* (*beecheyi*; Plate CCX.E), and *Spermophilus* (*citillus = citellus*; Plates CCXI.A–CCXI.B). *Arctomys* was restricted to marmots (*marmota* and *empetra=monax*) by Cuvier (1825: 160). Type species: *Marmota marmota* (Plate CCVII).

1780 *Lagomys* Storr. Renaming of *Arctomys* (Storr 1780: 39). "Although Storr and Schreber (= *Arctomys*) bear the same apparent date, it appears safe to take Schreber as the earlier, since Storr alludes to the genus *Arctomys*" (Miller 1896).

1811 *Lipura* Illiger. Type species: *Hystrix hudsonius* (= *Marmota monax*).

1922 *Marmotops* Pocock. Type species: "*M. monax*" (footnote on p. 1200). Proposed as a genus for marmots having "Pollex retained" as opposed to *Marmota* with "Pollex suppressed". The following species were included into *Marmotops*: *bobak*, *himalayana*, *hodgsoni* (= *himalayana*), and *caudata*, as well as "*M. monax* and other N. American species." (Pocock 1922: 1200). Howell (1938: 38) ranked *Marmotops* as a subgenus.

1999 *Petromarmota* Steppan, Akhverdyan, Lyapunova, Fraser, Vorontsov, Hoffmann et Braun. Type species: *Marmota caligata*; proposed as a subgenus; entirely Nearctic.

Marmots are heavy and thickset ground squirrels of a badger appearance. Tail is short (< ½ HbL), densely haired and not flattened; cheek pouches are rudimentary or absent. The head is short, with broad and rounded muzzle. Eyes are large and the inconspicuous ears are concealed in fur. Feet are robust with 4 front and 5 hind digits bearing long, slightly curved and fossorial claws. The vestigial first digit in fore foot has a small nail in all marmots except in *M. marmota*. Palm and sole are naked, with 5 and 6 pads, respectively. Marmots are plantigrade in gait. All Palaearctic species, excluding *M. marmota*, possess dark-tipped guard hairs, which are softer and finer than the underfur. The colour is typically shades of brown and grey, often with streaks or patches of white, black, reddish or yellow in dorsal surface; only *M. caudata* with its golden-reddish fur differs strikingly from the remaining marmots. Females of Palaearctic species have nipples in (4)5–6 pairs (1–2 pectoral, 2 abdominal, 2 inguinal; Ognev 1947). Baculum is a relatively small, irregularly flattened rod of sigmoid shape bearing in some species few denticles at its expanded distal end. Skull of *Marmota* resembles that of *Spermophilus* (sensu lato) in most essential features, but is of much greater size and more powerfully ridged for muscle attachment. Dorsal profile is less convex and the braincase is flattened, consequently the occipital height equals the height of rostrum at the level of anterior alveoli. Interorbital region is broad and depressed, postorbital processes are very thick and heavy, nearly transverse, and curve out and down. Supratemporal ridges converge into a prominent sagittal crest on the posterior half of the braincase. Squamosals are expanded, lambdoid crest is high, occiput is strong and prominent, paroccipital process is short but robust. Nasals abruptly bent downward anteriorly; infraorbital canal is not well opened; masseteric knob is prominent. Zygomatic arches are heavy, with well ridged upper border of zygomatic plate. Mandible is less angular than in *Spermophilus*. Maxillary tooth-rows diverge slightly. Upper incisors are wide, with anterior surface slightly flattened. Enamel pattern of cheek-teeth is essentially as in *Spermophilus*, except that inner tubercles are lower and less compressed in upper teeth, and cusps are more robust (Fig. 11), lower and with larger crushing surfaces in lower teeth. The anterior premolars are functional. In the upper row, molariform teeth have two transverse ridges each; the third molar is the largest. Each of the lower teeth bears two low external cusps. Dental formula: 1/1, 0/0, 2/1, 3/3 = 22 (Miller 1912, Allen 1940, Ellerman 1940, Ognev 1947, Gromov et al. 1965). A 38-chromosomal karyotype of mostly biarmed (meta- and submetacentrics) chromosomes

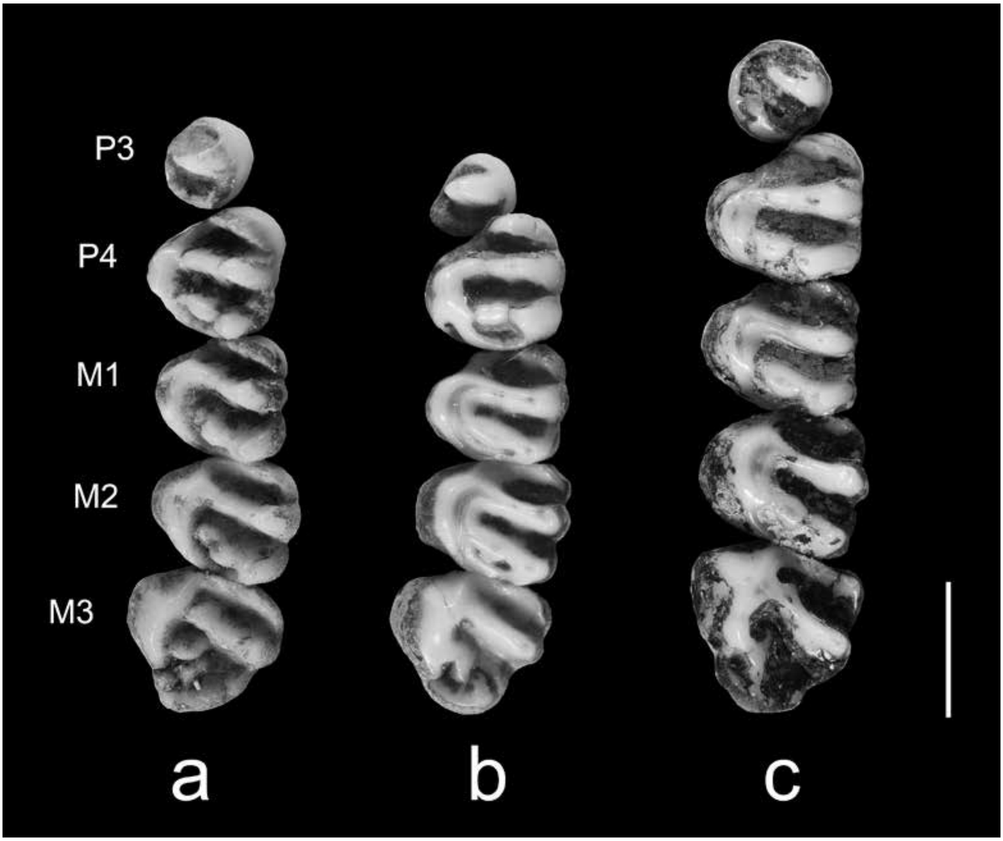


Fig. 11. Maxillary cheek-teeth in marmots: a – *Marmota marmota* (Schladming, Styria, Austria; ZFMK 78.77); b – *M. caudata* (Pandjir Valley, 10 km north of Astana, Afghanistan; ZFMK 93.444); c – *M. kastschenkoi* (near Akademgorodok, Novosibirsk District, Russia; ZFMK 87.789). Scale bar = 5 mm. Photo by Boris Kryštufek.
Obr. 11. Horní řady zubů svišťů: a – *Marmota marmota* (Schladming, Styria, Austria; ZFMK 78.77); b – *M. caudata* (Pandjir Valley, 10 km severně od Astana, Afganistan; ZFMK 93.444); c – *M. kastschenkoi* (blízko Akademgorodku, Novosibirsk, Rusko; ZFMK 87.789). Měřítko = 5 mm. Foto Boris Kryštufek.

is supposedly the ancestral in *Marmota* and prevails in majority of recent species (Brandler et al. 2008). Diploid number is low in all marmots, but number of chromosomal arms is high (fundamental number = 62–66; Lâpunova & Voroncov 1969).

Marmots are a Holarctic group, and they occupy the niche of giant sousliks. They mainly occupy montane pastures, meadows in a rolling country, steppes, tundra and rocky habitats. The solitary Nearctic *M. monax* inhabits deciduous forest habitats and *M. kastschenkoi* prefers a wooded forest steppe (“lesostep”). Various species of *Marmota* are considered as typical component of a periglacial fauna (Zimina & Gerasimov 1973). Marmots in general have poor abilities to dump excess heat and face problems at high ambient temperatures. Thermoregulatory constraints are putatively important determinant of species ranges and set the lower limit of their altitudinal distribution (ARNOLD 1992). Closely related species of *Marmota* tend to stay in similar environments (DAVIS 2005). All Palaearctic marmots are diurnal, social and live in extended families (ARMITAGE 2000); they all hibernate for up to eight months per year (ARNOLD 1992).

The genus *Marmota* originated in North America (known since the Miocene at 9.5 mya; HOFFMANN & NADLER 1968), while Asia was invaded via Bering land bridge at about 4.6 mya (STEPPAN et al. 2011); a subsequent expansion across Eurasia was rapid. The extant Palaearctic lineages appeared within a period of <1 million years (STEPPAN et al. 2011). Modern species emerged by allopatric speciation during the Middle Pleistocene or afterwards. Although the earliest fossils in the Palaearctic date back to the late Pliocene (ZIMINA & GERASIMOV 1973), fossil history is traceable only in six species (ERBAJEVA & ALEXEEVA 2009a, b). Despite of low genetic divergences among species (LYAPUNOVA & BRANDLER 2001, BRANDLER & LYAPUNOVA 2009, BRANDLER et al. 2010) the interspecific hybridization is much less common in marmots than in ground squirrels (*Spermophilus*). Slight overlap of ranges is known in the following tandems: *bobak – baibacina*, *baibacina – sibirica*, *baibacina – caudata*, *caudata – himalayana*, and *caudata – menzbieri*; hybrids (individuals of the intermediate phenotype) were reported only between *baibacina* and *bobak*, and *baibacina* and *sibirica*.

During the last century, the taxonomic arrangements oscillated between three species in ELLERMAN & MORRISON-SCOTT (1951) and the present nine species (e.g. THORINGTON et al. 2012). The intraspecific variation in different features and traits (body size, colouration, annual cycle, physiology, alarm calling) is evident in all marmots, much of this is phenotypic however (ARMITAGE 2005).

Division into subgenera and species groups follows STEPPAN et al. (1999) and BRANDLER & LYAPUNOVA (2009). All Palaearctic marmots are in the subgenus *Marmota*, which includes also the Nearctic *M. monax* and *M. broweri*. The remaining 4 Nearctic species are in the subgenus *Petromarmota.* Cranial traits that allow discrimination of *Petromarmota* from *Marmota* are present early in development and are conserved during post-natal ontogeny (CARDINI & O'HIGGINS 2005). Within the Palaearctic marmots, analyses based on skull morphology failed to cluster species in accordance to their phylogenetic affiliations (CARDINI 2003, CARDINI & O'HIGGINS 2005). Palaearctic *Marmota* is divided into four species groups (Fig. 12): (1) *marmota* group with *M. marmota* as the only species; (2) *caudata* group with *M. caudata* and *M. menzbieri* (not sister species in the results by STEPPAN et al. 2011); (3) *camtschatica* group with *M. sibirica*, *M. himalayana* and *M. camtschatica*, and (4) *bobak* group with *M. bobak*, *M. baibacina*, and *M. kastschenkoi*. The terminal clades in the subgenus *Marmota*, i.e. the *bobak* and the *camtschatica* groups (Fig. 12), were traditionally clumped into *bobak* group (e.g. BIBIKOW 1996). Segregation of the *bobak* and the *camtschatica* groups is supported also in karyological analyses (BRANDLER et al. 2008).

Key to Species

1 Guard hairs rush, with pale tips; head blackish, muzzle contrastingly pale in some animals (Fig. 13); the vestigial first digit in fore foot lacks a nail; range is to the west of the Dnieper River (Alps, Carpathians, Pyrenees). .... *M. marmota*

1* Guard hairs usually soft, rarely rush, with dark tips; head without a contrastingly pale muzzle; the vestigial first digit in fore foot bears a small nail; range is to the east of the Dnieper River. 2

2 Tail thick and long, usually >40% of HbL. .... *M. caudata*

2* TL <40% of HbL. 3

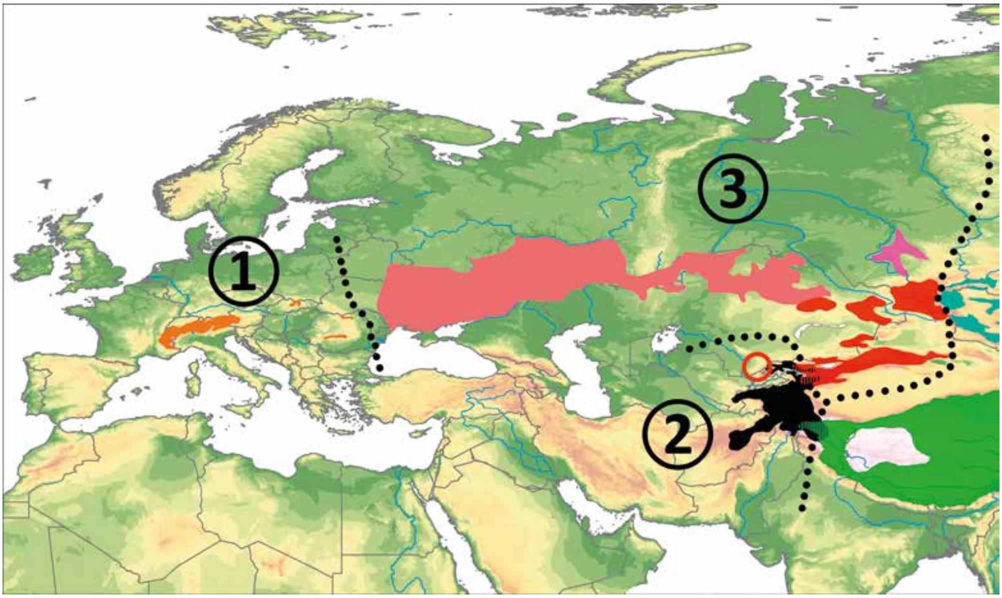


Fig. 12. Ranges of species groups of Palearctic marmots. Tentative phylogenetic relationships among these groups are shown right bottom. Range of *Marmota menzbieri* is encircled.

3 The anterior end of nasals pointed (Fig. 50); the entire animal bi-coloured (most evident in dark pelage during the second half of the season): pale fur on the anterior body contrasts the dark posterior part (Figs. 48, 49). .... *M. menzbieri*

3* The anterior end of nasals rounded; the entire animal not bi-coloured in the anterior-to-posterior direction. 4

4 Pelage is of black-and-white appearance; head is dark-brown to black from the nose to behind the ears (Figs. 38, 39 and 42). .... *M. camtschatica*

4* Pelage is buff or grey; dark area on the head is absent or does not expand behind the ears. 5

5 Muzzle is buff (Fig. 34); the distribution area is to the south of 40° northern latitude. .... *M. himalayana*

5* Muzzle is dark-brown or black; the distribution area is to the north of 40° northern latitude. 6

6 Pelage is normally light fulvous; the distal part of tail dark for ~$^1/_2$ of TL; *processus nasalis ossis premaxillae* is wider than the nasal bone (Fig. 32). .... *M. sibirica*

6* Pelage is buff, brown, yellow or grey; the distal part of tail dark for <$^1/_2$ of TL; *processus nasalis ossis premaxillae* is narrower than the nasal bone. 7

7 Diploid number of chromosomes 2n = 36. .... *M. kastschenkoi*

7* Diploid number of chromosomes 2n = 38. 8

8 Tail longer, with 21–23 caudal vertebrae; auditory bullae elongate (Fig. 26); karyotype with 66 autosomal arms. .... *M. baibacina*[1]

8* Tail shorter, with 19–20 caudal vertebrae; auditory bullae rounded (Fig. 22); karyotype with 62 or 64 autosomal arms. .... *M. bobak*[1]

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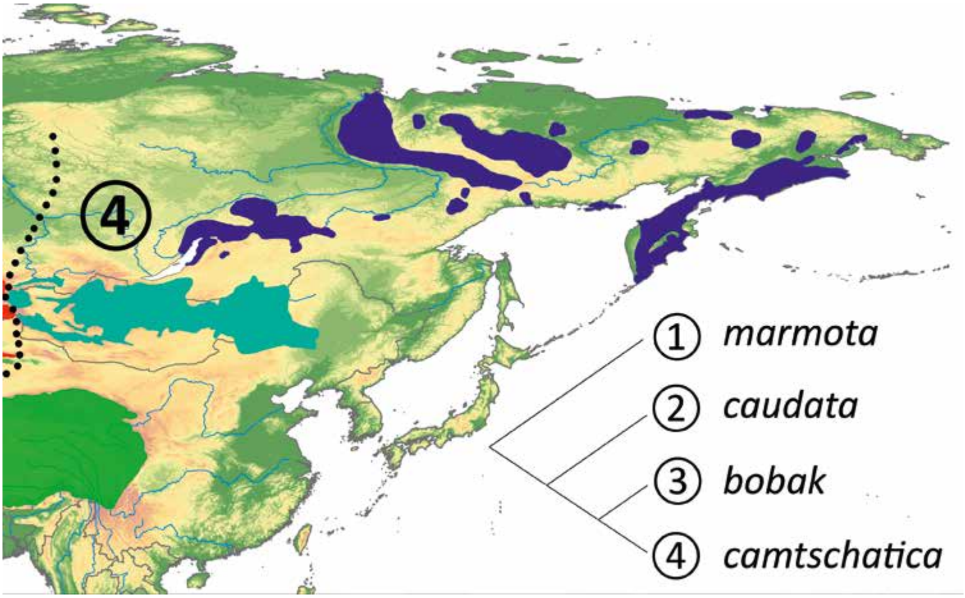
[1] For further comparison between *M. bobak* and *M. baibacina* see Remarks under the later.



Obr. 12. Areály rozšíření druhových skupin palearktických svišťů. Jejich přibližné fylogenetické vztahy jsou znázorněny vpravo dole. Areál *Marmota menzbieri* je zakroužkován.

Species group *marmota*

Included is a single species which is basal to the Palaearctic clade of marmots. Characteristic are shaggy fur and absence of pollex on the fore foot. Endemic to the Alps and the Carpathians (Fig. 12).

Marmota marmota (Linnaeus, 1758) – Alpine marmot

1758 *Mus marmota* Linnaeus. Type locality: "Habitat in alpibus Helveticis, Tridentinis" (= Inhabits the Alps in Switzerland and Trentino-Alto Adige [northern Italy]). Type locality restricted to "Swiss Alps" (Thomas 1911) but mainly reported as the "Alps" (Miller 1912, Ellerman & Morrison-Scott 1951).

1762 *Marmota alpina* Brisson. Type locality: "Habitat in Alpibus" (= Occupies the Alps; p. 117). Unavailable name. Brisson (1762) was rejected for nomenclatorial purposes (ICZN 1998) because his names are not Linnean or binomial.

1779 *Marmota alpina* Blumenbach. Substitution of *marmota* (Ellerman & Morrison-Scot 1951: 513).

1801 *Arctomys marmota alba* Bechstein. Type locality not given.

1801 *Arctomys marmota nigra* Bechstein. Type locality not given.

1844 *Arctomys marmotta* Brandt. Misspelling (lapsus calami) of *marmota* (p. 364).

1891 *Arctomys marmotta* Flower et Lydekker. Misspelling (lapsus calami) of *marmota*; cf. caption to Fig. 2 on p. 455.

1904 *Marmota marmotta* Trouessart. Lapsus calami.

Fig. 13. Alpine marmots *Marmota marmota marmota* from various parts of their Alpine range to show variability in colour. a – Gran Paradiso, Italy; b and c – Hohe Tauern, Austria; d – Mangart, Julian Alps, Slovenia. Animals a–c are relict populations; d is from introduced population. Photo courtesy Nedko Nedyalkov (a); Dare Šere (b), Jan Matějů (c); Tomi Trilar (d).
Obr. 13. Svišti horští *Marmota marmota marmota* z různých částí jejich alpského areálu rozšíření vykazují variabilitu ve zbarvení. a – Gran Paradiso, Itálie; b, c – Hohe Tauern, Rakousko; d – Mangart, Julské Alpy, Slovinsko. Jedinci a–c pocházejí z reliktních populací, jedinec d je z introdukované populace. Foto Nedko Nedyalkov (a); Dare Šere (b), Jan Matějů (c); Tomi Trilar (d).

1961 *Marmota marmota latirostris* Kratochvíl. Type locality: "Kriváňský žleb", (= Kriváň trench, ca. 6 km east of village Podbanské, West Tatra Mts., Slovakia). Kratochvíl (1961) reported two different toponyms for the type specimen: Kriváňský žleb (pp. 290, 301) and Podbansko (p. 298). The actual locality where the specimen was collected is evidently Kriváňský žleb; Podbansko (correctly Podbanské) is a village below Kriváňský žleb, located within the forest zone and therefore too low to qualify as a marmot habitat.

Characteristics. (Figs. 13–15, 19). A medium sized marmot with moderately long tail (on average ~$^1/_3$ HbL; range = 20–40% HbL). The Alpine marmot is exceptional among the Palaearctic marmots due to the absence of polex on fore feet. Fur is long (33–35 mm on mid-

-back, 35–45 along flanks) and shaggy, colour noticeably varies (Figs. 13, 14, 19). Upper parts are a grizzle of black and buff; hairs are slate at bases, with wide buffy or grey terminal band. Top of head is usually blackish and contrasts less dark neck, a whitish to grey muzzle, and paler (a grizzle of blackish and buffy white) cheeks; this contrast is obscured in dark individuals. Underparts are yellowish tawny-buff, feet are buff, and the tail is darker than back, being mainly black for at least the terminal 1/3. Baculum (length up to 7 mm) is a simple and slightly asymmetrical rod with expanded base and rudimentary spatula which is irregularly denticulate (Pocock 1923). Females have 10 (rarely 8) nipples (Krapp 1978). The skull shows no peculiarities (Fig. 15); it is relatively narrow across zygomatic arches (ZyB = 58.8–69.8% CbL) and depressed in the medial portion at the interorbital region; postorbital processes not much bent downward. Enamel on front surface of incisors deep orange brown, rarely yellow. Number of alveoli in the maxilla (P4 → M3): 1-3-3-3-3; in the mandible (p4 → m3): 3-4-4-4 (Niethammer & Krapp 1978). Ranges for dimensions (in mm, weight in grams; sexes pooled): W = 1950–8000, HbL = 420–690, TL = 135–200, HfL = 78–105, EL = 19–34, CbL = 87.4–99.2, ZgB = 53.9–64.0, MxT = 19.4–24.0. Males are larger; in a sample from the Alps, male CbL_{52} = 93.5 (87.4–98.7), female CbL_{31} = 92.8 (87.8–97.3) (Krapp 1978). However, *M. marmota* is the least sexually dimorphic Palaearctic marmot with a male/female ratio in CbL = 1.007 (Matějů & Kratochvíl 2013). Karyotype: 2n = 38 (Zima & Král 1984).

Fig. 14. Skin of an adult female *Marmota marmota marmota* from the Basses Alpes, France (BMNH 8.8.10.65). Photo by Boris Kryštufek.

Obr. 14. Balk adultní samice *Marmota marmota marmota* z Nízkých Alp, Francie (BMNH 8.8.10.65). Foto Boris Kryštufek.

Range (Fig. 16) was restricted during the Holocene to the Alps and the Carpathians (Krapp 1978). The Quaternary range was more extensive, and encompassed the Pyrenees, the western Balkans, and the periglacial environments in the plains northward to Belgium and the Netherlands, and eastward to Moldavia (Kowalski 2001). Range oscillated already during the Pleistocene, as a consequence of climate change, and shrank significantly during the Holocene (Preleuthner & Bauer 2001, Herrero et al. 1992). Krapp (1978) concluded that autochthonous marmots survived in the High Tatra Mts. (the Carpathians) and the Western Alps. All the remaining extant populations were (re)introduced. Marmots were exterminated in many parts of the Eastern Alps (Preleuthner et al. 1995) and during the 19th century in the majority of the Carpathians: Romania (Popescu & Murariu 2001), Ukraine (possibly survived until WWI;

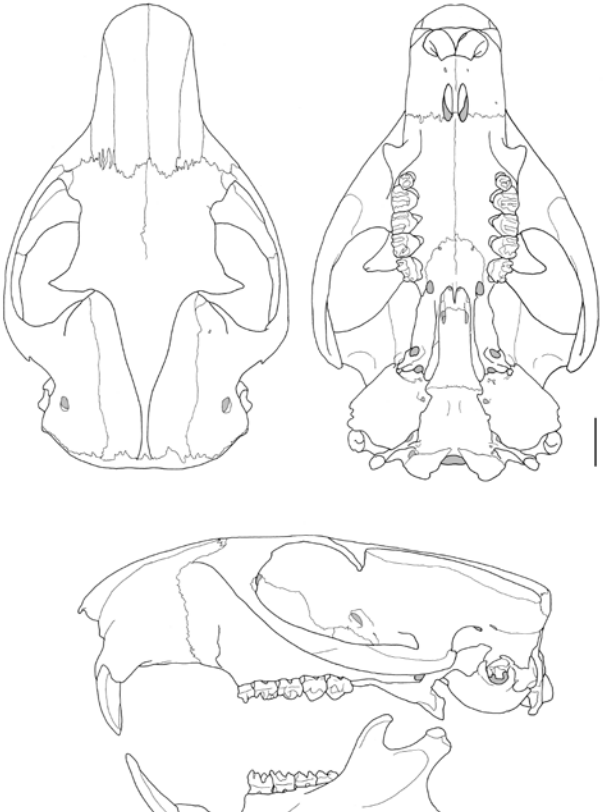


Fig. 15. Skull and mandible of an adult *Marmota marmota marmota* from Schladming, Styria, Austria (ZFMK 78.77). Scale bar = 1 cm.
Obr. 15. Lebka a mandibula dospělého jedince *Marmota marmota marmota* ze Schladmingu, Štýrsko, Rakousko (ZFMK 78.77). Měřítko = 1 cm.

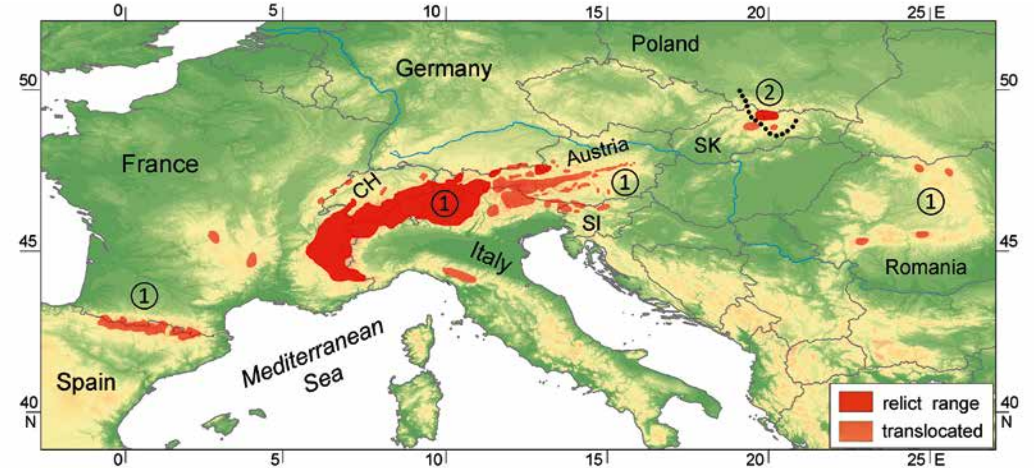


Fig. 16. Distribution of *Marmota marmota*. Compiled from the following sources: the overall range – Krapp (1978); Austria – Preleuthner et al. (1995); France – Ariagno (1984); Italy – Amori et al. (2008); Poland – Pucek (1983); Pyrenees – Barrio et al. (2012); Romania – Popescu & Murariu (2001); Slovenia – Vidic (1994); Slovakia – Chovancová & Krištofík (2012); Switzerland – Müller (1995). Subspecies: 1 – *Marmota marmota marmota*; 2 – *M. m. latirostris*. Country acronyms: CH – Switzerland, SI – Slovenia, SK – Slovakia.

Obr. 16. Rozšíření *Marmota marmota*. Sestaveno z následujících zdrojů: celkový areál – Krapp (1978); Rakousko – Preleuthner et al. (1995); Francie – Ariagno (1984); Itálie – Amori et al. (2008); Polsko – Pucek (1983); Pyreneje– Barrio et al. (2012); Rumunsko – Popescu & Murariu (2001); Slovinsko – Vidic (1994); Slovensko – Chovancová & Krištofík (2012); Švýcarsko – Müller (1995). Poddruhy: 1 – *Marmota marmota marmota*; 2 – *M. m. latirostris.* Zkratky názvů států: CH – Švýcarsko, SI – Slovinsko, SK – Slovensko.

Bashta & Potish 2007) and the Low Tatra Mts. (Nízké Tatry) of Slovakia (Feriancová 1955, Chovancová & Krištofík 2012).

Currently, autochtonous marmots are widespread in the French Alps (Haute-Alpes, Savoie, Maritime Alps, Ligurian Alps; Krapp 1978), in the entire Alpine arch in Switzerland (Müller 1995), in the Dolomites, the Ligurian Alps, Piedmont, Aosta valley, and the western Carnic Alps in Italy (Krapp 1978, Amori et al. 2008), and in western Austria (Vorarlberg and western Tirol), as well as in Berchtesgaden area on the German-Austrian border (Preleuthner et al. 1995). The only truly autochtonous marmots in the Carpathians are restricted to ~40 km of mountain ridge of the Western Tatra Mts. (Západné Tatry) and the High Tatra Mts. (Vysoké Tatry) in Slovakia and adjacent Poland (Chovancová & Krištofík 2012). Population in the Low Tatra Mts. was introduced between 1859 and 1881 from the High Tatra Mts. and the Alps, and inhabits currently ~85 km of the main mountain ridge (Feriancová 1955, Chovancová & Krištofík 2012).

Extant range is to a great deal a consequence of translocations and re-introductions; Preleuthner et al. (1995) identified 119 releases in Austria alone. The entire Pyrenean population, whose extant range covers ~8200 km^2 (Barrio et al. 2012), results from introduced marmots. Marmots were translocated to the Pyrenees of France (starting in 1948) wherefrom they expanded their range into Spain (established in 1968 at the latest; Herrero et al. 1992). Further introductions were to various localities in Jura Mts. (known from four populations in south-western Switzerland: Noirmont, Chasseron, Crex-du-Van, Chasseral; Neet 1992), Vosges Mts., and Massif Central (Mann et al. 1993), to Dolomites (in 2006–2007; Borgo et al. 2009), to north-western Apennines between Parma and Bologna (since 1950s; Sala et al. 1992), to the Eastern Alps in Austria (since 1860; Preleuthner et al. 1995) and in Slovenia (since 1954; Kryštufek 1991), and into the Carpathians in Romania (since 1973; Făgăraş Mts., Retezat Mts., and Călimani Mts.; Isuf 1996, Popescu & Murariu 2001, Benedek 2006). In Slovakia, marmots were re-introduced to Low Tatra Mts. (since 1859) and to the Belianske Tatra Mts. (in 2008 and 2009; Chovancová & Krištofík 2012). As a result of the above activities, the overall range mainly expanded during the 20th century, despite some regional extirpations, e.g. between the rivers Adda and Oglio in the Central Alps of Italy in 1911–1953 (Toschi 1954).

Majority of translocations (including some of those to the Low Tatra Mts.) involved marmots from the Alps. There is a single documented translocation of Tatra marmots to Tosco-Emiliano region in the north-eastern Apennines (Amori et al. 2008). Some of translocations failed, e.g. to Czech Republic (Anděra 2006), and the one to Schwarzwald Mts. (Germany) where marmots survived from 1954 into 1970s (Braun 1989). Contrary to claims in Hoffmann & Thorington (2005) and Thoringon et al. (2012), marmots were never introduced to Serbia and Montenegro.

The Alpine marmot is a high mountain animal, occupying altitudes from 800 to 3200 m a. s. l. (Krapp 1978), but this varies among regions: 900–2700 m in Austria (Preleuthner et al. 1995), 1350–2600 m in the Tatra Mts. (Chovancová & Krištofík 2012), and 1200–3000 m in Switzerland (Müller 1995); preferred elevations are 1800–2200 m in Austria (Preleuthner et al. 1995), 1800–2400 m in the Pyrenees (Herrero et al. 1994), 1770–2100 m in Belluno, Italy (Corona 1992), 2100–2500 in Aosta valley, Italy (Bassano et al. 1992), and below 2350 m in the Tatra Mts. (Chovancová & Krištofík 2012). In Switzerland, the optimal habitat starts

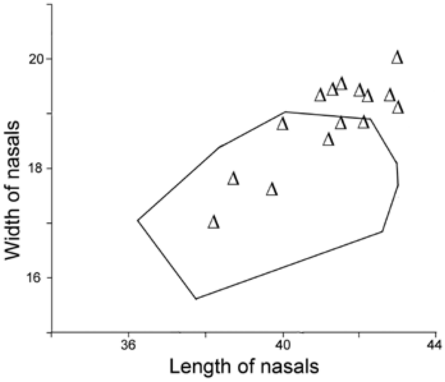


Fig. 17. Plot of greatest width of nasal bones against their length for *Marmota marmota*. Polygon encloses extremes for the nominotypical subspecies; individuals of a ssp. *latirostris* in the plot are shown by triangles.

Obr. 17. Korelační diagram největší šířky nosních kostí a jejich délky u *Marmota marmota*. Polygon ohraničuje extremní hodnoty nominotypického poddruhu; jedinci poddruhu *latirostris* jsou znázorněni trojúhelníky.

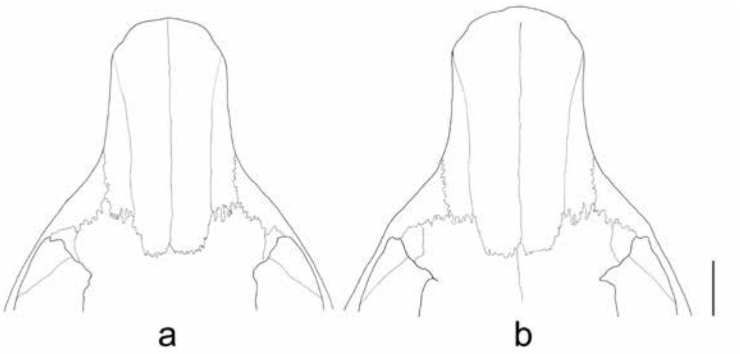


Fig. 18. Shape of nasal bones which are supposedly characteristic for subspecies of *M. marmota*: a – *M. m. marmota* (Alps; NMP 47119); b – *M. m. latirostris* (Tatra Mts., Slovakia; NMP 47122). Scale bar = 1 cm.
Obr. 18. Tvar nosních kostí, u kterého se předpokládá, že je charakteristický pro jednotlivé poddruhy *M. marmota*: a – *M. m. marmota* (Alpy; NMP 47119); b – *M. m. latirostris* (Tatry, Slovensko; NMP 47122). Měřítko = 1 cm.

400–600 m above the upper forest edge (Müller 1995). The habitat is highly seasonal, with short vegetation period. Most suitable are open alpine meadows (*Nardus*, *Sesleria*, *Carex*) on alluvial terraces with deep soil, or on a rocky slopes (inclination of 15^0–45^0, southern exposure; plant cover of 25–75%; Rodrigue et al. 1992); shrubs (*Pinus mugo*, *Rhododendron*, *Salix*, *Vaccinium*) and woods are avoided. The importance of the alpine meadows and pastures is subordinate to the presence of rocks (e.g. Borgo 2003). Hibernation lasts for 6.5–7 months, i.e. from the first decade of October till the second half of April (Chovancová & Krištofík 2012).

Subspecies. The population which is isolated in the Tatra Mts. is nearly invariably recognized as subspecifically distinct (*latirostris*) from the nominotypical subspecies (Krapp 1978, Hoffmann & Thorington 2005, Thoringon et al. 2012). Morphological variability of the Alpine marmot was never assessed comprehensively and the genetic makeup of the Tatras population is still not known. We follow the established practice and keep marmots from the Alps and the Tatras as distinct taxa. We stress however that morphological dimensions for *latirostris* are entirely within the range for the Alpine population, except for a slightly wider anterior expansion of nasals in the former (Figs. 17, 18). Differences between the subspecies are therefore far from being categorical, as suggested by Kratochvíl (1961), which makes classification of individuals and even populations into a subspecies uncertain (see also Chovancová & Krištofík 2012).

Marmota marmota marmota (Linnaeus, 1758)

Synonyms. *alpina* Brisson, *alpina* Blumenbach, *alba*, *nigra.*

Description (Figs. 13–15). Anterior end of nasals less expanded: greatest width of nasals = 15.5–19.0 mm; n = 62 (Fig. 18a). Dimensions (in mm, weight in grams; sexes pooled): W_{29} = 4341 (1950–8000), HbL_{51} = 489.4 (420–690), TL_{27} = 161.5 (135–200), HfL_{30} = 86.5 (78–105), EL_{23} = 25.6 (19–34), CbL_{120} = 93.3 (87.4–98.7), ZgB_{111} = 59.5 (53.9–64.0), MxT_{125} = 22.2

(19.4–24.0) (Kratochvíl 1961, Krapp 1978; specimens in NMW, ZSM, BMNH, IVB, AMNH, NMNH, NMP, and PMS). Genetic variability is low among marmots from the Alps, probably a consequence of ancient bottlenecks and/or inbreeding (Preleuth & Pinsker 1993, Rassmann et al. 1994). Even in the autochthonous populations the microsatellite diversity decreases in west-to-east direction (Kruckenhauser & Pinsker 2008).

Geographic range (Fig. 16). The entire range except for the High Tatra Mts. (see under *latirostris*).

Marmota marmota latirostris Kratochvíl, 1961

Synonyms. No junior synonyms.

Remarks. Kratochvíl (1961) refers directly to the type of *M. marmota latirostris* on three occassions: (i) on p. 292 by figuring (Fig. 2) a male skull, collected by M. Blahout in Kriváňsky žleb in 1960; (ii) on p. 298 by reporting skull dimensions of a male, collected by M. Blahout in Podbansko in 31. V. (= May) 1960 (cf. the individual under #1 in the top line; the Table (at the bottom) is not numbered); (iii) on p. 300 by reporting the external measurements ("Rozměry těla"; cf. the right-hand column) for the type: "tělo (= HbL) 480 mm, tlapka (= HfL) 83 mm, ocas (= TL) 145 mm". Kratochvíl published the paper while at the IVB and his material is normally deposited in the Mammal Collection of the IVB. This, however, does not hold for the type specimen of *latirostris*. There are 11 individuals from the High Tatras in IVB, and 10 of them are from "Kriváň" (i.e. from the type locality of *latirostris*) but none is designated as the type. All topotypes are either flat skins (4 vouchers) or round skins (6 vouchers). The only skull

Fig. 19. Mounted specimen of *Marmota marmota latirostris* from the High Tatra Mts., Slovakia, collected in 1938 (NMP 57397). Photo by Boris Kryštufek.
Obr. 19. Vycpaný exemplář *Marmota marmota latirostris* z Vysokých Tater, Slovensko, ulovený v r. 1938 (NMP 57397). Foto Boris Kryštufek.

(with a skeleton) is labeled “Teryho chata” (Petr Koubek, personal information in 2013), and is therefore not from the type locality. The skull of the type specimen was not in the collection on 26 January 1992 when one of us (B.K.) examined cranial material of marmots in IVB, and is evidently lost. The type specimen is possibly a voucher skin recorded in the files of IVB as “5a”. Dimensions of this individual match the values for the type published by Kratochvíl (l. c.) on p. 300, except for HfL which is recorded as 85 mm in the IVB files, but reported as 83 mm in Kratochvíl (1961: 300).

Description (Fig. 19). Anterior end of nasals more expanded: greatest width of nasals = 17.0–20.0 mm; n = 15 (Fig. 18b). Dimensions (in mm, weight in grams); a female (IVB specimen) and a male (the type; Kratochvíl 1961), ranges in parentheses (from Chovancová & Krištofík 2012; sexes pooled): W = 2050, 3530 (3400–7000), HbL = 450, 480 (433–650), TL = 145, 145 (141–175), HfL = 83, 85 (81–85), EL = 26, 27. Cranial measurements (*sample size relates to the variation range): $CbL_{10/15*}$ = 93.5 (90.6–99.2), ZgB_{10} = 59.4 (57.3–61.2), MxT_{10} = 22.1 (21.2–22.8) (Kratochvíl 1961, Chovancová & Krištofík 2012).

Geographic range (Fig. 16). Endemic to the High Tatra Mts. in Slovakia and adjacent Poland; population mixed with marmots of the Alpine origin inhabits the Low Tatra Mts. Introduced to Tosco-Emiliano region in north-eastern Apennines (Amori et al. 2008). Inhabits high mountain pastures from 1350–1380 to 2280–2350 m a. s. l. (exceptionally to 2600 m) in the Tatra Mts. (Chovancová & Krištofík 2012). The entire population was estimated in 2008 at ~1175 individuals: 474 individuals in the Western Tatra Mts. and 700 in the High Tatra Mts. (500 in Slovakia, the remaining 200 in Poland). Additional 300–350 marmots inhabit the Low Tatra Mts. A pre-WWII census (~1200 marmots in Slovakia) suggests the entire population to be stable (Chovancová & Krištofík 2012).

Species group *bobak*

Included are short tailed marmots from steppes, forest-steppes, and mountain pastures between the Dniester River and Xinjang (Fig. 12). This is one of two terminal clades (*camtschatica* is the other) in the subgenus *Marmota*. Interspecific genetic divergences are lower than in other marmot groups. Despite their external and cranial similarities, these species are well defined karyologically. Three species are recognized: *bobak*, *baibacina*, and *kastschenkoi*.

Marmota bobak (Müller, 1766) – Baibak, Bobak marmot

1762 *Marmota polonica* Brisson. “Habitat in Polonia” (= occupies Poland; p. 116). Unavailable name. Brisson (1762) was rejected for nomenclatorial purposes (ICZN 1998) because his names are not Linnean or binomial.

1776 *Mus bobak* Müller. Type locality: “Der Aufenthalt ist in Polen” (= residence is in Poland). “Poland” in Miller (1912: 937) and Ellerman & Morrison-Scott (1951: 514). Because the geographic scope of Poland varied over time, Ognev (1947) concluded that *terra typica* is “Pravobrežnaâ Ukraina”, which is translated in the English edition as “Ukrainian territory on the right bank of the Dnieper” (Ognev 1963: 221).

1780 *Arctomys bobac* Schreber. Unjustified emendation of *bobak* by changing the terminal letter (k) to (c) to accord standards of classical Latin script (Nikol’skij 1999, 2000 2007).

1801 *Arctomys marmota tigrina* Bechstein. Type locality: “Pultawa” (= Poltava, Ukraine). Miller (1912) and Ellerman & Morrison-Scott (1951) placed this name into synonymy of *M. marmota*, most probably because Bechstein’s book, as indicated in its title, covers the German territory. Note that

Fig. 20. Bobak marmots *Marmota bobak* from Tatarstan, Russia. Note variation in colour and the extent of a black facial mask. Right bottom individual displays dull rusty-brown belly. Photo courtesy Alenka Kryštufek.
Obr. 20. Svišti stepní *Marmota bobak* z Tatarstánu, Rusko. Povšimněte si variability ve zbarvení a v rozsahu černé obličejové masky. Exemplář vpravo dole má matně rezavo-hnědé břicho. Foto Alenka Kryštufek.

Bechstein (1801) reported *Arctomys marmota* to be inhabitant of the mountains of Europe and Asia: "Das Vaterland dieser Thiere sind die hohen Alpen Europens und Asiens". The type locality of *tigrina* is well within the range of *M. bobak*.

1811 *Arctomys baibak* Pallas. Terra typica: "In Poloniae, Rossiae et Sibiriae australioribus ..." (= in Poland, Russia and southern Siberia …; p. 155).

1844 *Arctomys baibac* Brandt. Unjustified emendation of *bobak* by changing the terminal letter (k) to (c) to accord standards of classical Latin script; cf. comment under *Arctomys bobac* Schreber, 1780.

1930 *Marmota bobak schaganensis* Bažanov. Type locality: "Okrestnosti sela Miroškino na r. Čegane v. Ural'skoj oblasti" (Ognev 1947) (= vicinity of the village Miroškino on the Čegan River, former Ural'skaâ Region (now Orenburg Region), Russia).

1966 *Marmota bobac kozlovi* Fokanov. Type locality: "... iz okrestnostej s. Verhnaâ Černavka, Vol'skogo r-na Saratovskoj obl." (= vicinity of village Verhnaâ Černavka, Volsk District, Saratov Region), Russia.

Remarks. In the past all the Palaearctic marmots with short fur and short tail (*baibacina*, *kastschenkoi*, *sibirica*, *himalayana*) were considered to be part of *M. bobak* (e.g. Ellerman & Morrison-Scott 1951, Bibikow 1996). The name is frequently misspelled *bobac* (Flower & Lydekker 1891, Trouessart 1910, Ognev 1947, Flint et al. 1965, Gromov et al. 1965).

In the Kazakh highlands where *M. bobak* is in contact with *M. baibacina*, marmots show transitional morphological characteristics. Animals from the western side of this zone (to the southeast of Karaganda) are classified as *M. bobak*, and those from the eastern side as *M. baibacina* (Sludskij et al. 1969). For comparison between *bobak* and *baibacina*, see under the later.

Remnants from the Middle Pleistocene are reported from various sites in the Urals, European Russia, the Caucasus, Ukraine and Crimea (Gromov et al. 1965, Markova 2000, Markova & Rumâncev 1999). During the Late Pleistocene, baibak occurred as west as the Carpathians (Radulesco & Kovács 1970).

Description (Figs. 20–22). Large and short-tailed marmot; tail accounts on average for $^1/_5$ HbL (range = 15.4–27% HbL). Differs from *M. marmota* in retaining the small thumb with a nail on the front paws. Fur is soft but short (mainly <20 mm). Colour is more or less uniform yellowish brown except for upper parts which are clouded with brown or black hair tips; dark-tipped hairs are most numerous in the posterior back. The front head down to the eyes (and in some animals to the cheeks) is dark brown to blackish; lips are cream or grey and the ears are buff. The tail is of same colour as back, its distal $^1/_3$ – $^1/_5$ is chestnut brown. Flanks and limbs are of same colour as the back although they tend to be tinted less black. The belly is yellow (like the back) or rusty to dull (Fig. 21). Underfur is yellow throughout the body and hair bases are slate. Claws are blackish. Juveniles are more dull and grey, with rusty head and dark brown nose. Females have 10–12 nipples (Miller 1912, specimen PMS 19408). The baculum is bent, with much expanded and uplifted base; number of denticles bordering the distal spatula is 2–5 (left side) and 1–3 (right side). Individual variation in the shape of baculum is significant (Fokanov 1966). Skull is wide and flattened (Fig. 22); ZgB accounts for 61.4–71.4% CbL. Interorbital region is wide and flattened; brain-case is broad; nasals bent down abruptly at their anterior tip; auditory bullae are circular. Mandible and cheek-teeth are more robust than in *M. marmota*; enamel on anterior surface of incisors is whitish to pale-yellowish, only exceptionally light--orange. In comparison with *M. baibacina*, the third lower molar is smaller in *bobak*, the lower incisor is narrower and the posterior root of fourth lower premolar (p4) is simple (bifurcates distally in 10% of *baibacina*). Hence, number of alveoli in the maxilla (P4 → M3): 1-3-3-3-3; in the mandible (p4 → m3): 2-4-4-4 (Niethammer & Krapp 1978). Dimensions (in mm, weight in grams) in baibaks from the two opposite parts of their range; Europe: (sexes pooled): W_2

Fig. 21. Skin of an adult female *Marmota bobak* from Fedotovka, Tatarstan, Russia (PMS 19408). Photo courtesy Ciril Mlinar.
Obr. 21. Balk adultní samice *Marmota bobak* z Fedotovky, Tatarstán, Rusko (PMS 19408). Foto Ciril Mlinar.

= 5500, 6700, HbL$_{13}$ = 531.6 (490–600), TL$_{10}$ = 121.1 (106–145), HfL$_{13}$ = 85.4 (80–90), EL$_{11}$ = 28.5 (19.0–33.5), CbL$_{42}$ = 95.5 (86.8–101.6), ZgB$_{40}$ = 64.2 (57.6–69.0), MxT$_{43}$ = 22.9 (20.0–24.8) (Miller 1912, Ognev 1947, specimens in PMS). Kazakhstan, males: W$_{14}$ = 4221.4 (2800–5400), HbL$_{16}$ = 508.7 (447–600), TL$_{15}$ = 97.9 (80–120), HfL$_{16}$ = 83.7 (76.9–96), CbL$_{15}$ = 89.6 (82.7–97.0), ZgB$_{13}$ = 58.9 (50.8–65.2), MxT$_{17}$ = 21.9 (20.0–23.0); females: W$_{16}$ = 3952.5 (2700–4650), HbL$_{17}$ = 501.2 (440–540), TL$_{16}$ = 100.1 (80–124), HfL$_{17}$ = 80.8 (74.0–89.0), CbL$_{16}$ = 86.7 (80.4–97.0), ZgB$_{15}$ = 57.6 (51.4–64.8), MxT$_{16}$ = 21.4 (19.9–23.0) (specimens in SZM).

Baibaks from the Orenburg Region, which are geographically intermediate are larger; averages for three monthly samples (n = 6 for each sample) vary between 6.8 (in June) and 8.5 kg (in August) in body mass, and between 587 (July) and 603 mm (June) in head and body length (Rudi et al. 1994). Body mass in Celinogradsk District, Kazakhstan (scored between April and June); males: W_{213} = 3496 (2300–5700); females: W_{164} = 2806 (2300–5700). Maximal external dimensions (in mm, body mass in grams) recorded in the Kharkov Region, Ukraine: W = 9400, HbL = 620, TL = 170, HfL = 100, EL = 35 (Zorya 2005). Secondary sexual dimorphism in size is more pronounced than in the majority of Palaearctic marmots; male/female ratio in CbL = 1.033 (Matějů & Kratochvíl 2013). Karyotype: 2n = 38, fundamental number of autosomal arms 62 or 64 (Lâpunova & Voroncov 1969).

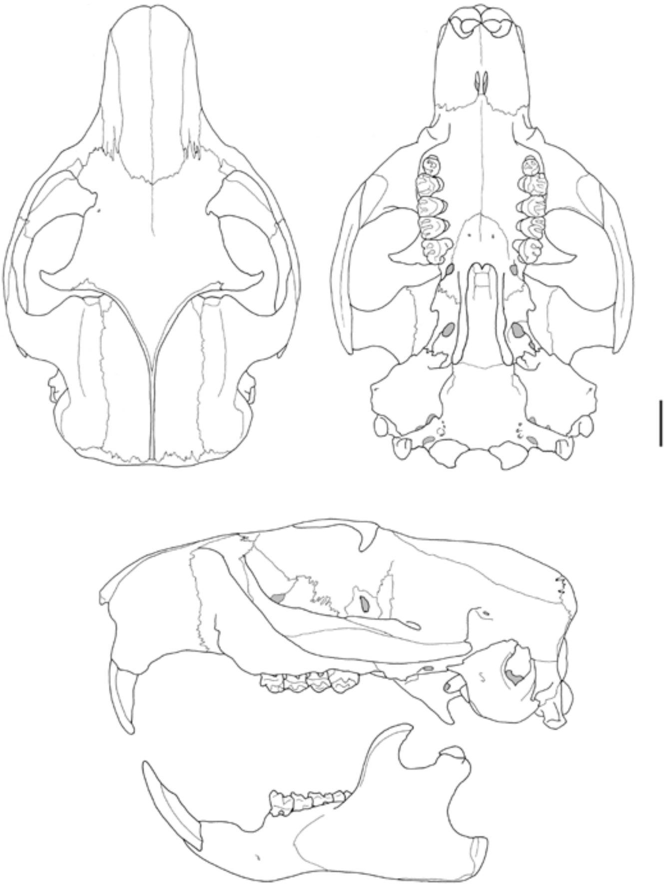


Fig. 22. Skull and mandible of an adult *Marmota bobak* from Sarabikulovo, Tatarstan, Russia (PMS 19638). Scale bar = 1 cm.
Obr. 22. Lebka a mandibula adultního jedince *Marmota bobak* z lokality Sarabikulovo, Tatarstán, Rusko (PMS 19638). Měřítko = 1 cm.

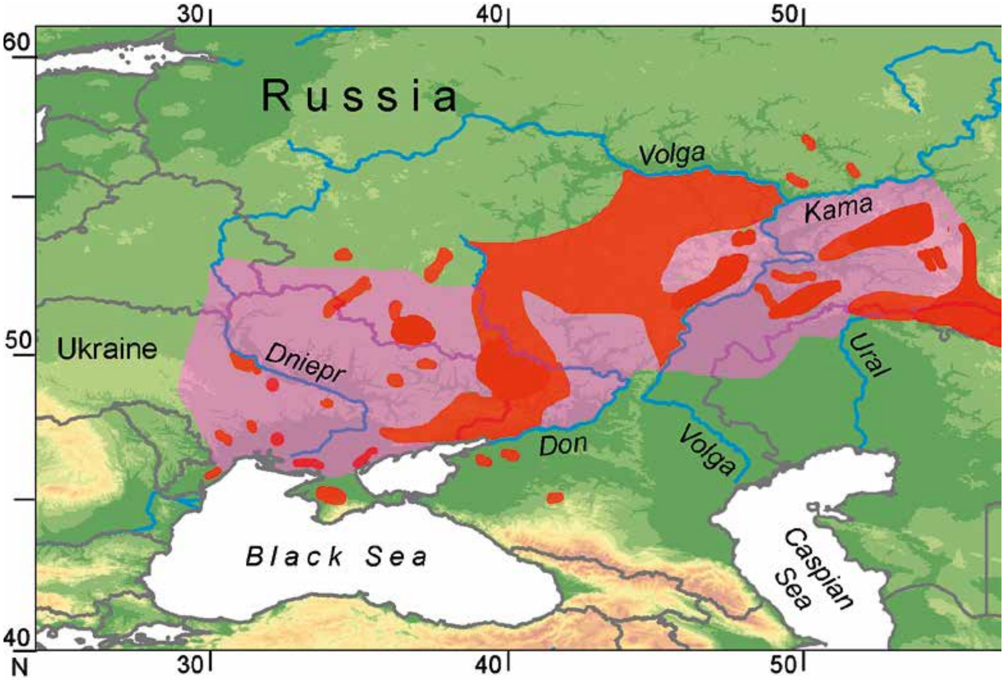
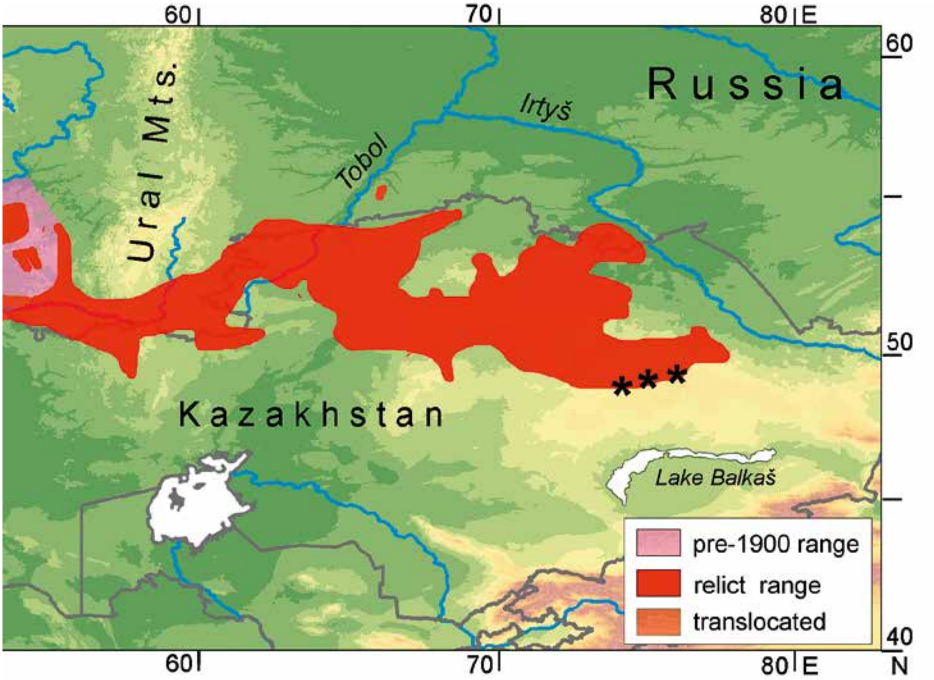


Fig. 23. Distribution of *Marmota bobak*. Compiled from the following sources: range in Europe and western Asia – Ognev (1947), Bobrov et al. (2008); Ukraine – Rumyantsev & Bibikov (1994); Kazakhstan – Sludskij et al. (1969). Asterisks indicate *M. bobak* with morphology which is transitional to *M. baibacina* (Sludskij et al. 1969).

Geographic range (Fig. 23). Formerly occupied a wide belt of chernozem soil in Ukraine, Russia and northwestern Kazakhstan, i.e. between the rivers Dniester in the west and the Irtyš in the east. The northern border was at ~51° northern latitude in Ukraine and ~55° to the east of the Volga; baibaks avoided the Ural Mts. (Sludskij et al. 1969). Since the late 18th century the range shrunk and populations declined as a result of spread of agriculture and unregulated cull; by mid-20th century only several thousand baibaks survived in Europe. Colonies were along the Don River (Kamennaâ steppe near Voronež, Strileckaâ and Derkulskaâ steppes near Lugansk, Velikij Burluk near Kharkov, and Kašarsk near Rostov on Don) and in a hilly zone on the right bank of the Volga, which was not suitable for a large-scale ploughing (Regions of Saratov, Samara, and Ulânovsk; Sokur 1961, Gromov et al. 1965, Bibikov 1991, Šlâhtin et al. 2009). Transformation of steppes in the southern Urals was postponed into 1950s. The colonies were subsequently largely isolated in 1960s and 1970s (Rudi et al. 1999); in the Region of Orenburg only several tens of colonies survived (Rudi et al. 1994). Although first reintroductions were undertaken in Ukraine already in 1936 (Kiris 1973), a significant population recovery started in 1970s following a series of large-scale translocations: 41,955 baibaks were released in 375 localities in Russia during 1977–1990 (Bobrov et al. 2008) and 2800 individuals in >40 sites



Obr. 23. Rozšíření *Marmota bobak*. Zkompilováno z následujících pramenů: areaál v Evropě a západní Asii – Ognev (1947), Bobrov et al. (2008); Ukrajina – Rumyantsev & Bibikov (1994); Kazachstán – Sludskij et al. (1969). Hvězdičky ukazují populace *M. bobak*, jejichž morfologie vykazuje přechodný stav směrem k *M. baibacina* (Sludskij et al. 1969).

in Ukraine between 1986 and 1993 (Rumyantsev et al. 2012). Ulânovsk Region, which was always an important donor, provided 2599 marmots for translocations between 1979 and 1989 (Abrahina & Dimitriev 1999). Baibaks were translocated also to southwestern Siberia (Region of Omsk; Mal'kova et al. 2003). Reintroductions in the northern part of the range yielded better results (Rumyantsev et al. 2012) and baibaks expanded range by 15–25 km every 20 years (Tokarsky 1994, 2005); in Mordovia, the average range expansion during 15 years was 1.2 km per year (Barmin 1999).

Population in Tatarstan nearly doubled its number in a single decade, from 11,946 baibaks in 1982 to 21,994 individuals in 1991 (Gorškov & Pavlov 1999). By 1990s *M. bobak* already reestablished along the Volga, being present in the administrative districts of Mary El, Nižnij Novgorod, Chuvashia, Mordovia, Ulânovsk, Penza, Saratov, Udmurtia, Tatarstan, Bashkortostan, Samara and Saratov (Dimitriev et al. 1994). Baibaks recolonized significant proportion of their historical range also elsewhere and are occasionally found also outside their former borders (e.g. on the right bank of the Kama River, on the left bank of the lower Don, and in Crimea; Fig. 23). There were 330–340,000 baibaks in Russia during 1990s: 70–74,000 in the Volga region, 110–114,000 in the Ural region, and 150–152,000 in the southern zone of cernozem (Maškin

1999). The major part of range in Kazakhstan is in the upper flow of the Išim River (south of Petropavlovsk–Omsk line). Evidently, there was no shrink in range in Kazakhstan although populations declined severely due to unsustainable cull; ~260,000 skins were harvested annually in mid-1920s compared to ~19,000 in 1940s and 1950s (Sludskij et al. 1969) and ~700,000 in 1880s (Bibikow 1996). Currently, baibak is the most abundant marmot in European Russia and Kazakhstan; in the former, 84% of about 1.5–1.9×10^6 marmots belonging to four species, are baibaks (Pole et al. 1994).

Baibaks populate steppes and open habitats in a forest-steppe (*lesnaâ step*) with various grasses and herbs from the genera *Poa*, *Taraxacum*, *Trifolium*, *Stipa*, *Festuca*, *Salvia*, and *Euphorbia*; grasses (*Stipa* and *Festuca*) dominate in southern Ural and eastward. Baibaks are among few marmot species which are tied mainly to low altitudes. Undulating landscape is preferred west of the Ural Mts. (Ronkin et al. 2009; own data), but flat steppe is the main habitat in Kazakhstan (Sludskij et al. 1969). Ismagilov (1961) distinguished 3 types of flat steppe inhabited by baibaks in Kazakhstan and characterized them by the dominant plants as (i) *Stipa sareptana* type, (ii) *Psathyrostachys juncea* type, and (iii) *Artemisia pauciflora* type. Large herbivores probably had significant impact on the range and population dynamics of baibaks by creating suitable habitats through grazing. Population densities of baibaks correlate positively with grazing pressure (Ronkin & Savčenko 1999). In Ukraine, baibak's historical range overlapped with regions of extensive livestock husbandry and population ups and downs during the 20th century recovery can be linked with the grazing pressure (Ronkin et al. 2009).

In regions which are under cultivation, baibaks occupy patches which are not suitable for agriculture, edges of fields and sides of dirt roads (Semikhatova & Karakul'ko 1994), but also crop fields and even deserted villages (Bibikov 1991, Suntsov et al. 1994). Baibaks hibernate between early September – end of November and March – early April (Šubin et al. 1978, Savchenko & Ronkin 2005). They are active for ~6 months in Russian plains and 4–5 months in Kazakhstan (Bibikow 1996); Bibikov (1967) reports hibernation to last on average 6–7.5 months. In Orenburg Province baibaks hibernate between mid-July–October and early April (Soroka 2000). Hibernation starts 30–40 days earlier in humid years than in dry years because fat can accumulate in a shorter time (Šubin 1963).

Subspecies. Two (Gromov et al. 1965) or three (Sludskij et al. 1969, Gromov & Erbaeva 1995) subspecies are recognized, replacing one another in a west to east direction: *bobak*, *kozlovi*, and *shaganensis*. Ssp. *kozlovi* is bordered by the Volga River in the west, but the eastern border is not defined. This marmot shows a noteworthy fusion of posterior pads on both, palms and soles (Fokanov 1966). The border between *bobak* and *shaganensis* is set either on the Volga (Semihatova 1972), on the uplands of the Obŝij Syrt (to the south of Samara; Gromov et al. 1965, Čašin 2006) or on the Or River in the Regions of Orenburg (Russia) and Aktûbinsk (Kazakhstan) (Barmin 2005). Baibaks from Europe (ssp. *bobak*) are larger (see above) and darker (yellowish brown pelage clouded with dark hair tips; head darker); those from Kazakhstan (*shaganensis*) are smaller and paler (dark hair tips barely noticeable; head brown; Ognev 1947). Baibaks from the left bank of the Volga, intermediate in size between the western and the eastern extremes, were interpreted as transitional between the two subspecies (Semihatova 1972). Because the variation is more likely clinal than categorical, we do not divide baibaks into subspecies. Geographic variability was also reported in the shape of baculum and in vocalization. Number of denticles on distal baculum is lower to the west of Volga (1 on the right margin of spatula, 1–3 on the left margin) and higher eastward (2–3 and 2–5, respectively; Fokanov 1966). Nikol'skii (2002) clustered 11 populations into four geographical populations and the basis of spectral analysis of their alarm call, but the variation was better explained by landscape topography than by traditional subspecific division.

Marmota baibacina (Kaŝenko, 1899) – Gray marmot

1844 *Arctomys baibacina* Brandt. Type locality: "Altaï" (= Altai Mts.). Ognev (1947) as well as Pavlinov & Rossolimo (1987) rejected this name as *nomen nudum*.

1854 *Arctomys lewisii* Audubon et Bachman. Type locality is not known and the name was proposed to be *nomen oblitum* (for details see Hoffmann 1977).

1899 *Arctomys baibacina* Kaŝenko. Type locality: "Altajskij kr., Gorno-Altajskaâ AO, Ust'-Koksinskij r-n., r. Mul'ta, Nižn. Ujmon" (Pavlinov & Rossolimo 1987) (= Russia, Altai Region, Gorno-Altajsk Autonomous Region, Ust'-Koksa District, Mul'ta River, Nižnyj Ujmon).

1909 *Arctomys centralis* Thomas. Type locality: "Mt. Boro-choro, Ak-sai Plateau, 120 miles N. of Kashgar", Tian-Shan Mts., north-west China.

1950 *Marmota baibacina ognevi* Skalon. Type locality: "Altajskij kr., Gorno-Altajskaâ AO, Koš-Agačskij r-n., r. Džumaly" (Pavlinov & Rossolimo 1987) (= Russia, Altai Region, Gorno-Altajsk Autonomous Region, Koš-Agač District, Džumaly River).

1965 *Marmota bobak aphanasievi* Kuznecov. Type locality: "gory Kyzyl-Raâ, Nur-Taâ, Kenta, Karkary i drugich gornyh grup" (= Kyzylraj Mts., Nur-Taj Mts., Kent Mts., Karkara Mts. and other mountain groups [Sic !]). Restricted by Pavlinov & Rossolimo 1987) to "Kazakhstan, Džezkazganskaâ obl., Aktogajskij r-n, gory Kyzylraj" (= Kazakhstan, Džezkazgan [known also as Zhezkazgan] Region, Aktogaj District, Kyzylraj [known also as the Kyzylaraj] Mts.).

Remarks. In the past frequently synonymized with *bobak*; Ellerman & Morrison-Scott (1951) and Rausch (1953) synonymized *baibacina* with *M. marmota*, and Ognev (1947) suggested it to be close to *sibirica* (now in the *camtschatica* group).

Morphological differences between *baibacina* and *bobak* are slight: *baibacina* has on average longer tail (25.5 and 24.5% HbL in males and females, respectively; 21–23 caudal vertebrae); corresponding values in males and females *M. bobak* are 21.3 and 18.3%, respectively (19–20 caudal vertebrae; Sludskij et al. 1969). Fur is longer in *M. baibacina*: hairs are ~22.9 mm long (~16.4 mm in bobak); the longest hairs measure up to 42 mm (31.6 mm in *bobak*; Sludskij et al. 1969). The two marmots differ in habitat selection: *bobak* occupies flat steppes throughout its range, while *baibacina* inhabits mountains (Sludskij et al. 1969). Karyotype is characterized by 66 autosomal arms in *M. baibacina* and 62 or 64 autosomal arms in *M. bobak* (Lâpunova & Voroncov 1969).

Skull and dentition of baibacina and bobak are very similar; the differences are in means and the non-overlapping extremes. For detailed comparison see Gasilin & Kosincev (2011). The angle at the junction of maxillary root of zygoma and the rostrum is smaller in *M. bobak* than in *M. baibacina*; individuals having the angle <117° are certainly *bobak* and those with the angle >125° are certainly *baibacina*. Lower molars are more delicate in *bobak* than in *baibacina* and individuals at the lower end of variation range are invariably *bobak* as are those at the high end *baibacina*; the cut-off thresholds (in mm) are: alveolar length of lower cheek-teeth <21.4 for *bobak*, >23.2 for *baibacina*; transverse length of third lower molar m3 <7.1 is *bobak*, >8.0 is *baibacina*; length of m3 <5.3 is *bobak*, >6.6 is *baibacina*; width of m3 <5.7 is *bobak*, >6.6 is *baibacina*; width of lower incisor <3.1 is *bobak*, >4.1 is *baibacina* (Gasilin & Kosincev 2011).

Phenotypic hybrids between *M. baibacina* and *M. sibirica* were reported from the zone (presumably a secondary contact) of their restricted sympatry around Dalun in the Mongolian Altai. The hybrids are rare and restricted to suboptimal marginal habitats on the slopes of the

Fig. 24. Grey marmot *Marmota baibacina* from Tašanta, the Altai Mts. in Russia. Photo courtesy Alenka Kryštufek.
Obr. 24. Svišť šedý *Marmota baibacina* z lokality Tašanta, pohoří Altaj v Rusku. Foto Alenka Kryštufek.

mountains (Smirin et al. 1985, Rogovin 1992). In the Kazakh highlands where *M. baibacina* comes in contact with *M. bobak*, marmots show transitional morphological characteristics. Animals from the western side of this zone (to the southeast of Karaganda) are classified as *M. bobak*, and from the eastern side as *M. baibacina* (Sludskij et al. 1969).

The oldest fossil evidence of *M. baibacina* is from the Upper Pleistocene (Gromov et al. 1965).

Description (Figs. 24–26). Large and relatively short-tailed marmot; tail accounts on average for ¼ of HbL (range = 20.0–40.0%; Sludskij et al. 1969). In general resembles *M. bobak*. Pelage is soft, hairs ~20 mm long, guard hairs exceed 3 cm; individual hairs with slate basal band, succeeded by a yellowish band which extends over $^1/_3$–$^2/_3$ of the hair; tip is brown or blackish. Ground colour of upper parts is pinkish-buff to grayish cream, clouded cinnamon brown to dark brown. Because of light subterminal band and dark tips the pelage is of grizzled appearance. Head is darker than back but there is no distinct black cap; snout is usually dark cinnamon-brown, ears are rusty straw, and cheeks are tinted with yellow (Fig. 24). Tail is of same colour as back,

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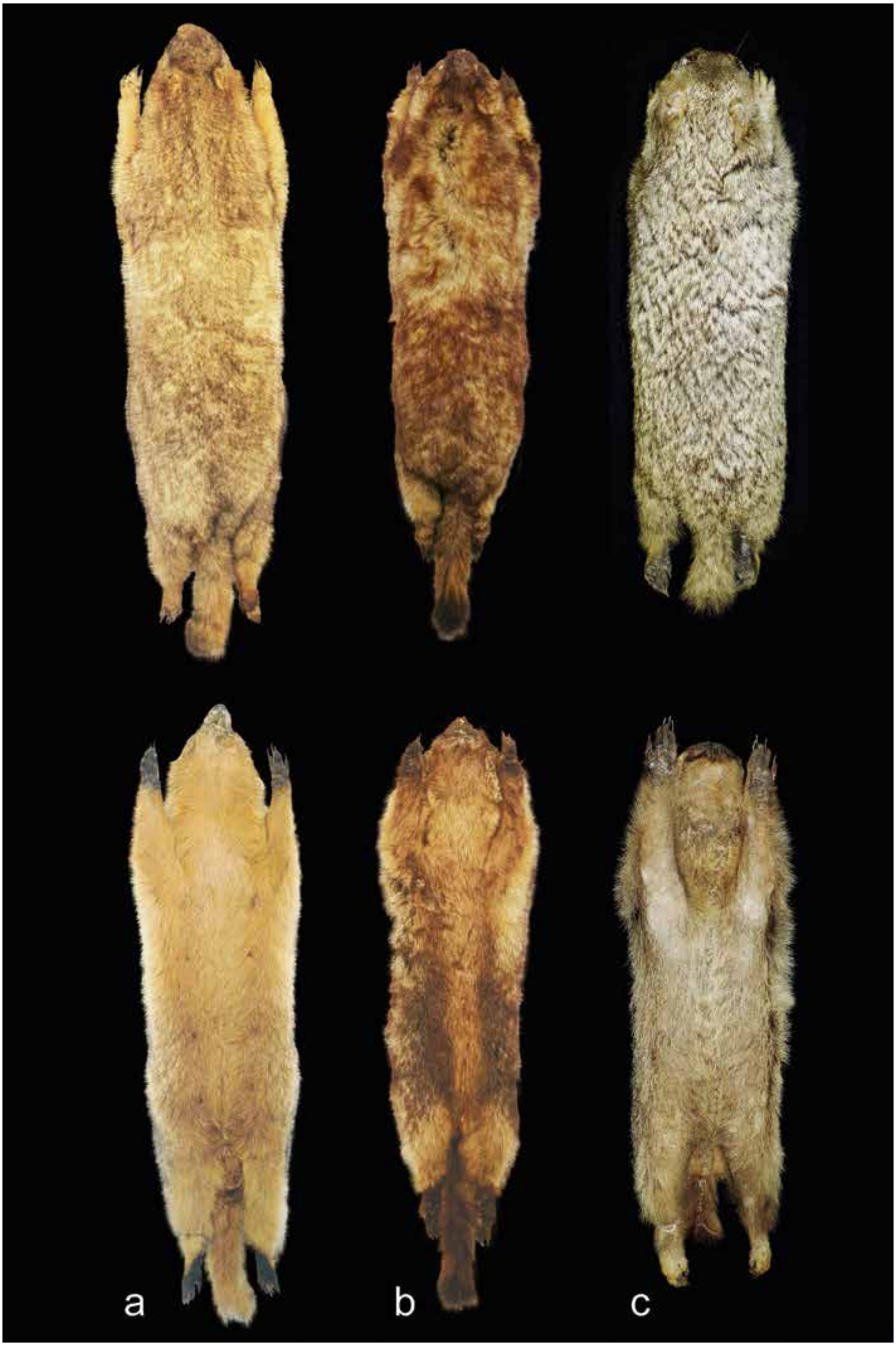
Fig. 25. Skins of *Marmota baibacina* from different parts of their range to show interpopulation variation in colour. a – adult female from Semireč'e (= Džeti-Suu), Kyrgyzstan (BMNH 14.5.10.74); b – adult male from the Altai Mts. (BMNH 12.4.1.38); c – adult male from Mon'-Chu, Cho-nan', Province of Jun-Xai, China (NMP 57681). Photo by Boris Kryštufek.

Obr. 25. Balky *Marmota baibacina* z různých částí jeho areálu rozšíření, které ukazují mezipopulační variabilitu v jeho zbarvení. a – adultní samice ze Sedmiříčí (= Džeti-Suu), Kirgizie (BMNH 14.5.10.74); b – adultní samec z pohoří Altaj (BMNH 12.4.1.38); c – adultní samec z Mon'-Chu, Cho-nan', provincie Jun-Xai, Čína (NMP 57681). Foto Boris Kryštufek.


a
b
c

with yellowish-brown to chestnut-brown tip; ventral side is variable, from ochre to dark brown. Flanks are as back, except for less marked brown hair tips; paws are cream yellowish to rusty brown. Belly varies in colouration: yellowish-rusty and darkened by brown hair tips, whitish grey and washed buff, or bright rust to hair bases (Fig. 25). Claws and whiskers are dark brown. Young animals are either greyer, or more yellow. Females have 10 nipples (BMNH specimens). Baculum has an expanded and uplifted base which is orthogonal with respect to the body of the bone (Bibikov 1967). Skull shows no peculiarities when compared to *M. bobak*, however zygomatic arches are less expanded (ZyB accounts for 58.0– 67.4% CbL) and auditory bullae

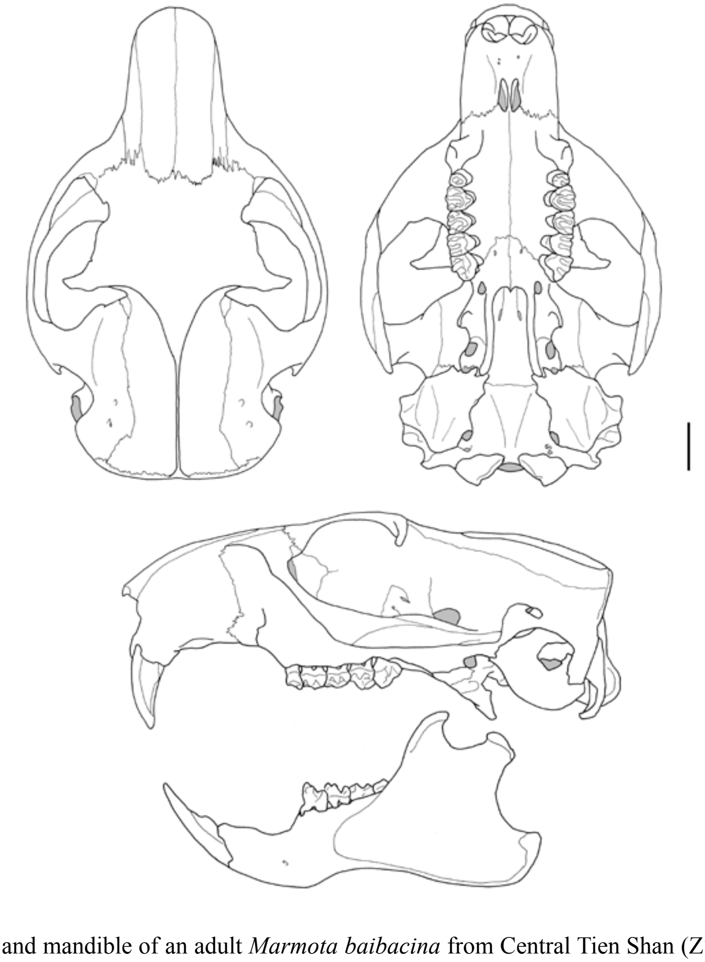


Fig. 26. Skull and mandible of an adult *Marmota baibacina* from Central Tien Shan (ZSM 1326/1906). Scale bar = 1 cm.
Obr. 26. Lebka a mandibula adultního jedince *Marmota baibacina* ze středního Ťan-Šanu (ZSM 1326/1906). Měřítko = 1 cm.

are more elongate (Fig. 26). Dentition as in *M. bobak*, the third lover molar, however, is more robust, the lower incisor is wider and the posterior root of third lower molar bifurcates in 10% of individuals (Gromov & Erbaeva 1995, Gasilin & Kosincev 2011). Dimensions (in mm, weight in grams), males: W_{101} = 5216.0 (2400–8200), HbL_{105} = 547.5 (490–670), TL_{104} = 151.5 (110–220), HfL_{104} = 90.5 (71–104), EL_{5} = 27.0 (24.0–33.0), CbL_{59} = 95.9 (89.8–105.7), ZgB_{47} = 60.0 (54.0–65.0), MxT_{54} = 22.6 (20.4–25.5); females: W_{100} = 4872.5 (2900–7300), HbL_{96} = 527.9 (450–630), TL_{96} = 148.5 (115–215), HfL_{96} = 87.3 (70–105), EL_{3} = 27.3 (27.0–28.0), CbL_{61} = 93.5 (84.4–102.2), ZgB_{57} = 59.2 (53.4–66.0), MxT_{57} = 22.4 (20.9–24.4) (Sludskij et al. 1969, and specimens in BMNH, NMNH, PMS, SMF, SZM, and ZISP). Males are on average larger; male/female ratio in CbL = 1.020 (Matějů & Kratochvíl 2013). Karyotype: 2n = 38; 66 autosomal arms (Lâpunova & Voroncov 1969, Voroncov et al. 1969, Brandler 1999). Marmots from Koš Agač (the Altai Mts. in Russia) displayed 2n = 37 which is due to a fusion of submetacentric and metacentric chromosomes with subsequent loss of the small arm of the submetacentric (Brandler 2003).

Geographic range (Fig. 27) is fragmented in the mountains surrounding the large depression of the Balkhash Lake, i.e. in Kazakhstan, Kyrgyzstan, Russia, Mongolia, and China. The main fragments to the north of the lake are (west to east) Akčatau (part of the Kazakh highlands), Tarbagatai Mts. (Kalbinsk Altai), and the Altai Mts. proper in Russia, the adjacent northwestern Mongolia and very marginally in China; to the south of the Balkaš grey marmots occupy Džungarian Alatau and north-eastern Tien Shan Mts. from around the Lake Issyk-Kul (Kyrgyzstan) eastward to Chinese Xinjiang. Batbold et al. (2008a) plotted presence of *M. baibacina* for the Kyrgyz Alatau but we were unable to find supporting evidence for this in the major Russian sources (Kuznecov 1948, Sludskij et al. 1969, Bibikov & Berendaev 1978). Furthermore, Bibikov (1967) explicitly set the western border of *M. baibacina* in this part of Kazakhstan and Kyrgyzstan at ~74° eastern longitude (i.e. slightly west of Biškek).

During the 20th century, the grey marmot was poisoned in extensive campaigns aimed to eradicate plague. Besides, grey marmots were hunted extensively for skins, meat and fat. Populations in the Tien Shan Mts. declined 4–12-fold during the second half of the century (Toropova 2005), and in Trans-Baikal Russia number of annual provision of skins dropped steadily from 2.5 million in 1910, to 280,000 in 1924, 95,000 in 1932, and 70–90,000 in 1947, to merely ~200 in 1970; in 2000, *M. baibacina* was declared to be a species of conservation concern (Kardaš et al. 2002). It seems, however, that pressures did not much affect the overall range.

Before WWII there were several attempts in the former Soviet Union to introduce grey marmots from the Altai Mts. into Europe where the bobak marmot *M. bobak* was extirpated in large parts of its former range (see above). First translocation dates back to 1920 when 31 grey marmots were released in Bashkortostan. During 1960s, grey marmots were still reported from many localities (Kiris 1973, Long 2003) but none survived up to now (Oleg Askeev, personal information in 2012). Next release was in 1934 to Gunibskij Plateau in the northern slopes of the Caucasus Mts., Daghestan (Šidlovskij 1976); 113 animals were released. There were 1000 marmots in several colonies in 1962, but the population crashed in 1963 and perished entirely by 1966 (Kiris 1973), possibly due to poaching (Tembotov 1972). Long (2003) reports further releases of grey marmots from Altai to "Onpudaiskom and Alekmonarskom" regions of the Caucasus, but any of these is mentioned in major compilations of the Caucasian rodents (Tembotov 1972, Šidlovskij 1976). Kiris (1973) recorded a release of 234 grey marmots in Gornyj Altajsk in 1937 in order to help a local population to recover after excessive cull.

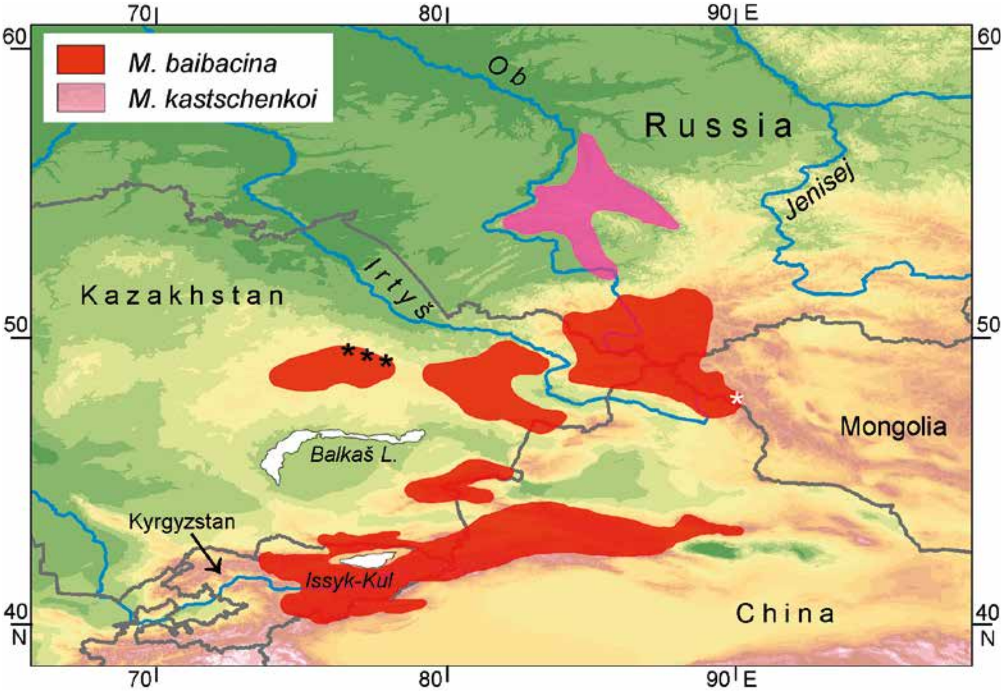


Fig. 27. Distribution of *Marmota baibacina* and *M. kastschenkoi*. Compiled from the following sources: *M. baibacina* – Bannikov (1954), Bibikov & Berendev (1978), Galkina et al. (2005a), Sludskij et al. (1969), Smirin et al. (1985) and Zhang (1997); *M. kastschenkoi* – Bibikov & Berendev (1978) and Taranenko (2011). Asterisks indicate *M. baibacina* with morphology which is transitional to *M. bobak* (black symbols) and to *M. sibirica* (white symbol); from Sludskij et al.(1969) and Smirin et al. (1985), respectively.
Obr. 27. Rozšíření *Marmota baibacina a M. kastschenkoi*. Zkompilováno z následujících pramenů: *M. baibacina* – Bannikov (1954), Bibikov & Berendev (1978), Galkina et al. (2005a), Sludskij et al. (1969), Smirin et al. (1985) a Zhang (1997); *M. kastschenkoi* – Bibikov & Berendev (1978) a Taranenko (2011). Hvězdičky označují *M. baibacina* jejichž morfologie vykazuje přechodný stav směrem k *M. bobak* (černé symboly) a k *M. sibirica* (bílý symbol); podle Sludskij et al.(1969) a Smirin et al. (1985).

Although the grey marmot is regarded to be a typical mountain animal (e.g. Rogovin 1992), a significant part of its range in Kazakhstan is at low elevations, e.g. in Kalbinskij Altai at 400–1500 m and in Tarbagataj at 1300–2000 m (Sludskij et al. 1969). Altitudinal range in the Southern Altai Mts. is 1450–2800 m (Zinčenko & Prokopov 2002) with optimal habitats between 2000 and 2800 m a. s. l. (Prokopov & Zinčenko 2002); the range in the Altai is 720–3500 m in Russia (Ûdin et al. 1979) and the upper border is >3000 m in Mongolia (Rogovin 1992); in Tien Shan the elevational range is 1200–4500 m (Pole 1994). The highest elevations are 3400 m in Džungarian Alatau (Sludskij et al. 1969), 3500–4000 m in Tien Shan (Zimina 1965, Toropova 2005), and 4525 m in Kyrgysztan (Kuznecov 1948). Main habitats are river valleys, slopes, mountain ridges and plateaus; vegetation varies from forest steppe (e.g. in Tien Shan; Pole 1994), mesic meadows and mountain steppes to xeric alpine tundra (Sludskij et al. 1969, Bibikov & Berendev 1978, Ûdin et al. 1979, Prokopov & Zinčenko 2002). In the Southern Altai gray marmots select steep slopes which abounds with rocky cover but have only a thin soil layer, scanty vegetation and are >250 m away from the nearest water source (Ricankova et al. 2005). In a sympatric zone with *M. sibirica*, *M. baibacina* occupies tops of ridges with alpine vegetation. Grey marmots hibernate, depending on the region, for 6.5–7.5 months on average but this may extend to eight months at high altitudes (Bibikov & Berendev 1978). Normally, they become lethargic in September–October, exceptionally already in late July, and emerge from burrows in March–April (Kuznecov 1948).

Subspecies. Variability in colour (Fig. 25), size and proportions is well pronounced. Populations from dry regions tend to be paler (Ognev 1947). In six samples from Kazakhstan the mean HbL varied between 512 and 565 mm (males) and 493–545 mm (females), and the mean relative tail length (% HbL) ranged 25.5–33.4% (males) and 24.5–32.9% (females; Sludskij et al. 1969). Other traits show interpopulation variability as well, e.g. vocalization. On the basis of rhythmical organization of the alarm call, Nikol'skii (1994) recognized 4 dialects among 6 populations. Pole (1994) reports interpopulational heterogeneity in frequencies of blood groups and non-metrical cranial traits, and in the morphology of baculum.

Number of subspecies recognized is either two (the nominotypical and *centralis*; Ognev 1947, Thorington et al. 2012) or three (also *ognevi*; Gromov et al. 1965, Gromov & Erbaeva 1995). Main difference is in colouration: belly is "vivid-rust-red" in *centralis* v. brown washed black in the typical race (Ognev 1963); *ognevi* is reportedly intermediate in this respect (Gromov & Erbaeva 1995). A reconstruction of relationships based on immunological differentiation retrieved two clusters which cut across subspecies boundaries: *M. baibacina baibacina* from the eastern Kazakhstan (Lake Markakol') grouped with *M. b. centralis* from Tien Shan, and not with the nominotypical subspecies from the Altai Mts. (Žolnerovskaâ 2002). Because no clear evolutionary lineages were retrieved so far in grey marmot, we refrain from adopting any subspecific division.

Marmota kastschenkoi **Stroganov et Ûdin, 1956 – Forest-steppe marmot**

1956 *Marmota baibacina kastschenkoi* Stroganov et Ûdin. Type locality: "Tomskaâ obl., okr. g. Tomska, s. Lâzgino" (Žolnerovskaâ et al. 1989) (= Russia, western Siberia, Tomsk Region, vicinity of Tomsk, village Lâzgino).

Remarks. The forest-steppe marmot was for long considered to be a well defined subspecies of *M. baibacina* (e.g. Bibikov & Berendev 1978, Ûdin et al. 1979, Brandler et al. 1999, Galkina & Taranenko 2002) but was erected to a level of a species on its own on the basis of distinct diploid number: 2n = 36 in *kastschenkoi* and 38 in *baibacina* (Brandler et al. 1999, Brandler & Bogdanov 2002, Brandler 2005). For the 36 form Brandler (2003) suggests an origin from the 38 cytotype through a fusion of submetacentric and metacentric chromosomes with a subsequent loss of small arm of the submetacentric element. No matter how impressive is a record of a deviant diploid number in karyologically conservative group as are marmots, the available body of chromosomal evidence on its own provides only weak support for separation of these two cytotypes as distinct species. A centric fusion is fairly simple change and was documented also in a population of *M. baibacina* proper from the Altai Mts. (Brandler 2003). A small number of grey marmots karyotyped so far in Koš Agač leaves open door for various speculations on the frequency of centric fusions in the ancestral population. Genetic divergence between *kastschenkoi* and *baibacina* (Brandler et al. 2010, Steppan et al. 2011)

Fig. 28. Skin of *Marmota kastschenkoi*; adult male from the vicinity of Tomsk, Russia (SZM 6884, type specimen). Photo by Boris KRYŠTUFEK.
Obr. 28. Kůže *Marmota kastschenkoi*; adultní samec z okolí Tomska, Rusko (SZM 6884, typový jedinec). Foto Boris KRYŠTUFEK.

can be interpreted either as a low interspecific or as a deep intraspecific divergence; it is only slightly higher than the distance separating the two subspecies of *M. caudata* (cf. STEPPAN et al. 2011). Therefore, we believe that *kastschenkoi* could be equally well treated as a subspecies of *M. baibacina*. Because *kastschenkoi* shows at least two attributes of rarity (small range and small population size) it would be highly desirable from the conservation point to advance understanding on its taxonomic status.

DESCRIPTION (Figs. 28, 29). A marmot of same appearance as *M. baibacina*; tail accounts for 22–35% HbL. Hair is soft and short: 20–25 mm in summer pelage, up to 33 mm in winter pelage. Hairs are yellow-brown except for brown tips and slate bases; the latter frequently narrow. The overall appearance is grizzled brown, ochre and cream; head is dark-brown to blackish brown. Tail is of same colour as back, with yellowish-brown to chestnut-brown terminal tip. Ventral side is buff and claws are black (Fig. 28). Baculum is cylindrical with distal spatula split into two lobes edged with denticles (Galkina et al. 2005b). Skull and dentition as in *M. baibacina*; ZyB accounts for ~63% CbL (Fig. 29). Enamel on upper incisors cream to light yellow. Dimensions (in mm, weight in grams; sexes pooled): W_5 = 6026.0 (4330–8900), HbL_8 = 527 (450–590), TL_8 = 144.1 (100–181), HfL_7 = 86.7 (80–92), EL_4 = 20.4 (15.5–27.0); cranial measurements are based on 2 males & 1 female: CbL = 92.0, 100.4, 98.0, ZgB = 57.7, 63.1, 61.1, MxT = 25.1, 24.4, 23.1 (Brandler 2003, and specimens in SZM and ZFMK). Galkina & Taranenko (2002) and Galkina et al. (2005b) report ranges in body mass 3–6.3 kg in spring and 4.6–8.9 kg in the autumn; CbL = 101.1 (94.5–107.5 mm); the following maximal values are also quoted: W = 12 kg (needs confirmation), HbL = 660 mm. Karyotype: 2n = 36 (Brandler 1999, 2003), differs from a 38 cytotype which is typical of *M. baibacina* in a tandem fusion TSI 5/7 (Beklemisheva et al. 2011).

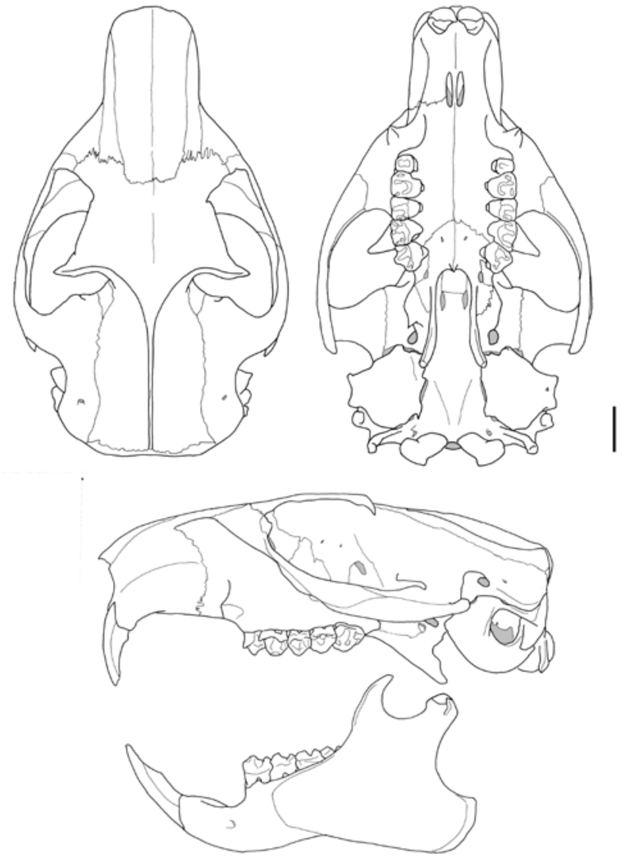


Fig. 29. Skull and mandible of *Marmota kastschenkoi*; adult male from the vicinity of Tomsk, Russia (SZM 6884, type specimen). Scale bar = 1 cm.
Obr. 29. Lebka a mandibula *Marmota kastschenkoi*; adultní samec z okolí Tomska, Rusko (SZM 6884, typový jedinec). Měřítko = 1 cm.

GEOGRAPHIC RANGE (Fig. 27). It is in southwestern Siberia (Novosibirsk District and the northern--most part of Gorno Altajsk) and is bordered by the following rivers: Ob to the west, Tom' to the northeast, and Ob and its tributary the Biâ in the south (BIBIKOV & BERENDEV 1978). Rivers pose strict borders: all known localities are on the right bank of the Ob; very few localities are on the right bank of the Tom' and on the left bank of the Biâ (BIBIKOV & BERENDEV 1978, TARANENKO 2011). In the past forest-steppe marmots possibly reached rivers Ket' and Vasûgan in the north (LAPTEV 1958) and fossils were reported from the Enisej river basin around Krasnodarsk (TARANENKO 2011). Current population of *M. kastschenkoi* is most probably isolated from the Altai population of *M. baibacina* by the forest zone; in the north forest-steppe marmots are bounded by the taiga zone (TARANENKO 2011).

The entire range is <300 km in a north-south direction (from Tomsk till Bijsk) and <200 km in west-east direction (estimated as 500 km and 400 km, respectively, by GALKINA & TARANENKO 2002). Population was estimated at 7500 individuals in 2000 and 7900 in 2004 (MASHKIN & KOLESNIKOV 2005); an estimate from 1960s reported 18,000 marmots (BIBIKOV & BERENDEV 1978) and ÛDIN et al. (1979) stated 13,000 individuals for forest-steppes of the Salair range. TARANENKO (2011) claims that number remained stable at ~14–16,000 individuals over the last 50 years.

No other Palaearctic marmot is so closely tied to a forest as *M. kastschenkoi*. Its range entirely overlaps with a narrow west to east stretching zone of forest-steppe (lesostep), which is bounded by taiga in the north, and dry steppes and mountain forests to the south. Marmots inhabit undulating landscape, steep terraces and slopes, but avoid flat surface. Preferred are floristically rich grasslands in a shadow of scattered birch (*Betula*), ash (*Fraxinus*) and pine trees (*Pinus*) (LAPTEV 1958, BIBIKOV & BERENDEV 1978). In late 1990s, this marmot was reported for the first time from close proximity of human settlements (KALÂGIN 2002). Altitudinal range is 180–350 m a. s. l., exceptionally up to 450 m (TARANENKO 2011). Forest-steppe marmot hibernates from mid-August – early September till late March–April (TARANENKO 2011), i.e. 6.5 months on average (BIBIKOV & BERENDEV 1978).

SUBSPECIES. None recognized, a monotypic species.

Species group *camtschatica*

Traditional phylogenetic reconstructions which relied on morphological characters failed to recognize close relationships among the 3 species which are currently in this group. More frequently, *M. sibirica* and *M. himalayana* were linked to *M. bobak*, while *M. camtschatica* was regarded to be close to *M. marmota* (ELLERMAN & MORRISON-SCOTT 1951), or as an intermediate between *bobak* and *marmota* (GROMOV et al. 1965). Monophyly of the *camtschatica* group received strong support in molecular analyses. *M. camtschatica* hold basal position in the group and *M. sibirica* and *M. himalayana* are sister species (STEPPAN et al. 2011). The group diversified in the easternmost periphery of the Palaearctic marmots.

Marmota sibirica (Radde, 1862) – Tarbagan marmot

1859 *Arctomys bobak*, var. *sibirica* Maak. Nomen nudum.

1862 *Arctomys bobak* var. *sibirica* Radde. ALLEN (1940: 714) stressed that "Radde unintentionally became the authority for the subspecies, stating that Brandt in a forthcoming publication proposed to call the variety of Siberia by the name *A. b.* [= *Arctomys bobak*] *sibirica*, basing his account largely on that of Pallas" and concluded "It is not known to me whether any of his material is still extant."

Indeed, there are three specimens in the Zoological Institute of Russian Academy of Sciences in St. Petersburg (ZISP), collected by G. I. Radde himself (Baranova & Gromov 2003: 21); Ognev (1947: 273) designated as a lectotype the voucher "No. 2095" (Baranova & Gromov 2003: 21), collected on 25 March 1856 in "Kulusutaj bliz oz. Torej-Nor, Ûgo-vost. Zabajkale" (= Kulusutaj near lake Torej-Nor, Čita [also Chita] Region, south-eastern Siberia, Russia). The type locality is therefore Kulusutaj.

1910 *Arctomys robustus* Kaŝenko. From Ognev (1963: 235), who stressed: "Not *Arctomys robusta* of Milne-Edwards". Kaŝenko (1910) attributed *robustus* to Milne-Edwards (see under *M. himalayana*) which means that Ognev's (l. c.) combination of the species name and the authority is erroneous.

1922 *Arctomys dahurica* Dybowski. Type locality: "Daurskie stepi" (= Daurian steppes) (Ognev 1947: 273). All authorities (Ognev 1947, Ellerman & Morrison-Scott 1951, Pavlinov & Rossolimo 1987) consider this name to be nomen nudum.

1949 *Marmota sibirica caliginosus* Bannikov et Skalon. Type locality: "Mongoliâ, Hangaj, Šara-usu" (= Mongolia, Khangai Mts., river Shara-Usu Gol).

Remarks. In the past, *M. sibirica* was frequently reduced to a subspecies of *M. bobak* (Allen 1940, Ellerman & Morrison-Scott 1951, Bannikov 1954, Bibikov 1967, Corbet 1978, Stubbe & Chotolchu 1968, Bibikow 1996, Zhang 1997); rank of species on its own was claimed for *sibirica* by a number of Russian authors: Ognev (1947), Gromov et al. (1965), Letov (1978), Nekipelov (1978), Švecov (1978), Sokolov & Orlov (1980), Pavlinov & Rossolimo (1987), Rogovin (1992), Gromov & Erbaeva (1995), and Pavlinov & Lissovsky (2013).

Phenotypic hybrids between *M. baibacina* and *M. sibirica* were reported from the zone of their sympatry in Mongolian Altai around Dalun. Contact zone is presumed to be due to a secondary contact. Tarbagans occupy river valleys with high primary productivity while grey marmots (*M. baibacina*) occur on slopes of ridges. The hybrids, which are rare, are restricted to suboptimal marginal habitats on mountain slopes. In allopatry tarbagans slightly expand their niche and populate also the ridges (Smirin at al. 1985, Rogovin 1992).

M. sibirica or its ancestor occupied the Trans-Baikal region already during the Middle Pleistocene (Erbajeva & Alexeeva 2009b).

Fig. 30. Siberian marmot or tarbagan *Marmota sibirica*. a – Hustai, Mongolia (photo courtesy Hermann Ansorge), b – Central Mongolia (photo courtesy Nedko Nedyalkov).
Obr. 30. Svišť sibiřský neboli tarbagan *Marmota sibirica*. a – Hustai, Mongolsko (foto Hermann Ansorge), b – střední Mongolsko (foto Nedko Nedyalkov).


a
b
c

Description (Figs. 30–32). Medium sized marmot with tail equaling ~¼ HbL (range = 24–33% HbL). Fur is short (~11–20 mm, guard hair in summer pelage 18–20 mm long, in winter pelage up to 30 mm) and thick; hairs with short slate basal band, followed by a broad whitish to

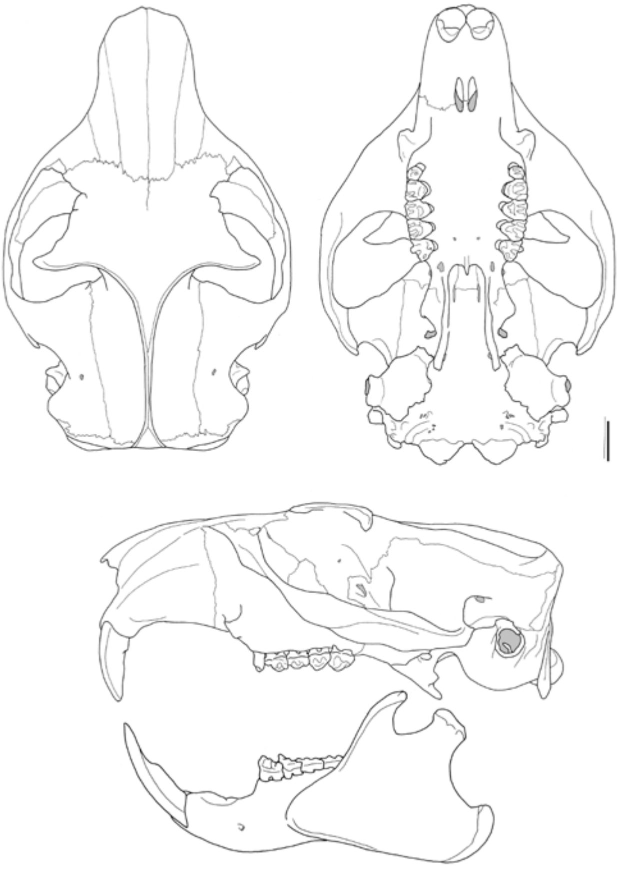


Fig. 32. Skull and mandible of *Marmota sibirica*; adult specimen from the Mongun-Tajga Mts., Tuva, Russia (SZM 23792). Scale bar = 1 cm.
Obr. 32. Lebka a mandibula *Marmota sibirica*; adultní jedinec z pohoří Mongun-Tajga, Tuva, Rusko (SZM 23792). Měřítko = 1 cm.

←

Fig. 31. Skins of *Marmota sibirica* in dorsal and ventral view to show variability in colour. a – a fulvous individual from Mongolia (BMNH 1937.6.12.9); b – subadult from Burun Urt, Mongolia (MNM 74.2.2); c – adult male from the Mongun-Tajga Mts., Tuva, Russia (SZM 25974). Photo by Boris Kryštufek.
Obr. 31. Balky *Marmota sibirica* z hřbetní a břišní strany, které ukazují variabilitu v jeho zbarvení. a – žlutavý jedinec z Mongolska (BMNH 1937.6.12.9); b – suadultní jedinec z Burun Urt, Mongolsko (MNM 74.2.2); c – adultní samec z pohoří Mongun-Tajga, Tuva, Rusko (SZM 25974). Foto Boris Kryštufek.

cream-fulvous band and an extensive buffy or brown tip. The overall appearance is lighter and more fulvous than in other marmots (Fig. 30); light underfur is mottled by brown tips from the occiput to tail. Some animals tend to be browner, other more fulvous (Fig. 31). The top of the head from the nose to about the level of the ears is uniformly brown (from "seal brown" to "vandyke brown"; Allen 1940); cheeks are light yellow to buff, and the ears are whitish-fulvous. Flanks are lighter than back; the limbs and feet are nearly uniformly pale ochraceous to buffy. Belly and lips are fulvous to ochraceous, usually more intense on a throat and on chests, shaded light-gray on the belly. The inguinal region is stained blackish in some individuals. The proximal tail is of same colour as body, the terminal $^1/_3$–$^1/_2$ is darker (rusty-brown to black). Young are paler (olive-grey; Ognev 1947) with light-brown head. Baculum is of conical shape, tapering towards its uplifted tip; the base is robust (Bibikov 1967). Females have six pairs of nipples (Moore 1961). Skull shows no peculiarities; zygomatic arches are moderately expanded (ZgB = 53.9–69.1% CbL; Fig. 32). In western Mongolia, tarbagans have on average wider skull relative to its length (ZgB = 62.2–69.8%) than grey marmots (ZgB = 59.1–67.6% CbL; Smirin et al. 1985). Posterior edge of nasals frequently truncated and shifted backward (cf. Smirin et al. 1985); their anterior edge ends more posteriorly than in *baibacina*. The rostrum is more robust than in the *bobak* group, and *processus nasalis ossis premaxillae* is wider than the nasal bone (narrower in the *bobak* group). Teeth with no peculiarities; enamel on the anterior surface of incisors yellowish-white to light orange. Dimensions (in mm, weight in grams), males: W_{27} = 4936.5 (2350–7200), HbL_{31} = 498.6 (428–570), TL_{17} = 132.2 (90–155), HfL_{13} = 86.9 (77–110), EL_{13} = 26.5 (21–33), CbL_{54} = 91.3 (81.3–103.2), ZgB_{57} = 57.1 (49.0–63.6), MxT_{42} = 21.5 (20.1–22.9); females: W_{15} = 4096.3 (2450–6400), HbL_{15} = 458.7 (402–503), TL_{10} = 128.3 (115–145), HfL_{6} = 84.2 (76–90), EL_{6} = 23.0 (20–29), CbL_{46} = 87.2 (78.1–97.3), ZgB_{47} = 55.3 (47.7–62.4), MxT_{32} = 21.1 (19.0–22.4) (Ognev 1947, Tinnin et al. 2002, Stubbe & Chotolchu 1968, and specimens in AMNH, MNM, SMF, SZM, and ZISP). Ognev (1947) reports body mass of up to 8 kg. Males are larger; male/female ratio in CbL = 1.060 (Matějů & Kratochvíl 2013). Karyotype: 2n = 38 (Lâpunova & Voroncov 1969).

Geographic range (Fig. 33). Main part of the range is in Mongolia, wherefrom extends to adjacent Russia in the north and China (Nei Mongol and Heilongjiang) in the east. In the west, the Altai Mts. pose the main barrier to tarbagans; in the east these marmots cross a north-to-south oriented Great Khingan Mts. and reach in the east the rivers Liao-che and Nun-fiang. In the north, tarbagans occupy Trans-Baikal region (Russia) in the Province of Tuva (the northern border is on the southern-most tributaries of the Enisej River), in Buryatia (south of Baikal Lake), and in the Čita Region (between the rivers Ingoda and Amur). In the south tarbagans occupy the Džungarian Gobi and the range border is posed by Gobi itself. To the north of Gobi, tarbagans are widely spread, except for the Great Lakes Depression in western Mongolia.

Tarbagan is characteristic for "empty stretches with open horizons" (Ognev 1947) and of a high-altitudinal steppe (Bannikov 1954, Ûdin et al. 1979). Inhabited is short-grass steppe in flat plains, rolling hills, mountain slopes and plateaus, and river valleys. Grass is mainly low (10–20 cm high) and covers ~30–80% of the ground (Švecov 1978). The preferred habitat is gently undulating landscape of steppe and rocky outcroppings (Ognev 1947), however extensive areas of scree are avoided (Švecov et al. 1980a). Proximity of water is avoided and tarbagans stay for at least 100–150 m (preferably 300–350 m) away from the banks of rivers and lakes (Bannikov 1954). These marmots occupy marginally also forest-steppe, but only exceptionally inhabit sparse woodland (Ognev 1947). In the mountains they go up to 3600–3800 m a. s. l. (Bannikov 1954). Tarbagans hibernate from mid-September – October until March – mid-April,

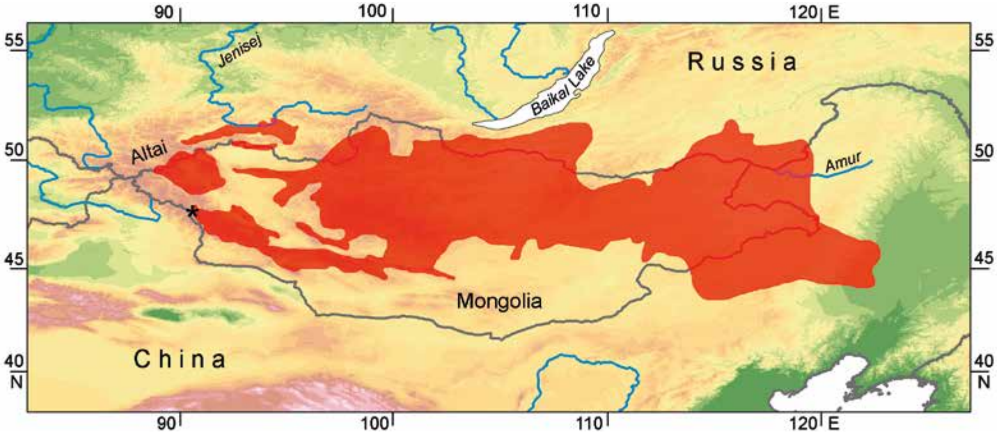


Fig. 33. Distribution of *Marmota sibirica*. Compiled from: total range – Clark et al. (2006); Mongolia – Bannikov (1954), Smirin (1985), Bibikov et al. (1990); Russia – Letov (1978), Nekipelov (1978), Švecov (1978), Švecov et al. (1984); China – Zhang (1997). For explanation of the asterisk see Fig. 27.
Obr. 33. Rozšíření *Marmota sibirica*. Zkompilováno z: celkový areál rozšíření – Clark et al. (2006); Mongolsko – Bannikov (1954), Smirin (1985), Bibikov et al. (1990); Rusko – Letov (1978), Nekipelov (1978), Švecov (1978), Švecov et al. (1984); China – Zhang (1997). Hvězdička viz obr. 27.

i.e. 6–7 months (Bibikov 1967). Tarbagans were hunted by man since ever and the cull was very high already a century ago; e.g. 2.984 million skins were sold in Mongolia in 1907 and 3.22 million in 1910 (Bannikov 1954). In a relatively small Tuva population the annual bag was >20,000 marmots before 1946, 6500–21,000 animals in 1950s and 1960s, but dropped to 70 skins in 1971 (Ûdin et al. 1979); note that population estimate in 2000 for the entire Russian range was 92,000 tarbagans (Mashkin & Kolesnikov 2005). Excessive hunting in Mongolia caused a 70% population decline since 1990 and fragmented the range (Batbold et al. 2008b). A survey in 2007 yielded ~8 million tarbagans for Mongolia (Kolesnikov et al. 2009).

Subspecies. Two subspecies are recognized, the nominotypical from northeastern Mongolia and adjacent China, and *caliginosus* from western and central Mongolia, and probably Tuva in Russia (Gromov et al. 1965). Their geographic borders are seemingly not resolved and we are unaware of any evidence that these subspecies represent distinct evolutionary lineages. Because Thorington et al. (2012) claim that "No description is available" for *caliginosus*, we repeat a brief diagnosis as quoted in Gromov et al. (1965): in comparison with the nominotypical subspecies, *caliginosus* is said to have larger dimensions, longer fur, darker back, and narrower anterior part of nasals.

Marmota himalayana **(Hodgson, 1841) – Himalayan marmot**

1841 *Arctomys himalayanus* Hodgson. Type locality: "The habitat of this species is the Himalaya, and Kachar rarely, and very commonly the sandy plains of Tibet". Blanford (1875) noted that the species was described from "the Kachar of Nepal and the plains of Tibet". Ellerman & Morrison-Scott (1951) fixed "Nepal" to be the type locality; Zhang (1997) quotes "Southern Qinghai – Xizang Plateau", China.

1843 *Arctomys hemachalanus* Hodgson. Type locality: "Habitat the Himalaya with the Bhote pergannahs or Cachâr in the immediate vicinity of the snows". Ellerman & Morrison-Scott (1951) quoted "Nepal".

1846 *Arctomys tibetanus* Gray. New name to replace *Arctomys hemachalanus* Hodgson 1843 (see Blanford 1875).

1847 *Arctomys tataricus* Jameson. Blanford (1875) wrote: "In 1847 the 'larger Himalayan marmot' was described by Dr. Jameson as *Arctomys Tataricus*." Although Blanford abbreviated citation of Jameson's paper ("L' Instit. 1847, XV, p. 384"), he claimed subsequently (Blanford 1879: 36) that "this reference is quoted from 'Wiegman's Archiv', no copy of the work named being available". We were unable to trace the quoted paper by Jameson.

1872 *Arctomys robustus* Milne-Edwards. Type locality: "Moupin" (= Baoxing County, Sechuan, China). Rode (1945: 25) gives the locality of the type specimen as "Thibet oriental".

1879 *Arctomys hodgsoni* Blanford. New name proposed for *Arctomys hemachalanus*.

Remarks. In the past considered either as a subspecies of *M. bobak* (Jerdon 1867, Ellerman & Morrison-Scott 1951, Corbet 1978) or a species on its own (Blanford 1891, Allen 1940, Gromov et al. 1965, Bibikow 1996, Zhang 1997).

Description (Figs. 34–36). Large and robust marmot with tail of ~$^{1}/_{4}$ HbL (range = 17.4–32.7% HbL). Fur is short (15–20 mm) and rush, dense above, scanty on the belly. Hairs are dark-brown

Fig. 34. Himalayan marmots *Marmota himalayana.* a – Xiahe, Gansu Province, China, 3050 m a. s. l. (photo courtesy David Král); b, c – Ladakh, India (photo courtesy Vít Tejrovský). Note the worn-out stage of pelage in specimens on Fig. c.

Obr. 34. Svišť himalájský *Marmota himalayana.* a – Xiahe, provincie Gansu, Čína, 3050 m n. m.(foto David Král); b, c – Ladak, Indie (foto Vít Tejrovský). Zajímavé je opotřebení srsti u svišťů na obr. c.

Fig. 35. Skin of *Marmota himalayana*; adult male from between the Mekong and the Yellow River, China (BMNH 22.9.1.82). Photo by Boris KRYŠTUFEK.
Obr. 35. Balk *Marmota himalayana*; adultní samec z oblasti mezi Mekongem a Žlutou řekou, Čína (BMNH 22.9.1.82). Foto Boris KRYŠTUFEK.

to slate at base (up to the proximal ½ of length), light-yellow or sandy-brown for the rest; black tips give the dorsal side a uniformly mottled yellow-black appearance. Front-head is darker brown, occasionally black. Brown face has pale-buff orbicular ring; the snout is rusty in some animals, cheeks and ears are buff or rufescent (Fig. 34). Proximal tail is of same colour as the back, and the tip is brown to blackish. Flanks are paler and less grizzled than back, feet are buff or yellow. Underside is "orange-buff" (ALLEN 1940), hairs usually yellow to base (Fig. 35). Fur is softer and more greyish in young marmots. Females have 12 nipples. Skull shows no peculiarities; zygomatic arches are moderately expanded (ZgB = 59.1–68.5% CbL), braincase is elongate and the auditory bullae are relatively short (Fig. 36). Enamel on the incisors is white to light yellowish. Dimensions (in mm, weight in grams): W_9 = 5931.4 (3250–8000), HbL_{25} = 589.8 (460–730), TL_{23} = 155.9 (112–193), HfL_{16} = 93.3 (78–105), EL_{10} = 25.9 (19–37), CbL_{28} = 103.5 (92.1–114.9), ZgB_{32} = 64.9 (58.1–67.0), MxT_{24} = 24.1 (22.0–25.5) (ALLEN 1940, ELLERMAN 1940, GROMOV et al. 1965, ROBERTS 1997, and specimens in BMNH, NMNH, ZISP, and ZSM). HOFFMANN & SMITH (2008) give the range for body mass: W = 4000–9215 grams. Sexual dimorphism in size is well pronounced by marmot's standards; male/female ratio in CbL = 1.029 (MATĚJŮ & KRATOCHVÍL 2013). Karyotype: 2n = 38 (LI et al. 2006).

Geographic range (Fig. 37) covers the high plateau of Tibet and Qinghai in China, reaching marginally (in a northwest-to-southeast direction) the southern Xinjiang and Gansu, western Sechuan and northern Yunnan (all in China); there is either lack of data in the western Tibet plateau, or a genuine absence of the Himalayan marmot there. The southern margin is in the Himalayas from (east-to-west) India (Arunachai Pradesh, western Assam, Sikkim, Uttar Pradesh, Uttaranchal, Himachal Pradesh, Jammu and Kashmir), Bhutan, Nepal and Baltistan in the extreme north-eastern Pakistan. The western border is possibly determined by the competitive exclusion by *M. caudata*. We accepted Zhang (1997) as the most reliable source of distributional data for China; map in Hoffmann & Smith (2008) plots the northern border much more northwards.

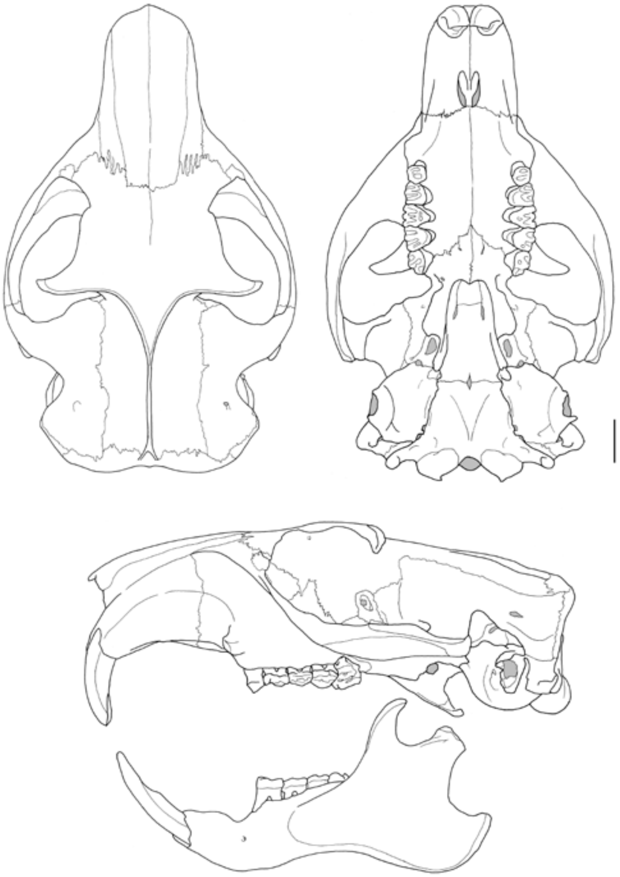


Fig. 36. Skull and mandible of *Marmota himalayana*; adult female from the elevation of 5370 m a. s. l. in "Tibet" (ZSM 1906/388). Scale bar = 1 cm.
Obr. 36. Lebka a mandibula *Marmota himalayana*; adultní samice z nadmořské výšky 5370 m v "Tibetu" (ZSM 1906/388). Měřítko = 1 cm.

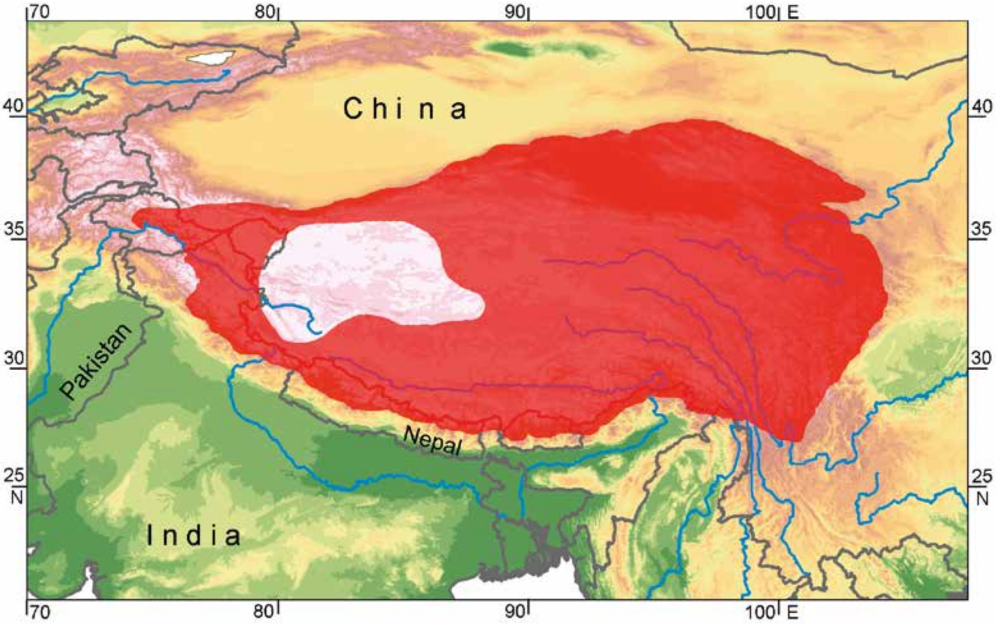


Fig. 37. Distribution of *Marmota himalayana*. Compiled from Zhang (1997) and Molur et al. (2005).
Obr. 37. Rozšíření *Marmota himalayana*. Zkompilováno z Zhang (1997) a Molur et al. (2005).

Himalayan marmots occupy short grass steppe and alpine meadows on plateaus, mountain slopes and in valleys, between the tree-line and the permanent snow line (>3000 m in the Himalayas; Jerdon 1867); precipitation is low and the habitat is described as "bleak dry plateau" (Blanford 1891) or "alpine desert" (Roberts 1997); occasionally rocky outcroppings are present (Mitchell 1977). Preferred is alluvial soil which allows for burrowing (Nikol'skii & Ulak 2006). Elevational range is 3000–5500 m a. s. l. in Nepal (Nikol'skii & Ulak 2006), 3960–4270 to 5500 m (13,000–14,000 to 18,000 ft; Blanford 1891), and 3750–5200 m in China (Hoffmann & Smith 2008). Hibernates for 7.5 months on average (Armitage & Blumstein 2002).

Subspecies. Two subspecies are frequently recognized: *robusta* and the nominotypical (Allen 1940, Gromov et al. 1965, Zhang 1997, Hoffmann & Smith 2008); Ellerman (1940) and Thorington et al. (2012) questioned their validity and we accept their reservation.

Marmota camtschatica (Pallas, 1811) – Black-capped marmot

1811 *Arctomys baibak camtschatica* Pallas. Type locality: "... vivit et in Camtschatcam ..." (= lives in [the peninsula of] Kamchatka), north-eastern Siberia, Russia.

1844 *Arctomys baibac* varietas *camtschatica* Brandt. Unjustified emendation of *baibak* by changing the terminal letter (k) to (c) to accord standards of classical Latin script. See comments under *M. bobak*.

1901 *Arctomys bungei* Kaŝenko. Type locality: "v'verhovâh r. Omoloâ (severnyj konec' Verhoânskago hrebta)" (= in the upper reaches of the Omoloj River, the northern end of the Verhoânsk Mts.), north-eastern Siberia, Russia.

1902 *Arctomys cliftoni* Thomas. Type locality: “Verkiansk Mountains, Yakutsk, N. E. Siberia” (= Verhoânsk Mts., north-eastern Siberia, Russia).

1922 *Marmota doppelmayri* Birula. NASONOV (1922: 8) was the first who mentioned “*Marmota doppelmayri* (Bir.)” in a list of new acquisitions of the Zoological Museum of the Russian Academy of Sciences, St. Petersburg. No further information is provided. Most probably, no other description was published, however the name was considered as available by OGNEV (1947) who assigned the lectotype from the locality “Istoki reki Nergili (bereg Bajkala), v 50 km k severu ot Svâtogo Nosa” (= Upper reaches of the Negrila River (eastern shore of the Lake Baikal), 50 km north from the Svâtoj Nos peninsula, Central Siberia, Russia).

REMARKS. Earlier authors saw the closest relative to *M. camtschatica* in two Nearctic marmots, *M. caligata* (ELLERMAN & MORRISON-SCOTT 1951, OGNEV 1947) or *M. broweri* (RAUSCH 1977, HOFFMANN et al. 1979, LYAPUNOVA et al. 1992); both hypotheses were rejected in a phylogenetic analysis based on cyt *b* gene (STEPPAN et al. 1999). Late Pleistocene remnants are known from Anadyr (shores of the Bering Sea; GROMOV et al. 1965) and from Trans-Baikal region (ERBAJEVA & ALEXEEVA 2009b).

DESCRIPTION (Figs. 38–40). Small marmot with short tail (TL = 20–25% HbL). Fur is thick, soft, long (up to 40 mm) and fluffy; winter fur is longer and more soft, summer fur is more shaggy, greyer and less speckled black (Fig. 38). The overall appearance of dorsal side is of black and white (or black and buff) and is due to the presence of three bands on guard hair: dark at the base, light in the middle, and dark again at the tip; the wooly underfur is dark with white tips (HOFFMANN et al. 1979). The back is darkest along the spine. Characteristic is a black-brown cap from the tip of the snout to below the eyes and behind the ears; sandy to orange ears strongly contrast the dark cap (Figs. 38, 39). The cheeks are pale yellow or buff, flanks like back but

Fig. 38. Black-capped marmot *Marmota camtschatica camtschatica* (Kamchatka, Russia). Photo courtesy Vít TEJROVSKÝ.

Obr. 38. Svišť černohlavý *Marmota camtschatica camtschatica* (Kamčatka, Rusko). Foto Vít TEJROVSKÝ.

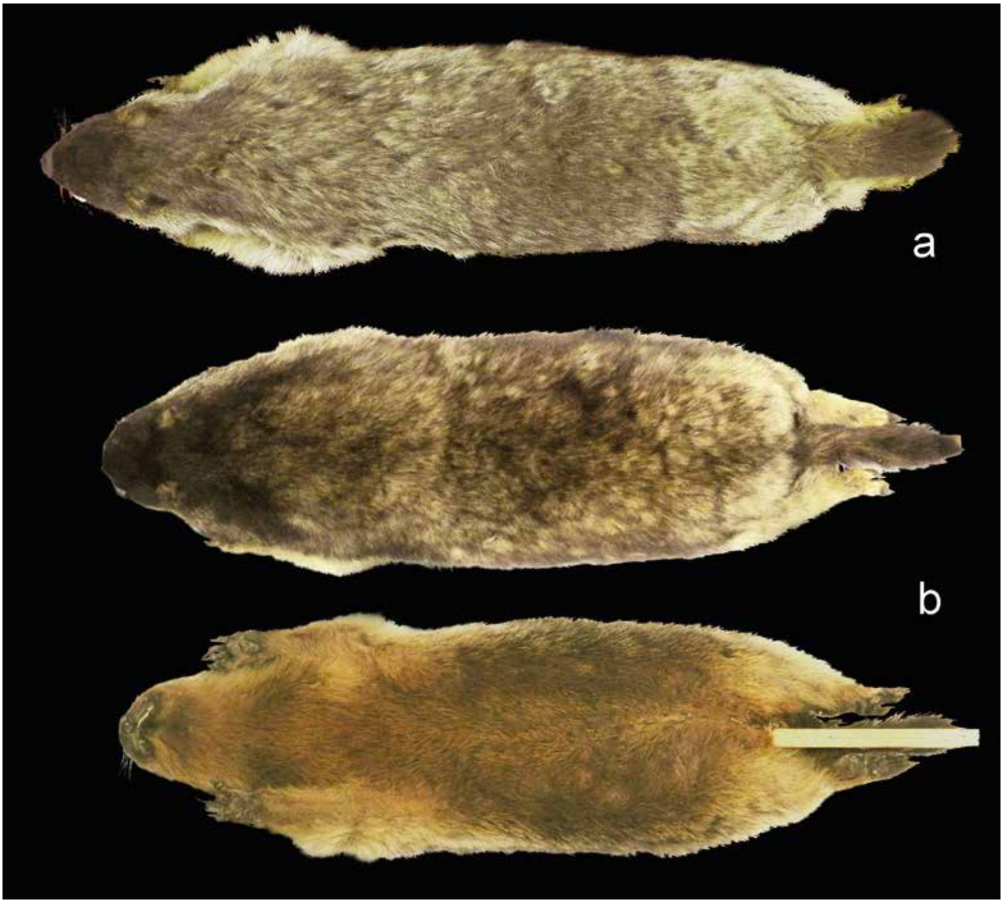


Fig. 39. Skins of *Marmota camtschatica camtschatica* from Kamchatka, Russia: a – unsxed adult (BMNH 58.11.18.3), b – adult male (BMNH 69.4.20.1). Photo by Boris Kryštufek.
Obr. 39. Balky *Marmota camtschatica camtschatica* z Kamčatky, Rusko: a – adultní jedinec neznámého pohlaví (BMNH 58.11.18.3), b – adultní samec (BMNH 69.4.20.1). Foto Boris Kryštufek.

paler. The thick, cylindrical tail is heavily clouded by dark hair tips and is blackish brown on its distal half. The ventral side is intense rusty-ocher, and speckled with brown hairs. Paws are ocher, and the two proximal plantar pads are distinctly elongate (Hoffmann et al. 1979). Baculum has a distal spatula with up to 5 denticles on its edge (Kapitonov 1978a). Females have 5–6 nipples (Hoffmann et al. 1979). Apart from its small size the skull does not differ appreciably from other marmots. It is low and rather narrow (ZgB = 60–65% CbL), with a long rostrum and small bullae. The mandible is long and low, coronoid process is rather weak (Fig. 40). Teeth show no peculiarities; enamel on the incisors is whitish to light-yellowish. Ranges for dimensions (in mm, weight in grams): W = 1650–5400, HbL = 394–615, TL = 110–155, HfL = 65–91, EL = 24–30, CbL = 80.4–100.4, ZgB = 49.9–62.2, MxT = 18.0–23.0 (KRIVOŠEEV 1984 and sources quoted below under "Subspecies"). Black-capped marmot is sexually dimorphic with a male/female ratio in CbL = 1.024 (MATĚJŮ & KRATOCHVÍL 2013); dimensions are subjected to considerable geographic variation (cf. account on "Subspecies"). Karyotype: 2n = 40 (LYAPUNOVA et al. 1992).

GEOGRAPHIC RANGE (Fig. 41). A species endemic to Russia with fragmented range extending from the Lena River and the Baikal Lake in the west to the Sea of Bering in the east; the northern border is on the shores of the Arctic Sea, the southern one is on the Okhotsk Sea and the Baikal. The largest contiguous populations are in three main parts: (i) along the Bering coast in Kamchatka and the Koriaksk Highlands, (ii) between the rivers Lena – Aldan and the

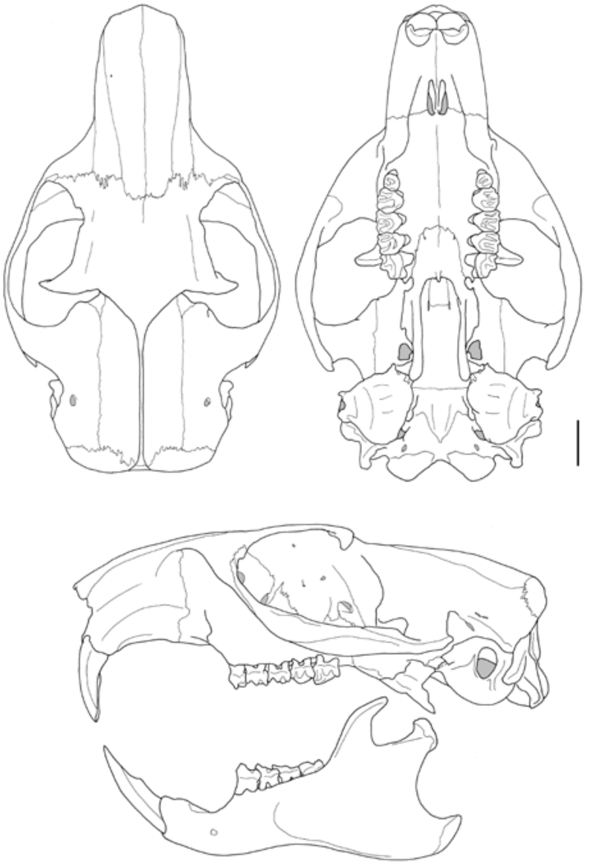


Fig. 40. Skull and mandible of *Marmota camtschatica camtschatica*; adult male from Kamchatka, Russia (SZM 50042). Scale bar = 1 cm.
Obr. 40. Lebka a mandibula *Marmota camtschatica camtschatica*; adultní samec z Kamčatky, Rusko (SZM 50042). Měřítko = 1 cm.

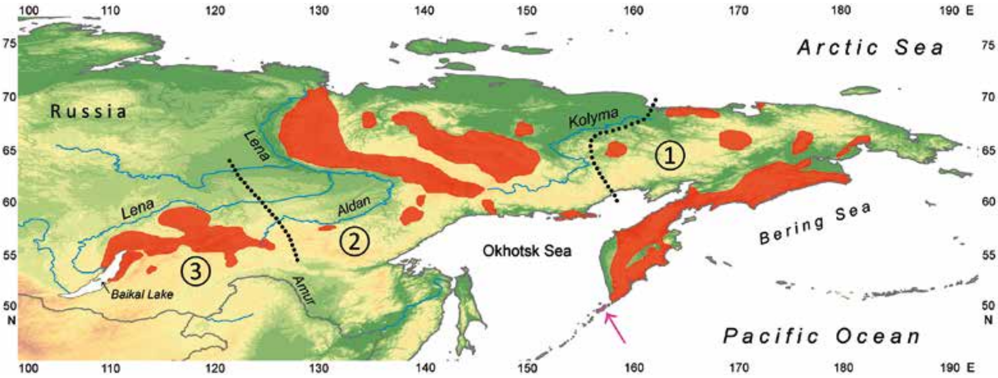


Fig. 41. Distribution of *Marmota camtschatica*. Compiled from the following sources: total range – Kapitonov (1978a), Bobrov et al. (2008); north-eastern Siberia – Krivošeev (1993), Baikal region – Švecov et al. (1984). Borders among subspecies are from Kapitonov (1978a) and Bibikow (1996). Introduction to northern Kuriles is shown in scarlet colour. Subspecies: 1 – *Marmota camtschatica camtschatica*; 2 – *M. c. bungei*; 3 – *M. c. doppelmayeri*.

Obr. 41. Rozšíření *Marmota camtschatica*. Zkompilováno z následujících pramenů: celkový areál rozšíření – Kapitonov (1978a), Bobrov et al. (2008); severovýchodní Sibiř – Krivošeev 1993, oblast Bajkalu – Švecov et al. (1984). Hranice mezi poddruhy jsou podle Kapitonova (1978a) and Bibikowa (1996). Vysazení na severní Kurily je vyznačeno fialově. Poddruhy: 1 – *Marmota camtschatica camtschatica*; 2 – *M. c. bungei*; 3 – *M. c. doppelmayeri.*

Kolyma in the Momsk, Čersk and Verhoânsk highlands, and (iii) to the north and northeast of the Baikal Lake. There is number of small isolates scattered throughout the entire range. Our map relies primarily on Kapitonov (1978a); presence on the Tajgonos Peninsula, not recorded by Kapitonov (l.c.) seems to be well supported (Krivošeev 1993, Bobrov et al. 2008) and was therefore included. On the other hand, we did not accept the presence in the central part of the Kolyma Highlands which is mapped only in Tsytsulina (2008).

The habitat is barren arctic tundra and alpine vegetation. Large proportion of range is on permafrost (Kapitonov 1978a) and in some areas (e.g. Kamchatka) the snow cover is absent for only 3.5–4 months (Mosolov & Tokarsky 1994). Specifically, the black-capped marmot is tied to dry plateaus and slopes (frequently steep ones with inclination of up to 30–50°), short-grass meadows on more gentle (15–30°) slopes of volcanic plateaus ("doly"), glacial circques, accumulations of rocks and boulders in moraines, and rocky coastal slopes. Elevational range is from sea level up to 2000 m (Kapitonov 1978a, Švecov et al. 1984) but there are significant differences among regions. Along the Arctic coast marmots go up to 200–400 m a. s. l., in the mountain tundra further south up to 400–500 m, in taiga and the forest-tundra they occupy a zone from the timber line and up to 600–1200 m a. s. l. (Zheleznov 1994); in the Baikal region the black-capped marmot similarly occurs from the timber line at 1300–1400 m a. s. l. up to the highest mountain peaks at 2000 m (Švecov et al. 1984); altitudinal range in Yakutia is from 20–25 m a. s. l. in the delta of the Lena, till 1400–1500 m (Tavrovskij et al. 1971); in eastern Kamchatka marmots go up to 1600 m a. s. l. (Mosolov & Rassohina 1999). These animals hibernate longer than other marmots, i.e. from the second half of September – early October until May; they are active for 5.5–6 months near the sea and for 4–4.5 months further inland (Bibikov 1967, Kapitonov 1978a).

Black-capped marmots were in steady decline throughout the entire 20th century in all main population segments: in the Baikal region (Švecov et al. 1984), between the Lena and the Kolyma in the Yakutsk area (Tavrovskij et al. 1971), and to the east of Kolyma in the Kamchatka segment (Krivošeev 1993). The entire population was estimated at 130,000 individuals in 1965–1970 (Bobrov et al. 2008), at 289,000 in 2000, and at 160,000 in 2004 (Mashkin & Kolesnikov 2005). A population on the Hologos River (a tributary of the Indigirka), which was extirpated, was re-established in 1954 through a translocation using black-capped marmots from the Momsk Highland. Another translocation was in 1963 of marmots from the Tuora-Sis Highlands which were released on the right bank of the Lena (Kapitonov 1978a). And finally, 43 marmots from Kamchatka were released in 2003 on the Is. Paramušir (Kuril Islands). This population, still present in 2005 (Bobrov et al. 2008), is the only insular occurrence of *M. camtschatica*.

Subspecies. Of the tree subspecies, which are recognized by the great majority of authors (Ognev 1947, Gromov et al. 1965, Gromov & Erbaeva 1995, Boeskorov et al. 1999, Thorington et al. 2012), *doppelmayeri* is morphologically the most distinct. In general, the eastern nominotypical subspecies is the largest and the darkest, the western-most *doppelmayeri* is the smallest and the least black, and the geographically intermediate *bungei* is transitional also in morphology. Besides, there is significant variation in the position of NORs in chromosomes, and Boyeskorov et al. (1994) suggested that *M. camtschatica* should be regarded as a "superspecies". Molecular markers, however, retrieved modest divergence between the two subspecies (*camtschatica* and *doppelmayeri*) which are geographically the most apart and morphologically the most divergent (Steppan et al. 2011). Museum specimens can be reliably classified into one of these two subspecies by size alone; *bungei* however overlaps, particularly with the nomintypical race, and cannot be satisfactory defined morphologically.

Marmota camtschatica camtschatica

Synonyms. No junior synonyms.

Description (Figs. 38–40). The largest subspecies, with the longest tail and ears, and with the darkest pelage. Back is dark brown to blackish, i.e. of same colour as the front head which is, together with the terminal tail, the darkest part of the animal (Ognev 1947, Boeskorov et al. 1999). The central band in dorsal guard hair is buff to ivory-yellow, ventral guard hairs tend toward deep-chestnut (Hoffmann et al. 1979). Baculum is longer, distal spatula is less expanded, with up to one single ill-developed denticle (invariably on the left half) (Kapitonov 1978a). Incisive foramen is a dot- or a slit-like; interpterygoid space is narrower (Boeskorov et al. 1999). External dimensions for both sexes (in mm, weight in grams): W_{10} = 4550.0 (3400–5400), HbL_{12} = 501.7 (498–540), TL_{2} = 115, 132, HfL_{2} = 85, 91, EL_{1} = 30. Mosolov & Tokarsky (1994) report the following maxima for a population from the Yartinaya River: HbL = 57 cm, W = 4.5 kg. Skull dimensions (in mm), males: CbL_{22} = 95.8 (90.2–100.4), ZgB_{22} = 58.9 (56.7–62.2), MxT_{22} = 21.3 (19.3–23.1); females: CbL_{21} = 90.1 (87.8–92.6), ZgB_{21} = 56.0 (53.0–58.1), MxT_{23} = 20.8 (20.0–22.1) (Kapitonov 1978a, Černâvskij 1984, Boeskorov et al. 1999, and specimens in SZM and ZISP).

Geographic range. The eastern portion of the species' range eastward of the Kolyma River (Fig. 41). Population estimated at 234,000 individuals in 2000 and 105,000 in 2004 (Mashkin & Kolesnikov 2005).

Marmota camtschatica bungei

SYNONYM. *cliftoni.*

DESCRIPTION. The subspecies *bungei* shows transitional characteristics in all morphological traits which were studied so far: size, colouration, and the peculiarities of cranial structure. It is paler than ssp. *camtschatica*, and dark front-head is clearly distinct from the back (OGNEV 1947, BOESKOROV et al. 1999). The central band in dorsal guard hair is ivory to light-yellow, ventral guard hairs tend towards rufous (HOFFMANN et al. 1979). Incisive foramen is oval, dot-like or slit-like; width of interpterygoid space varies (BOESKOROV et al. 1999). There is considerable amount of interpopulation variability in this subspecies (BOESKOROV et al. 1999). External dimensions for both sexes (in mm, weight in grams): W_{25} = 3539.6 (2150–5010), HbL_{25} = 541.2 (460–615), TL_{14} = 129.1 (110–145), HfL_{15} = 77.1 (65–85), EL_{15} = 25.8 (24–28). Skull dimensions (in mm), males: CbL_{53} = 90.5 (84.0–98.8), ZgB_{48} = 56.0 (50.6–59.5), MxT_{53} = 20.4 (18.9–22.1); females: CbL_{44} = 88.3 (85.6–93.7), ZgB_{44} = 54.6 (51.5–58.8), MxT_{45} = 19.8 (18.0–21.1) (TAVROVSKIJ et al. 1971, KAPITONOV 1978a, ČERNÂVSKIJ 1984; BOESKOROV et al. 1999, and specimens in AMNH and ZISP).

Fig. 42. Skin of a female *Marmota camtschatica doppelmayeri* from Barguzinskij Reserve in the upper reaches of the Urdikan River, Buryatia, Russia (SZM 49341). Photo by Boris KRYŠTUFEK.
Obr. 42. Kůže samice *Marmota camtschatica doppelmayeri* z Barguzinské reservace na horním toku řeky Urdikan, Burjatsko, Rusko (SZM 49341). Foto Boris KRYŠTUFEK.

GEOGRAPHIC RANGE is between the rivers Lena on the west and Kolyma in the east (Fig. 41). For the last 60 years local extirpations were reported for the lower reaches of the Ingidirka River, around Sakha, and the Momsk Highland (SOLOMONOV et al. 1994). The entire population declined from 80,000 individuals in 1950, to 30,000 in early 1990s; densities dropped from 25 individuals per 100 km^2 to a current nine per 100 km^2 (LUKOVTSEV & YAKOVLEV 1994). In two recent counts (in 2000 and 2004) the population was estimated at 33,000 individuals (MASHKIN & KOLESNIKOV 2005).

Marmota camtschatica doppelmayeri

SYNONYMS. No junior synonyms.

DESCRIPTION (Fig. 42). The smallest subspecies with a relatively shorter tail and ears; pelage is lightly tinted with dark. The front-head and terminal portion of the tail are dark rusty-brown; the back is paler than the front-head, with more pronounced yellow to light reddish-brown tints (OGNEV 1947, BOESKOROV et al. 1999). The central band in dorsal guard hair is buff, ventral guard hairs tend toward cinnamon or tawny (HOFFMANN et al. 1979). Baculum is robust although it is shorter than in ssp. *camtschatica*; the distal spatula with four denticles (one denticle on the right lobe) (KAPITONOV 1978a). Incisive foramen is oval; interpterygoid space is wider (BOESKOROV et al. 1999). External dimensions for both sexes (in mm, weight in grams): W_6 = 1800 (1650–2000), HbL_9 = 422 (394–450). Skull dimensions (in mm), males: CbL_{15} = 86.1 (82.1–90.6), ZgB_{15} = 53.2 (50.5–54.7), MxT_{16} = 19.4 (18.8–19.7), females: CbL_{14} = 82.8 (80.4–86.2), ZgB_{12} = 52.1 (49.9–53.9), MxT_{15} = 18.8 (18.0–20.4) (KAPITONOV 1978a, BOESKOROV et al. 1999, and specimens in SZM and ZISP).

GEOGRAPHIC RANGE. Between the Baikal Lake and the upper reaches of the Aldan River. Still widespread at the end of 20th century but suppressed afterwards (ŠVECOV et al. 1984). In two counts (in 2000 and 2004) the population was estimated at 22,000 individuals (MASHKIN & KOLESNIKOV 2005).

Species group *caudata*

Monophyly of the *caudata – menzbieri* tandem steams from molecular analyses. This clade is possibly in a sister position against the Nearctic *M. broweri* (STEPPAN et al. 2011). Its range is small, restricted to a broken landscape within the triangle: western Tian Shan Mts. – western Himalayas – central Afghanistan (Fig. 12).

Marmota caudata (Geoffroy Saint-Hillaire, 1844) – Long-tailed marmot

1844 *Arctomys caudatus* Geoffroy Saint-Hillaire. Type locality: “La haute vallée où le Sind et le Gombour se séparent” (= Gombour in the upper valley of the Sind River [not the Sindhu (= Indus) River], Jammu and Kashmir, India). RODE (1945: 25) reports the origin of the type as “Hautes Vallées de l’Himalaya”.

1875 *Arctomys aureus* Blanford. Type locality: “Kaskasu between Yárkand and the Pámir” (= pass Kaska-Su, ca. 130 km west of Yarkant (known also as Shache), prov. Xinjiang, China).

1875 *Arctomys dichrous* Anderson. Type locality: “mountainous country to the north of Kabul”, Afghanistan.

1909 *Arctomys littledalei* Thomas. Type locality: “Alai Mts., Pamir” (= Alai Mts., Kyrgyzstan).

1909 *Arctomys littledalei flavinus* Thomas. Type locality: “Hissar Mts, 100 miles E. of Samarkand, 10,000’ ”, Tajikistan. ALLEN (1940: 718) mistakenly regarded this form to be “*M. bobak sibirica*, of which Thomas had apparently none for comparison.”

1916 *Marmota stirlingi* Thomas. Type locality: “head of Chitral Nullah, 11,000’ ”, Chitrall, Pakistan.

Remarks. The long-tailed marmot is parapatric with three other marmots: *M. menzbieri*, *M. baibacina*, and *M. himalayana*. No hybrids were reported from any of the contact zones. The oldest evidence of *M. caudata* or a form very similar to it, is from the western-most part of its current range: from the Early Pleistocene (1.5 mya) in the Alai mountain range, Uzbekistan (Krakhmal 2005), and from the Middle Pleistocene of the Tien Shan Mts. (Gromov et al. 1965).

Description (Figs. 43, 45–47). Medium-sized to large marmot with tail longer than any other species of *Marmota*; tail length accounts on average for 43% HbL (range = 37–55%). Fur is rough, thick and long; hair on the mid-back 37–44 mm long, on the top of the tail up to

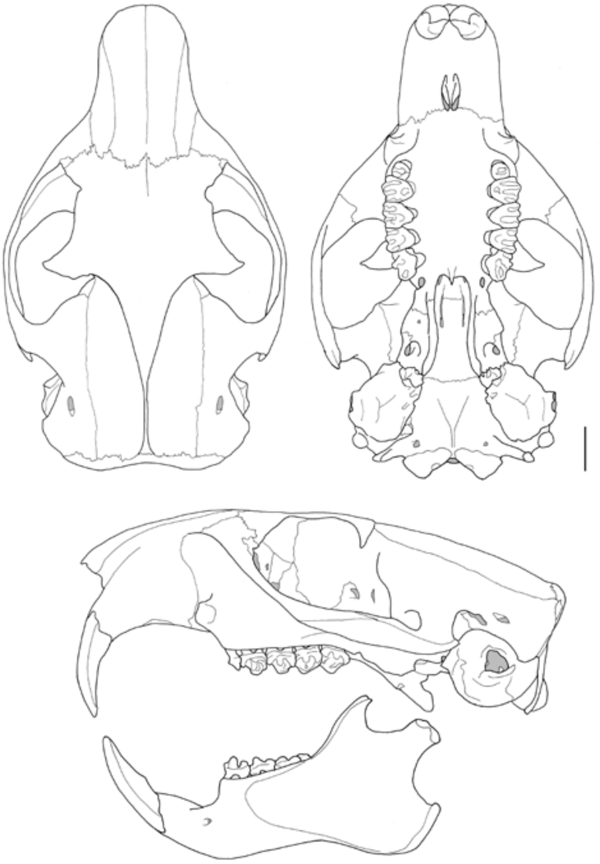


Fig. 43. Skull and mandible of *Marmota caudata aurea*; young adult from the Pamir Mts., Afghanistan, ~3900 m a. s. l. (ZFMK 93.435). Scale bar = 1 cm.
Obr. 43. Lebka a mandibula *Marmota caudata aurea*; mladý dospělý jedinec z Pamiru, Afghanistán, ~3900 m n. m. (ZFMK 93.435). Měřítko = 1 cm.

50–62 mm (Sludskij et al. 1969); belly is frequently only sparsely haired. Three bands are present on guard hair: a dark basal, yellow middle part, and dark tip. The basic colour throughout is reddish-yellow to rich-orange, usually darker on head, tail, and paws. The back is washed black in majority of individuals, but the extent varies tremendously among regions. In the nominotypical subspecies, the black "saddlepatch" (Ellerman 1940) extends as a wide stripe from the snout to the tip of tail, while in ssp. *dichrous* the animals lack rufous tint entirely, being light yellow to dark brown or black-brown above, and invariably black below (Fig. 45). In majority of populations however, the back is reddish and black patches are restricted to the head, or are even absent entirely (Fig. 46). For further notes on colour pattern see account on subspecies. Females have 5–6 pairs of nipples: 2–3 pectoral, one abdominal, and two inguinal; 13 nipples (due to a supernumerary pectoral nipple) were also recorded (Davydov 1974); Roberts (1997) reports 4–5 pairs of nipples. Baculum is a bent rod with uplifted distal spatula which bears few denticles; base is thick and circular (Bibikov 1967). Skull does not deviate from the form seen in other marmots. It is rather narrow across zygomatic arches (ZgB = 60.5–67.7% CbL), with wide interorbital region and short, blund postorbital processes (Fig. 43). Enamel on incisors is light yellow or light orange. Ranges for dimensions (in mm, weight in grams): W = 1500–7257, HbL = 370–800, HfL = 88–105, TL = 160–282, EL = 17–30, CbL = 83.4–106.0, ZgB = 53.0–65.4, MxT = 20.0–24.7. Body mass of adults varies depending on the season, e.g. in Kazakhstan between 2.1–4.3 kg in May and 4.4–6.7 kg in August (Sludskij et al. 1969); in animals just before the hibernation 27–28% of body mass is fat (data from Tajikistan; Davydov et al. 1978). Males are larger; male/female ratio in CbL = 1.023 (Matějů & Kratochvíl 2013). Karyotype: 2n = 38 (Voroncov et al. 1969).

Geographic range (Fig. 44). It is in broken mountain landscape in Central Asia in Kyrgyzstan, Tajikistan, Afghanistan, and marginally in Kazakhstan, Uzbekistan, Chinese Xingjian, Pakistan, and north-western India. The long-tailed marmots occupy the following major mountain ranges: western and Central Tien Shan, Pamir, Alai, Hindukush, and marginally also Kunlun-Shan, Karakoram, and north-western Himalayas.

Where not prevented by the snow line the long-tailed marmots ascend to the mountains peaks. Vertical range is 600–5200 m a. s. l. but this varies depending on the region. Range is 600–4500 m in Kyrgyzstan (Kizilov & Berendev 1978), 1500–5000 m in Tajikistan (Davydov et al. 1978), 2000–4000 m in Gissarsk range of Uzbekistan (Esipov et al. 1999), 2000–4000 m in Afghanistan (Habibi 2004), and between 8000 and 14,000 ft. (2440–4270 m) in India and Pakistan (Blanford 1891; up to 5200 m in Pakistan, cf. Roberts 1997). In Kyrgyz Alatau (altitudinal range 1200–4900 m), marmots are the most abundant at 2000–2200 m (Sludskij et al. 1969) and in Pamir (range 3600–4900 m) the optimal habitats are at 3800–4300 m (Saidov 2005). Habitats occupied by long-tailed marmots change depending on the elevation. In the western Tien Shan, marmots frequent steppe habitats from the foothills (600 m) up to the alpine zone above 4000 m a. s. l., while the forest steppe is occupied below 3000 m. At low elevations (600–1500 m) marmots live also in sparse woodland and between 1500 and 3000 m they occupy scrubs. At the altitude between 2500 and 4500 m the main habitat are high-elevational semi-deserts, sub-alpine meadows and moraines (Kizilov & Berendev 1978). In Pakistan long-tailed marmots occupy broken rocky ground interspersed with patches of alpine meadows and creeping brushes (Roberts 1997). In China the species "inhabits the zone of coniferous forests but also penetrates the alpine zone", specifically "dry, clifflike mountain slopes covered mainly by short grasses" and stands of 3–4 m high junipers (Hoffmann & Smith 2008). As it holds for all marmots, *M. caudata* hibernates for 7–7.5 months (Bibikov 1967), i.e. from the end of July – early September

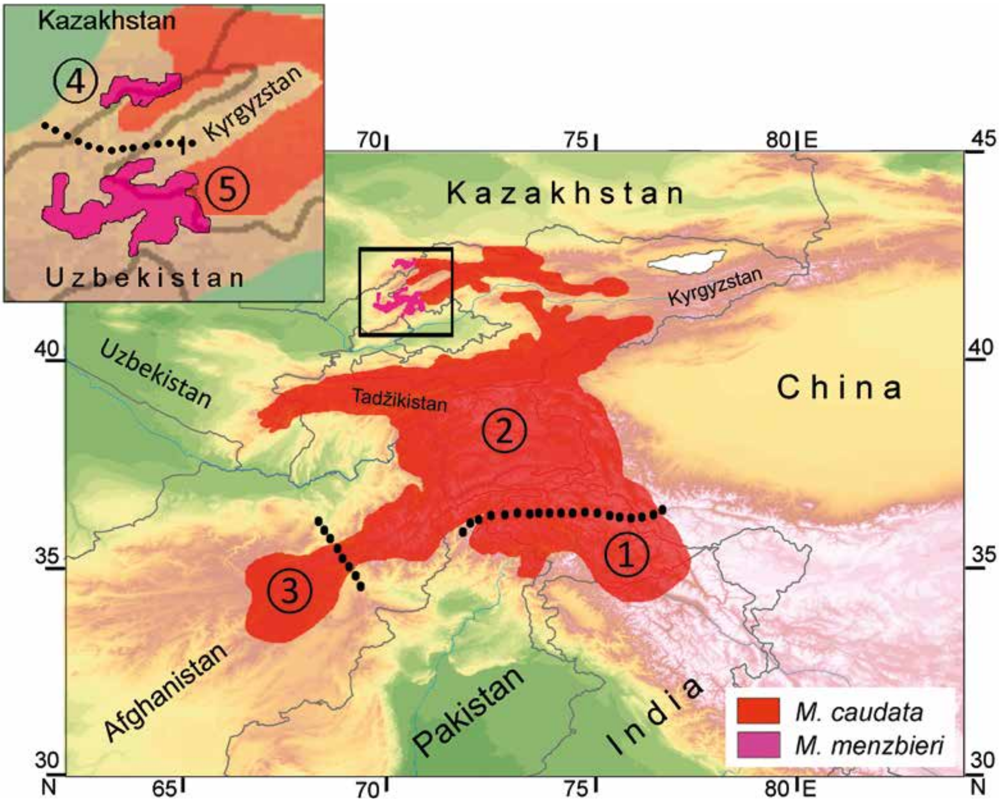


Fig. 44. Distribution of *Marmota caudata* and *Marmota menzbieri*. Compiled from the following sources: *Marmota caudata*: Kazakhstan – Sludskij et al. (1969); Kyrgyzstan – Kizilov & Berendev (1978); Tajikistan and Uzbekistan – Davydov (1974), Davydov et al. (1978); China – Zhang (1997); Afghanistan – Niethammer (1965), Habibi (2004); India and Pakistan – Roberts (1997), Molur et al. (2005). *Marmota menzbieri*: overall range – Petrov (1963) and Kapitonov (1978b); Tajikistan – Davydov (1964). Subspecies: 1 – *M. caudata caudata*; 2 – *M. caudata aurea*; 3 – *M. caudata dichrous*; 4 – *M. menzbieri menzbieri*; 5 – *M. menzbieri zachidovi*.

Obr. 44. Rozšíření *Marmota caudata a Marmota menzbieri*. Zkompilováno z následujících pramenů: *Marmota caudata*: Kazachstán – Sludskij et al. (1969); Kirgizie – Kizilov & Berendev (1978); Tadžikistán a Uzbekistán – Davydov (1974), Davydov et al. (1978); Čína – Zhang (1997); Afghanistán – Niethammer (1965), Habibi (2004); Indie a Pakistán – Roberts (1997), Molur et al. (2005). *Marmota menzbieri*: celkový areál – Petrov (1963) a Kapitonov (1978b); Tadžikistán – Davydov (1964). Poddruhy: 1 – *M. caudata caudata*; 2 – *M. caudata aurea*; 3 – *M. caudata dichrous*; 4 – *M. menzbieri menzbieri*; 5 – *M. menzbieri zachidovi*.

until mid-February – early April in Kazakhstan (Sludskij et al. 1969), from late August – early September until mid-March – April in Kyrgyzstan (Kizilov & Berendev 1978), and between late July – September and March – late April in Tajikistan (Davydov et al. 1978).

Long-tailed marmots tolerate aridity better than *M. baibacina*, and are therefore shifted towards drier habitats wherever these two species co-occur. Long-term changes in precipitation regime during the 20th century (with increase in precipitations) enabled *M. baibacina* to expand westwards on the expense of *M. caudata* (Sludskij et al. 1969). On the other hand, *M. caudata* expanded range for >10 km in the most exposed part of its occurrence in the western Tien Shan Mts. (Uzbekistan) and simultaneously also descended to lower elevations (down to 1377 m a. s. l.; Bykova & Esipov 2005). Populations were mainly in decline during the 20th century; e.g., in Kyrgyzstan a decline of 15–20-fold in high-elevation meadows between late 1930s and 1960s (Kizilov & Berendev 1978) was followed by a steady decay since 1960s (Tokmergenov et al. 2005). Along the northern range border in Kazakhstan the species was always rare (Spivakova et al. 2002).

Subspecies. Ellerman & Morrison Scott (1951) reduced number of "forms" (five were recognized in Thomas 1916) to three subspecies which are readily diagnosable on colouration. Gromov et al. (1965) list only 2 subspecies (*aurea* and the nominotypical), but *dichrous* is at least as distinct from any of them, as the two are between themselves. Scarce genetic evidence (Steppan et al. 2011) suggests deep divergence between *aurea* and the nominotypical subspecies; *dichrous* was so far not sequenced.

Key to Subspecies

1 Ventral side dark brown or black (Fig. 47). .... *M. caudata dichrous*

1* Ventral side rufous yellow (Figs. 45, 46). 2

2 A bold black stripe from occiput to rump (Fig. 45). .... *M. caudata caudata*

2* Back rufous yellow, clouded by black hair, but without bold black stripe (Fig. 46). .... *M. caudata aurea*

Marmota caudata caudata (Geoffroy Saint-Hillaire, 1844)

Synonyms. No junior synonyms.

Description (Fig.45). A large and long-tailed subspecies (on average TL = 45% HbL). Head is usually black, and bold black stripe extends along the spine from the occiput till the rump or the tail base; tail is black or mixture of black and yellow. Flanks, feet and belly are yellow with different degree of rufous tints; face is brown. Dimensions (in mm, weight in grams; sexes pooled): W_{10} = 5139.0 (3629–7257), HbL_{28} = 577.7 (490–800), TL_{28} = 252 (213–282), HfL_{26} = 98.7 (88–105), EL_{10} = 27.7 (25–30), CbL_{16} = 100.8 (90.4–104.9), ZgB_{15} = 62.4 (56.8–65.4), MxT_{16} = 23.4 (22.5–24.7) (Ellerman 1940, Roberts 1997, and specimens in BMNH and NMNH).

Geographic range (Fig. 44). It is to the south of Chitral in the Indian and Pakistani part of the species range (Ellerman 1940). The neighbouring parts of China (Zhang 1997) and Afghanistan (specimens in NMP and ZFMK) are already occupied by the ssp. *aurea*. In addition to Ellerman (1940), one of the best sources of detailed localities is Roberts (1997): Kaghan (Kagan) Valley, Nanga Parbat, at Dorah and Agram Passes, Lutko, Arkari Nullahs, Ayon Nullahs, Yarkhun, Besti, northern Hunza, Khunjerab, Deosai Plateau, Burzil, and Swat Kohistan. Altitudinal range is 3200–5200 m (Roberts 1997).

Marmota caudata aurea (Blanford, 1875)

Remarks. Nikol'skij & Blumstein (1999) claim that interpopulation differences in the alarm call justify split of *aurea* into two subspecies: one (*aurea* would be the proper name) occupying

Fig. 45. Skin of *Marmota caudata caudata* in dorsal and ventral view. Adult female from Kagan Valley, Mansehra District, Pakistan, 12,000 feet (= 3658 m a. s. l.) (BMNH 10.12.2.25). Photo by Boris Kryštufek. Obr. 45. Balk *Marmota caudata caudata* z hřbetní a břišní strany. Adultní samice z údolí Kagan, distrikt Mansehra, Pakistán, 12,000 stop (= 3658 m n. m.) (BMNH 10.12.2.25). Foto Boris Kryštufek.

Karakorum in Pakistan and the eastern Pamir, the other (*littledalei*) inhabiting mountain ranges of Tien Shan and Alai; the border is tentatively set on the rivers Bartang–Murgab–Aksu.

Synonyms. *littledalei*, *flavinus*, *stirlingi.*

Description (Fig. 46). A small and short-tailed subspecies (on average TL = 40% HbL) with the brightest pelage: rich orange-tawny to golden-buff throughout, tinged with black along the spine and at the tail tip. The slate basal band on guard hair is usually very narrow. Head is of same colour as back (in the Pamir Mts.), but is darker (brown, dark-brown or black) in majority of populations. Dark cap covers the entire front-head from nose to line of ears, and extends below the eyes; lips are also black. Dimensions (in mm, weight in grams; sexes pooled): W_{19} = 3726.7 (2041–5700), HbL_{24} = 491.0 (450–540), TL_{23} = 194.5 (160–250), HfL_{18} = 84.1 (63–97), EL_{16} = 21.8 (17–30), CbL_{36} = 91.5 (83.4–98.5), ZgB_{36} = 58.0 (53.4–64.0), MxT_{39} = 22.2 (20.5–24.5) (based on data in Ognev 1947 and Sludskij et al. 1969, and specimens in BMNH, NMNH, SMF, SZM, ZSM, and ZISP). Sample from Tajikistan (n = 132–142; sexes pooled): W = 3631 (2200–6000), HbL = 519.5 (450–610), TL = 225.3 (195–270), HfL = 96,3 (85–105), CbL = 93.5 (84.5–103.7), ZgB = 59.1 (54.1–66.3), MxT = 22.9 (20.5–25.0) (Davydov 1974).

Geographic range (Fig. 44). Chitral and the northernmost Kashmir in Pakistan and India, Pamir Mts. in Afghanistan, and the rest of the species' range in China, Kyrgyzstan, Tajikistan, Kazakhstan and Uzbekistan.


a
b
c

←

Fig. 46. Skins of *Marmota caudata aurea* in dorsal (top row) and ventral view (bottom row): a – adult female from Ojguing, western Tien Shan Mts., Uzbekistan (PMBg 30/60); b – adult male from the eastern Tien Shan Mts., 100 miles (= 160 km) east of Samarkand (BMNH 9.4.8.111); c – adult male from Chap Darrah, Afghanistan, 3700 m a. s. l. (NMP 37899). Photo by Milan PAUNOVIĆ (a) and Boris KRYŠTUFEK (b, c).
Obr. 46. Balky *Marmota caudata aurea* z hřbetní (horní řada) and břišní strany (dolní řada): a – adultní samice z Ojguing, západní Ťan-Šan, Uzbekistán (PMBg 30/60); b – adultní samec z východního Ťan-Šanu, 100 mil (= 160 km) východně od Samarkandu (BMNH 9.4.8.111); c – adultní samec z Čap Darrah, Afghanistán, 3700 m n. m. (NMP 37899). Foto: Milan PAUNOVIĆ (a) a Boris KRYŠTUFEK (b, c).

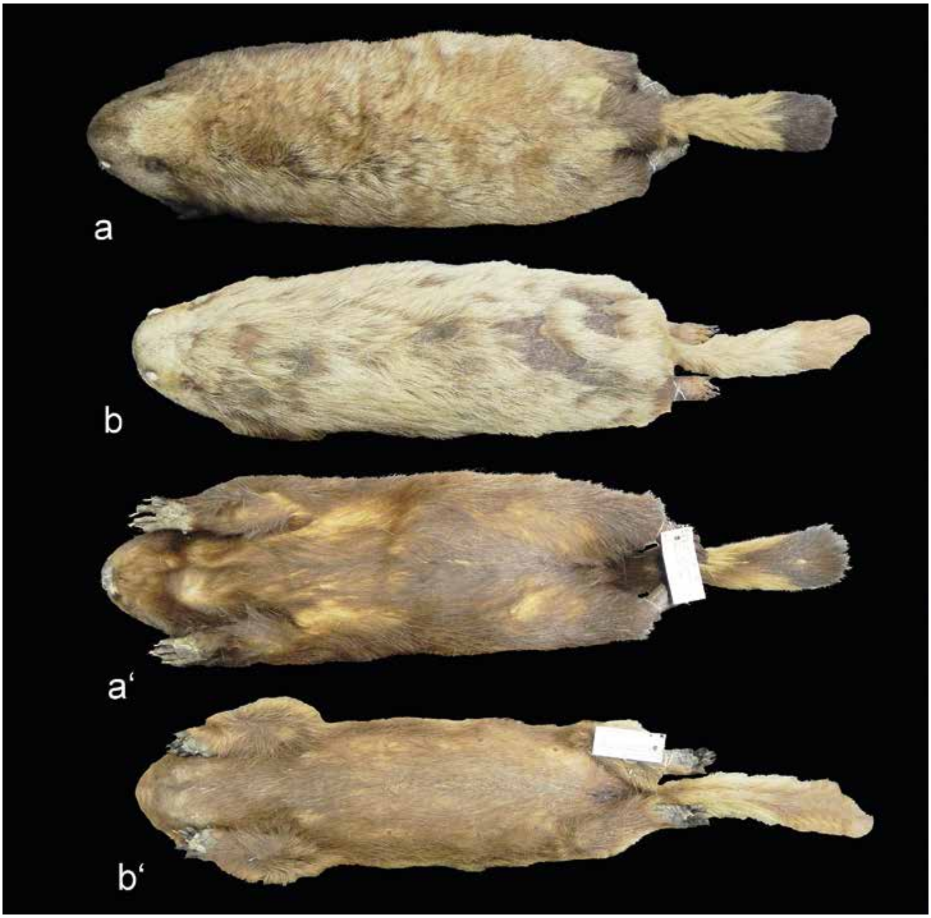


Fig. 47. Skins of *Marmota caudata dichrous* in dorsal (a and b) and ventral view (a’ and b’): a – adult female (ZFMK 93.431); b – adult male (ZFMK 93.430), both from Dasht-i-Nawar, Afghanistan. Photo by Boris KRYŠTUFEK.
Obr. 47. Balky *Marmota caudata dichrous* z hřbetní (a, b) a břišní strany (a’, b’): a – adultní samice (ZFMK 93.431); b – adultní samec (ZFMK 93.430), oba z Dasht-i-Nawar, Afghanistán. Foto Boris KRYŠTUFEK.

Marmota caudata dichrous (Anderson, 1875)

Remarks. considered as part of *baibacina* by some Russian authors (cf. Ognev 1947).

Synonyms. No junior synonyms.

Description (Fig. 47). Size as in *aurea*, relative tail length (on average 45% HbL) as in the nominotypical subspecies, longer than in *aurea*. Skins we saw (ZFMK) are of two distinct morphs, the dark and the pale. The basal band of guard hair is extensive (over ½ of hair length), slate in dark animals, brownish-yellow in pale ones. Dark morph is dull brown to blackish brown; feet are blackish-brown. Pale morph is light cream to light yellow from the nose to about mid-tail; the tail is of the same colour as back with light-brown terminal $^{1}/_{3}$; feet are light brown. Belly is black-brown in both morphs and hairs are dark throughout. For a photograph of a living individual see Niethammer (1965: 25). Dimensions (in mm, weight in grams; sexes pooled): W_5 = 2653.0 (1500–5000), HbL_6 = 442.5 (370–540), TL_6 = 207.5 (180–230), HfL_6 = 88.5 (70–100), EL_5 = 22.4 (18–25), CbL_{10} = 91.3 (88.3–94.3), ZgB_{11} = 59.3 (56.3–62.7), MxT_{11} = 22.4 (20.6–23.7) (based on specimens in ZFMK).

Geographic range (Fig. 44). Known from the mountains (above 2800 m a. s. l.; Niethammer 1965) around Kabul and Ghasni: Dashte Nawar, Hajigak, Panjshir, and ranges of Paghman and Baba. The identity of marmots occupying Nuristan (Habibi 2004) is not known.

Marmota menzbieri (Kaškarov, 1925) – Menzbier's marmot

1925 *Arctomys menzbieri* Kaškarov. Type locality: "Talasskij Alatau v uročiŝe Čigyr-Taš v verhovâh Ugama" (= Talas Alatau Mts., settlement Čigyr-Taš in the upper reaches of the Ugam River), ca. 50 km south-east of Shimkent, southern Kazakhstan.

1963 *Marmota menzbieri zachidovi* Petrov. Type locality: "Kyzyl-Nura (vysota 2900–3000 m), zapadnaâ okonečnost' Čatkalskogo hrebta, Taškentskaâ obl., Uzbekskaâ SSR" (= Mt. Kyzyl-Nura (altitude 2,900–3,000 m), western end of the Čatkal Mts., Toshkent Region, Uzbekistan).

Remarks. Along its eastern margin, *M. menzbieri* is in contact with *M. caudata*, and ranges of these two species partly overlap in both fragments of the former's range, i.e. in the Talas Mts. (Sludskij et al. 1969) and in the Čatkal Mts. (Petrov 1963); hybridization was not reported from any of the contact zones. The two marmots are capable of segregating ecological niches. In the Čatkal range *M. menzbieri* depends on higher level of moisture, occupies higher elevations (>2200–2400 m a. s. l.) within the zone of a high-mountain steppe, and prefers short grass; *M. caudata* tolerates aridity, populates lower elevations (1300–2200 m a. s. l.) in the juniper (*Juniperus* spp.) zone, and selects higher grass (Petrov 1963, 1966).

Description (Figs. 48–50). The smallest marmot with a short tail (18.5–23% HbL); vibrissae are longer (50–60 mm) than in *M. caudata*. Fur is long (up to 38 mm), very dense (2900 hairs cm^{-2} on average; in *M. caudata* 1608 cm^{-2}; Sludskij et al. 1969); underfur is dense and curly. Colour is more subjected to seasonal variation than in other Palaearctic marmots. Marmots are light during the first half of the season, dark afterwards. In the dark pelage, the underlying pinkish-buff on the head, back, shoulders, tights and tail is clouded with dull brown, cinnamon-brown or blackish hairs (Fig. 49). Head is the darkest (dull brown to black) from snout to ears; the black cap extends to the occiput, the neck and fore-most shoulders, reaching the tail base along the spine. Ventral side is grey-white, washed rusty or buff; the demarcation along the flanks is rather sharp. The tail is normally of same colour as back, indistinctly darker at the very tip; ears are light. Cream or light-yellow patch extends from the lips across cheeks and the side of

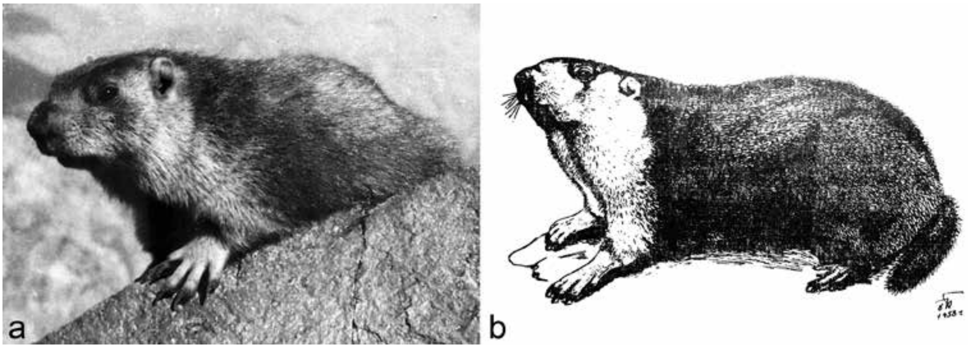


Fig. 48. Menzbier's marmot *Marmota menzbieri zachidovi* from the Čatkalski range, Uzbekistan, in dark pelage. Note the contrast between the light anterior and dark posterior fur which is clearly seen in the drawing (b). Photo and drawing by Boris M. Petrov.
Obr. 48. Svišť Menzbierův *Marmota menzbieri zachidovi* z Čatkalské oblasti, Uzbekistán, v tmavé srsti. Všimněte si kontrastu mezi světlou srstí vpředu a tmavou srstí vzadu, který je jasně vidět na kresbě (b). Foto a kresba Boris M. Petrov.

the neck, to the chest and the front paws. Pelage on the cheeks and around the eyes is tinted grey and light-buff; cheeks and area around the eyes is clouded grey or buff in some animals. The contrast between the light anterior part and the dark posterior (Fig. 48) is a unique feature of Menzbir's marmot, readily distinguishing this species from other marmots. The contrast is ill defined in the pale pelage which is light greyish-cream, washed buff or light fawn along the spine and on shoulders, rump and the proximal tail. The neck is darker than the shoulders; the front-head (from the snout to the ears) is dark brown. Tip of the tail is light yellow. Neck and flanks are light greyish; belly is as in dark pelage. The skull is small, with not much expanded zygomatic arches (ZgB = 61.6–66.9% CbL); nasals expand anteriorly, and have a pointed anterior margin. Interorbital region is flat and wide, the brain-case is relatively short, incisive foramina are extensive, interpterygoid vacuity is narrow (Fig. 50). Enamel on the anterior surface of incisors is light yellow. Baculum is a simple rod with small spatula and thick base (Bibikov 1967). Ranges for dimensions (in mm, weight in grams): W = 1850–4010, HbL = 345–500, TL = 72–130, HfL = 65–85, EL = 18–30, CbL = 79.8–91.8, ZgB = 51.3–59.1, MxT = 19.2–21.0. Body mass is reported to reach up to 5 kg (Sludskij et al. 1969); since August 750–1000 g of body mass is due to fat (Petrov 1965) what equals to 22.1% of body mass (Kapitonov & Lobačev 1964). This is sexually dimorphic species; male/female ratio in CbL = 1.023 (Matějů & Kratochvíl 2013). Karyotype: 2n = 38 (Voroncov et al. 1969).

Geographic range (Fig. 44) is the smallest of any Palaearctic marmot, restricted to the westernmost Tien Shan Mts. in Kazakhstan, Kyrgyzstan and Uzbekistan, and very marginally in northern Tajikistan. Furthermore, the range is in two parts which are separated by the valley of the Pskem River (which is populated by *M. caudata*; Mitropolskiy & Mitropolskaya 2005). The isolates are ~100 km apart: the northern isolate is in the Talas Mts. (Karažantau and Ugamsk mountain ridges), and the southern is in the Čatkal Mts. (Čatkal and Kuraminsk ridges). The range is further fragmented in both patches, e.g. into three major groups of populations in the northern isolate. These sub-populations are in the mountain ranges of (i) Badam (on a surface area of

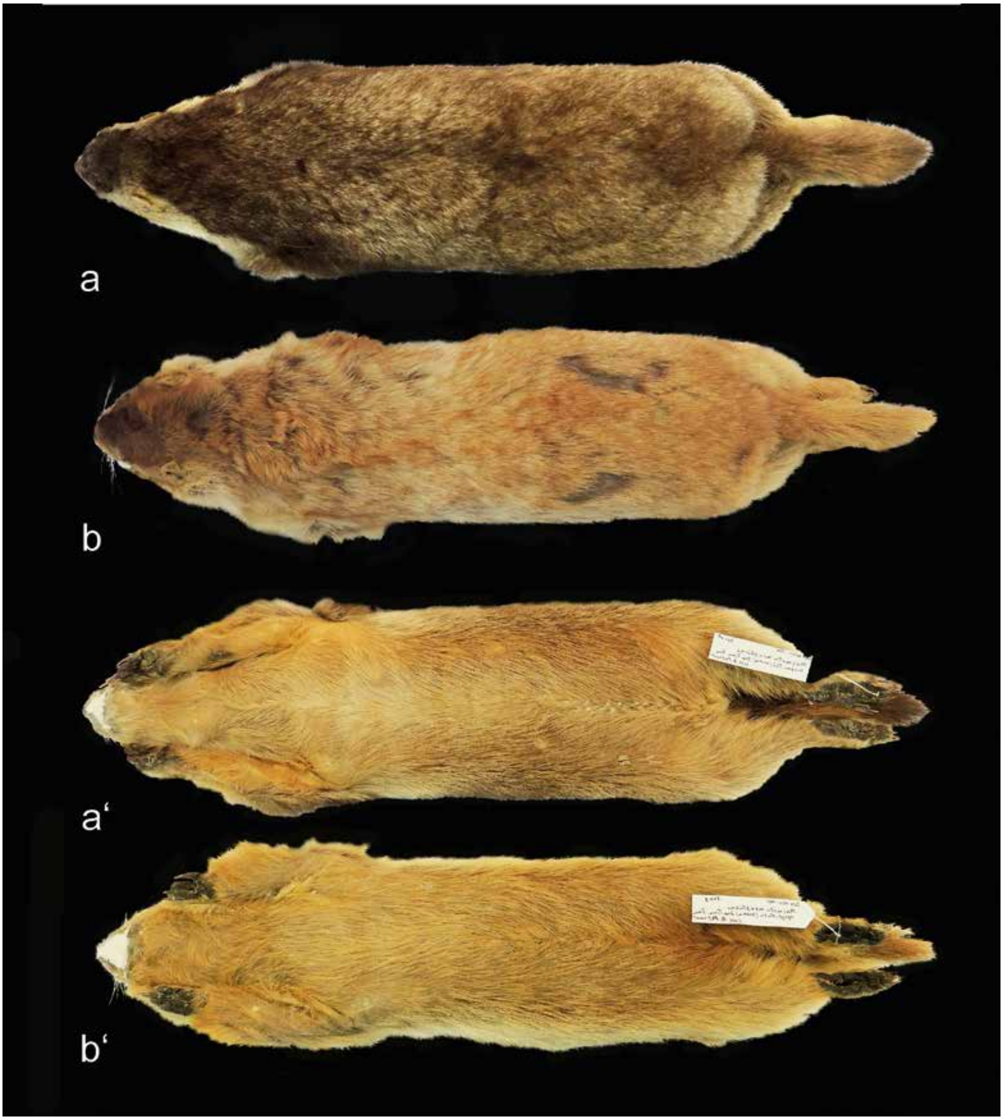


Fig. 49. Skins (dorsal and ventral view) of *Marmota menzbieri zachidovi* from western Tien Shan in Uzbekistan: a – adult male in dark pelage, collected on 20 August 1953 at 3000 m a. s. l. in Kurgan Taš; b – adult female in pale pelage, collected on 15 June 1961 at 3000 m a. s. l. in Kyzyl-Nura. Collection of Boris M. Petrov in PMBg. Photo courtesy Milan Paunović.

Obr. 49. Balky (pohled z hřbetní a břišní strany) *Marmota menzbieri zachidovi* ze západního Ťan-Šanu v Uzbekistánu: a – adultní samec v tmavé srsti, ulovený 20. 8. 1953 v 3000 m n. m. na lokalitě Kurgan Taš; b – adultní samice ve světlé srsti, ulovená 15. 6. 1961 v 3000 m n. m. na lokalitě Kyzyl-Nura. Sbírka Borise M. Petrova v PMBg. Foto Milan Paunović.

100 km^2 with an average density of 30 individuals km^{-2}), (ii) Sajram (100 km^2 and 50 km^{-2}, respectively), and (iii) Ugam (200 km^2 and 70 km^{-2}, respectively) (KAPITONOV 1978b). For the southern isolate PETROV (1965) gave an average estimate of 10 marmots km^{-2}, while patches of a suitable habitat may support up to 40–50 km^{-2}.

The entire range of Menzbier's marmot is relatively well supplied with precipitation. The northern segment is more wetted (1500–2500 mm year^{-1}) with a pronounced autumn peak. Summer is dry everywhere but marmots avoid excessive drought by concentrating around large accumulations of snow which provide water for the surrounding plants by melting (PETROV 1966). Main habitat in the wetter north are meadows (*Geranium*, *Myosotis*, *Anemona* etc.), and in the dryer south are steppes (*Prangos*, *Ferula*, *Eremostachis*, *Poa*, *Artemisia*, *Saxifraga* etc.).

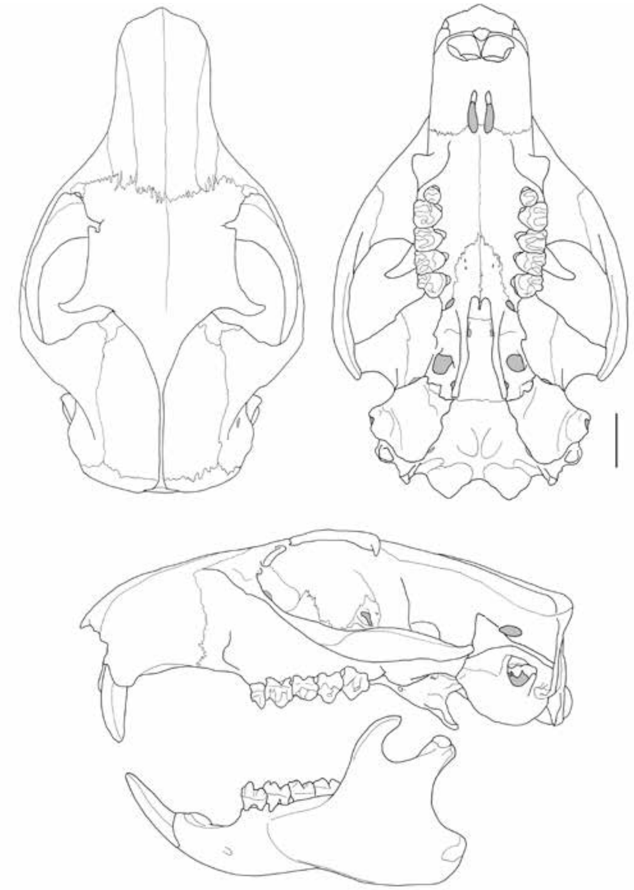


Fig. 50. Skull and mandible of *Marmota menzbieri zachidovi*; adult individual from Čatkal Reserve, Uzbekistan (SZM 50044). Scale bar = 1 cm.
Obr. 50. Lebka a mandibula *Marmota menzbieri zachidovi*; adultní jedinec z Čatkalské reservace, Uzbekistán (SZM 50044). Měřítko = 1 cm.

Particularly on dry slopes, *M. menzbieri* aggregates around valleys which retain snow long into summer and where melting water supports mesic vegetation (Petrov 1963). Elevational range is 2100–3300 m a. s. l. in the north v. 2200–3600 m in the south. In the north 60–70% of habitat is suitable for marmots, v. 10–15% in the south. Optimal habitats are 2300–2700 m in the Badam range (total altitudinal range is 2100–2800 m), 2500–3100 m in Sajram (total range of 2350–3200 m), and above 2500 m in Čatkal (range is 2200–3600 m). Depending on the elevation, Menzbir's marmots hibernate from mid-August – late-September till mid-April – early May (Kapitonov 1978b).

Already Petrov (1965) reported on low abundances of Menzbier's marmots throughout the entire range, and stressed a decline in Uzbekistan. Kapitonov (1978b) estimated the entire population in 1960s to be 60,000 individuals with each of the two fragments having half of the total; a census for the western Čatkal region gave an estimate of 20,000 individuals (Petrov 1965). Such a population was supposedly far below the carrying capacity of the habitat. Annual bag was small (e.g. 2500 skins in 1940s) and the fat was even more appreciated commodity than the fur (Kapitonov 1978b). Recently, Plakhov (2005) reported 20–25,000 animals for Kazakhstan alone but also claimed that the range is in shrink. Decline was also reported for Kyrgyzstan (Tokmergenov et al. 2005) and the Čatkal range in Uzbekistan (Tretyakov 2005). In both cases Menzbier's marmots shifted the lower border towards higher elevations, e.g. in the Čatkal range from 2600 m to 2800 m a. s. l. (Tretyakov 2005). Populations in the Čatkal range were affected by decline in precipitation and subsequently less melting snow during summer droughts, and by overgrazing of pastures (Esipov 2002).

Three translocations are documented (Kapitonov 1978b): to Aksu Džabag in Kazakhstan in 1944, and to Zaaminskij conservation area (Uzbekistan) in 1955 and 1957. The population occupying the Ugam range was a donor in all these attempts, which all proved to be failures.

Subspecies. Two subspecies are recognized, each of them tied to its own geographic isolate. Morphological differences are slight, but relatively deep genetic divergence was reported in this species (Steppan et al. 2011).

Key to Subspecies

1 Frontal bone partly displaces the suture between the posterior edge of the lachrymal bone and the the orbitosphenoidal bone (Fig. 51). .... *M. menzbieri menzbieri*
1* Frontal bone does not displace the suture between the posterior edge of the lachrymal bone and the orbitosphenoidal bone (Fig. 51). .... *M. menzbieri zachidovi*

Marmota menzbieri menzbieri

Synonyms. No junior synonyms.

Description. On average slightly larger than *M. m. zachidovi*. In the anterior side of orbital wall, the frontal bone partly displaces the suture between the posterior edge of the lachrymal bone and the orbitosphenoidal bone (Fig. 51). Dimensions (in mm, weight in grams), males: W_{35} = 2742.3 (1850–4080), HbL_{31} = 437.1 (354–490), TL_{31} = 98.5 (72–120), HfL_{31} = 74.0 (67.8–85), EL_{31} = 24.6 (20–30), CbL_{11} = 86.1 (82.3–91.8), ZgB_{11} = 55.6 (53.5–59.0), MxT_{11} = 20.3 (19.5–21.0); females: W_{20} = 2796.2 (1990–4070), HbL_{48} = 451.3 (365–500), TL_{48} = 97.8 (78–130), HfL_{48} = 78.8 (65–84), EL_{48} = 24.1 (18–28), CbL_{11} = 84.2 (80.1–87.9), ZgB_{11} = 56.0 (53.2–59.1), MxT_{11} = 20.0 (19.2–20.4) (modified from Kaškarov 1925, Ognev 1947, and Sludskij et al. 1969).

Geographic range. It is in the northern segment in the Talas mountain range (Fig. 44).

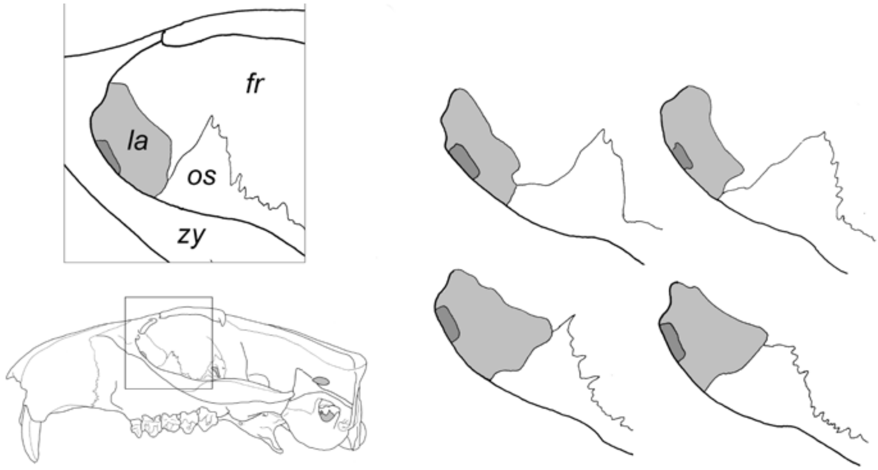


Fig. 51. Shape of the lachrymal-orbitosphenoidal suture in two subspecies of Menzbier's marmot: *Marmota menzbieri menzbieri* (top row); *M. m. zachidovi* (bottom row). Left insert shows the orbit with the lachrymal bone shaded. *fr* – frontal bone (*os frontale*); *la* – lachrymal bone (*os lacrimale*); *os* – orbitosphenoidal bone (*os orbitosphenoidale*); *zy* – zygomatic arch; lachrymal foramen (*foramen lacrimale*) is shaded dark. Morphotypes are from Petrov (1963).

Obr. 51. Tvar švu mezi slzní a klínovou kostí u dvou poddruhů sviště Menzbierova: *Marmota menzbieri menzbieri* (horní řada); *M. m. zachidovi* (dolní řada). Levý výřez ukazuje orbitu s vyšrafovanou slzní kostí. *fr* – kost čelní (*os frontale*); *la* – kost slzní (*os lacrimale*); *os* – kost klínová (*os orbitosphenoidale*); *zy* – jařmový oblouk; slzní otvor (*foramen lacrimale*) je tmavě vyšrafován. Morfotypy jsou podle Petrova (1963).

Marmota menzbieri zachidovi

Synonyms. No junior synonyms.

Description. On average slightly smaller than *M. m. menzbieri*. In the anterior side of orbital wall, the frontal bone does not displace the suture between the posterior edge of the lachrymal bone and the orbitosphenoidal bone (Fig. 51b). Dimensions (in mm, weight in grams), males: W_1 = 3500, HbL_1 = 440, TL_1 = 98, HfL_1 = 77, EL_1 = 27, CbL_3 = 85.9 (84.7–86.6), ZgB_2 = 53.6, 55.9, MxT_3 = 20.6 (20.3–20.8); females: W_4 = 2841.5 (1990–3800), HbL_4 = 448.8 (432–465), TL_4 = 96.8 (93–100), HfL_4 = 74.0 (73.0–76.2), EL_4 = 21.1 (20.7–21.6), CbL_5 = 82.9 (79.8–85.4), ZgB_5 = 53.5 (51.3–57.3), MxT_5 = 19.9 (19.4–20.4) (Sludskij et al. 1969, and specimens in SZM and ZISP). Ranges in marmots from the western part of the Čatkal range are: W = 2100–2600 (May–July), 2600–4000 (end of August), HbL = 407–462, TL = 84–121, HfL = 72.0–79.7, EL = 19.2–24.8, CbL = 79.8–90.7, ZgB = 49.9–57.7, MxT = 19.1–22.5 (Petrov 1961).

Geographic range. It is in the southern segment of the Čatkal Mts. (Fig. 44).

Tribe: Sciurotamiini Kryštufek et Vohralík, 2012 – Chinese rock squirrels

In the past, *Sciurotamias* (as the only genus in this tribe) was associated with various squirrels which are now in four different subfamilies of Sciuridae: Xerinae (with reference on close proximity with *Rhinosciurus* or *Dremomys* of Callosciurini, or resemblance of Xerini), Sciurinae (*Tamiasciurus*), Ratufinae (*Ratufa*), and Arctomyinae (Tamiini); for references see KRYŠTUFEK & VOHRALÍK (2012). Basal position of Sciurotamiini within Arctomyinae was re-confirmed in a phylogenetic reconstruction inferred from a molecular supermatrix (FABRE et al. 2012).

Since the tribe contains a single genus *Sciurotamias*, the description of the genus serves for the tribe.

Genus: *Sciurotamias* – Chinese rock squirrels

1901	*Sciurotamias* Miller. Type species: *Sciurus davidianus* Milne-Edwards, 1867.
1922	*Rupestes* Thomas. Type species: *Rupestes forresti* Thomas, 1922.

REMARKS. *Sciurotamias* contains two species in different subgenera. *Rupestes* was originally described as a full genus (THOMAS 1922) and still retained as such by ALLEN (1940). *Rupestes* is consistently treated as a subgenus of *Sciurotamias* since ELLERMAN (1940) who concluded that

Fig. 52. Skins of *Sciurotamias davidianus* (a, b) and *S. forresti* (c) in semilateral view: a – adult male *S. d. davidianus* from south-eastern Shensi, China (BMNH 10.5.2.19); b – *S. d. consobrinus* from Sechuan, China (BMNH 55.580); c – adult female from Lichiang, Sechuan, China (BMNH 23.4.1.39). Photo by Boris KRYŠTUFEK.

Obr. 52. Balky *Sciurotamias davidianus* (a, b) a *S. forresti* (c) ze semilateralního pohledu: a – adultní samec *S. d. davidianus* jihovýchodního Šensi, Čína (BMNH 10.5.2.19); b – *S. d. consobrinus* ze Sečuánu, Čína (BMNH 55.580); c – adultní samice z Lichiangu, Sečuán, Čína (BMNH 23.4.1.39). Foto Boris KRYŠTUFEK.

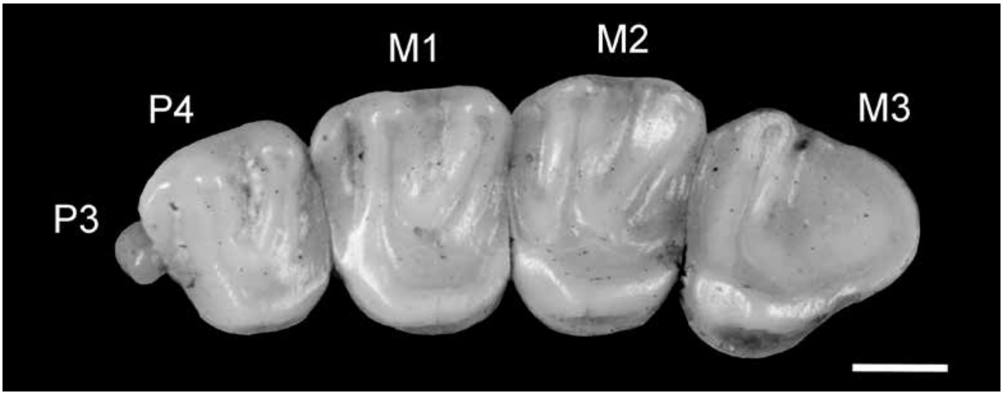


Fig. 53. Maxillary cheek-teeth in *Sciurotamias davidianus*; adult female from Shensi, China (BMNH 9.1.1.4). Anterior is to the left, labial is above; scale bar = 1 mm. Photo by Boris Kryštufek.
Obr. 53. Horní řada zubů *Sciurotamias davidianus*; adultní samice z Shensi, Čína (BMNH 9.1.1.4). Přední strana zubní řady je vlevo, vnější strana je nahoře; měřítko = 1 mm. Foto Boris Kryštufek.

"*Rupestes* … is not distinguishable in cranial and dental characters in any way that could be considered as of generic value". These subgenera differ in a whole set of stable character states: (i) colouration of flanks: plain greyish-brown in *Sciurotamias*; with a pale line between shoulder and hip in *Rupestes* (Fig. 52); (ii) colouration of a snout: greyish-brown in *Sciurotamias*, rusty in *Rupestes*; (iii) hind foot: broader in *Sciurotamias*, with sole hairy; narrower in *Rupestes*, with sole naked; (iv) plantar pads: 4 in *Sciurotamias*, restricted to the bases of proximal phalanges (the long metatarsal pad is absent); 5 plantar pads in *Rupestes* (the long metatarsal pad is present); (v) third upper premolar: present in *Sciurotamias* (Fig. 53), absent in *Rupestes*; (vi) nasal bones: long in *Sciurotamias* (their length exceeds the interorbital width; Fig. 56), short in *Rupestes* (length equals the interorbital width; Fig. 54); (vii) squamosal bone: high in *Sciurotamias* (nearly reaching the level of postorbital process; Fig. 56), lower in *Rupestes*, at about the level of lachrymal bone (Fig. 54); (viii) anterior edge of zygoma: ascends considerably higher in *Sciurotamias* (Fig. 56) than in *Rupestes* (Fig. 54); (ix) temporal ridges: weak or absent in *Sciurotamias* (Fig. 56), pronounced in *Rupestes* (Fig. 54); (x) postorbital process: well developed in *Sciurotamias* (>2 mm in length; Fig. 56); vestigial in *Rupestes* (Fig. 54); (xi) though diploid number is stable in the genus (2n = 38), subgenera differ in fundamental number of autosomal arms: NF = 64 in *Sciurotamias* (Wang et al. 1991), NF = 72 in *Rupestes* (Wang et al. 1980). The two subgenera are of about same size and body proportions; see below for *Sciurotamias*; *Rupestes* (in mm, sexes pooled): HbL_6 = 232.0 (194–290), TL_6 = 161.6 (130–180), HF_6 = 50.2 (47–57), EL_5 = 25.4 (25–27), PL_3 = 53.5, 56.4, 60.1, CbL_2 = 48.9, 50.1, ZgB_4 = 29.7 (28.9–30.8), MxT_7 = 8.8 (8.3–9.5) (Allen 1940, Moore & Tate 1965, and specimens in BMNH).

Fossils of *Sciurotamias* were reported from the Late Miocene of Shaanxi (Qiu et al. 2003) and the Middle Pleistocene of Quinhuangdao (Zhang et al. 2010). Further Miocene fossils which bear close resemblance on recent Chinese rock squirrels are known from various sites in Europe and Anatolia. These are classified into one of 4–5 fossil species under the generic name of either *Csakvaromys* Kretzoi, 1951, or *Spermophilinus* De Bruijn et Mein, 1968. These two names, which are synonymous (see below) are of interest because Gromov et al. (1965) and Gromov & Baranova (1981) consider *Csakvaromys* (= *Spermophilinus*) to be merely a subgenus of *Sciurotamias*.

Csakvaromys and *Spermophilinus* are based on the same type species and are therefore synonyms. Both names are valid and *Csakvaromys* clearly has priority over *Spermophilinus*. De Bruijn & Bosma (2012) argued that stability of nomenclature would benefit from a suppression of *Csakvaromys* in favor of *Spermophilinus*, but such an act would contradict the Principle of Priority (Article 23 of the International Code for Zoological Nomenclature; ICZN 1999). In the last years, authors interchangeably used either *Csakvaromys* (Hulva et al. 2007, Nicoara 2011) or *Spermophilinus* (Ruiz Sánchez et al. 2011, Bosma et al. 2013), always as full genera.

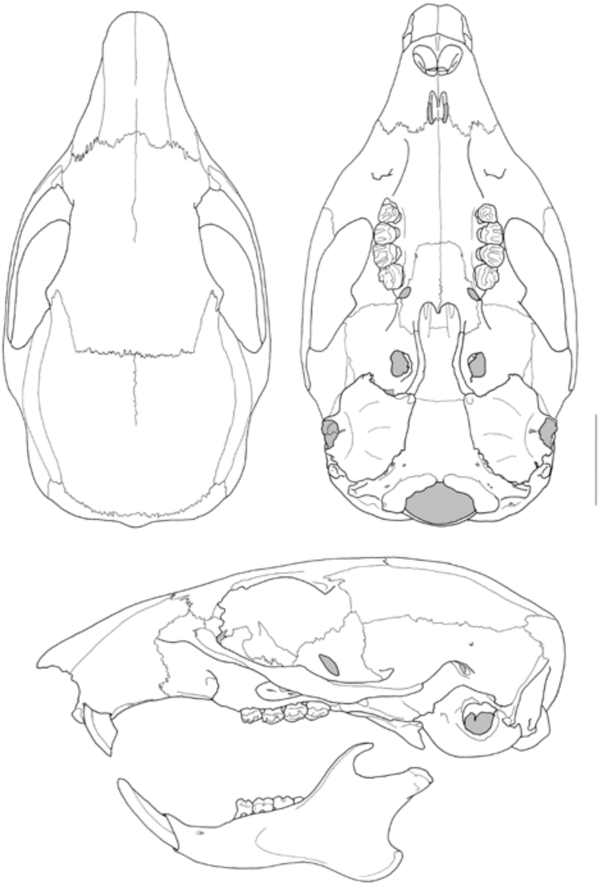


Fig. 54. Skull and mandible of *Sciurotamias forresti*. Adult male from northern Yunnan, China (BMNH 23.4.1.38). Scale bar = 10 mm.
Obr. 54. Lebka a mandibula *Sciurotamias forresti*. Adultní samec ze severu provincie Junan, Čína (BMNH 23.4.1.38). Měřítko = 10 mm.

The genus *Sciurotamias* was revised by Moore & Tate (1965).

Description (Figs. 52–56). Marmotines of moderate size and of squirrel-like external appearance. The tail is long (about $^{2}/_{3}$ of HbL) and thickly bushy; the ears are rounded and never tufted; the cheek pouches are present and normally developed (Fig. 55). There are three pairs of mammae (one pectoral and two inguinal pairs). The skull is long and relatively narrow, with elongate rostrum and much depressed postorbital processes; the braincase is low and smooth. The zygomatic plate is narrow and little tilted upwards, maseteric knob is weak, and the infraorbital foramen is constricted. The auditory bulla has three transbullar septa. Dentition essentially as in Tamiina; upper cheek-teeth are narrower, however, and upper incisors are rather short. Dental formula: 1/1, 0/0, 1–2/1, 3/3 = 20–22; third upper premolar (P3) much reduced in size (subgenus *Sciurotamias*; Fig. 53) or absent (*Rupestes*), P4 molariform. The anterior upper molariform cheek-teeth (P4–M2) bear two transverse enamel ridges each; the posterior M3 has only one ridge. Upper incisors are opisthodont.

Geographic range (Fig. 57) is restricted to the Palaearctic and Oriental China. In words of Moore & Tate (1965) *Sciurotamias* "... occupies an area of China which is almost entirely transitional between the Oriental and the Palearctic regions". Of the two species, which are allopatric, *S. forresti* is entirely Oriental occupying "forest and scrub in rocky mountains" (Zhang et al. 1997) to the south of the Tibetan Plateau in Yunnan, China; possible marginal presence in Myanmar and northern Indo-China (Fig. 57) requires confirmation. Tate (1947) reported "cliffy places at about 10,000 feet [= ~3050 m] above sea-level" to be the preferred habitat.

Sciurotamias davidianus (Milne-Edwards, 1867) – Père David's rock squirrel

1867 *Sciurus davidianus* Milne-Edwards. Type locality: "a découvert dans les montagnes de Pékin ..." (= found in the mountains of Peking [= Beijing]), China; "mountains near Peking" in Osgood (1932), "mountains of Pekin" in Moore & Tate (1965).

1868 *Sciurus consobrinus* Milne-Edwards. Type locality: "Moupin" ("Mouping" in Allen 1940, "Muping" in Moore & Tate 1965) (= Baoxing County), Sechuan province, China (= 30° 29' N, 102° 49' E; Moore & Tate 1965: 32).

1898 *Dremomys latro* Heude. Type locality: "... is evidently based on the form found in Shantung, although this is by implication only" (Allen 1940: 662). "? Shantung, China" (Ellerman & Morrison-Scott 1951). Original description not seen.

1898 *Dremomys saltitans* Heude. Type locality: "Although no type is mentioned in the original brief description, the specimen from which Père Huede's figures were drawn may be at the Sikawei Museum in Shanghai. It came from Hupeh apparently" (Allen 1940: 665). "Hupeh, China" (Ellerman & Morrison-Scott 1951). Original description not seen.

1898 *Dremomys collari*s Heude. Type locality: "... was recognized independently by Père Huede, who contrasted the Sechwan animal from that of Hopei and the middle Yangtze ..." (Allen 1940: 664). Therefore, from the context it is evident that the type locality was in Sechuan, China. Original description not seen.

1909 *Sciurotamias owstoni* J. A. Allen. Type locality: "Tai-pai-shiang Mountains, Shen-si, China".

1912 *Sciurotamias davidanus thayeri* G. M. Allen. Type locality: "from Washan, western Szechwan, China, at an altitude of 6,000 feet."

Description (Figs. 55, 56, and 58). See the account on the genus *Sciurotamias*. Fur is short and fairly rough. The bushy tail is on average 68% of HbL (range = 50–87% HbL). Hind feet are broad with densely hairy soles and four pads which are restricted to the bases of proximal phalanges. Limbs are slender, with four (fore foot) and five (hind foot) fingers. Dorsal side

Fig. 55. Père David's rock squirrel *Sciurotamias davidianus*. Note large cheek-pouches. Zoological Garden Görlitz, Germany. Photo courtesy Rainer HUTTERER.
Obr. 55. Veverka skalní *Sciurotamias davidianus*. Všimněte si velkých lícních toreb. Zoo Zhořelec, Německo. Foto Rainer HUTTERER.

generally gray brown to dark brown, grizzled due to a mixture of tri-coloured hairs (black--tipped with subterminal pale-ochraceous ring and slate base) and purely black hairs. The head is of same colour as back but cheeks tend to be darker; the eye is surrounded by a pale buffy ring, and there is buffy post-ocular strike reaching the ear base. Ears are densely clothed with very short gray hairs, slightly mixed with buff. There are generally faint whitish postauricular streaks. Flanks are slightly lighter than back and not sharply demarcated from the belly. The ventral side is whitish, clouded gray by slate hair bases, and washed buffy; chin is pure white in some individuals and the scrotum is blackish-brown. Feet are grey or mixture of grey and buff; claws are amber. Whiskers are black, stiff and long. The tail is of same colour as the back, with a pale-ochraceous central area on the ventral side. Hairs have pale rusty gray bases, black subterminal band and white tips which form a white margin (Fig. 58). In general appearance the skull resembles closely *Eutamias*. It is narrow; the breadth across zygomatic arches accounts for about 60% CbL (range = 57–63%). Rostrum is lengthened, nasals are long and projected forward, postorbital processes are depressed but still prominent. Brain case is rounded and low, temporal ridges are weakly pronounced. Zygomatic processes of squamosum are more powerful than in remaining Arctomyinae. Diastema is long, about 1.5-fold MxT, the incisive foramen is of about same relative length as in *Eutamias*. Interpterygoid fossa is wide, bullae are rounded and of normal size. Mandible is low and slender, but shows no peculiarities. The upper incisors are opisthodont and much shorter than in *Eutamias*; the enamel on front surface is dull orange. Females have three pairs of nipples. Glans penis is annulated and baculum is heavily bent dorsally (CALLAHAN & DAVIS 1982). Ranges for dimensions (in mm, sexes pooled): HbL_{45} = 172–235, TL_{44} = 103–200, HF_{46} = 45–59, EL_{37} = 18.0–29.5, CbL_{37} = 47.2–52.4, ZgB_{60} = 27.9–31.5, MxT_{64} = 8.0–11.1 (ALLEN 1940, MOORE & TATE 1965, and specimens in BMNH). Karyotype: 2n = 38 (WANG et al. 1991).

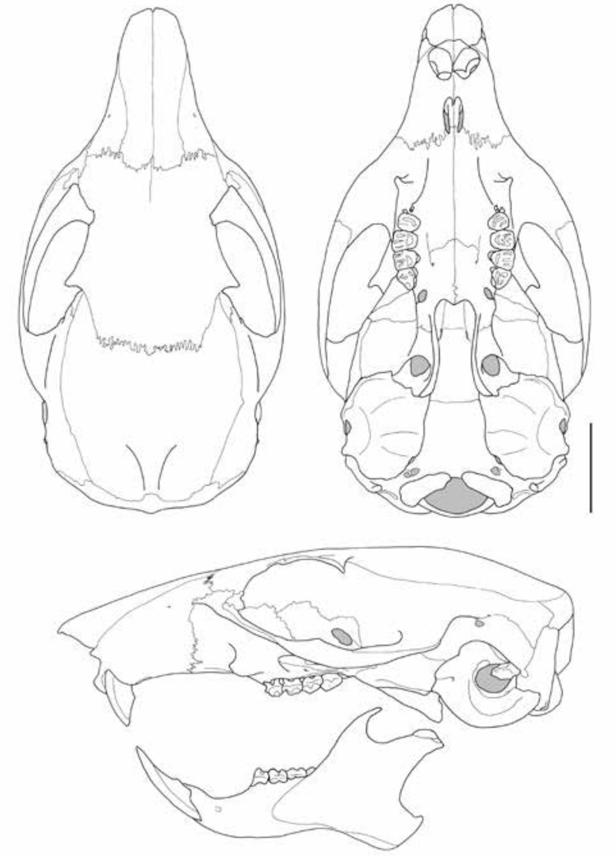


Fig. 56. Skull and mandible of *Sciurotamias davidianus davidianus*; adult male from south-eastern Shensi, China (BMNH 9.1.1.21). Scale bar = 10 mm.
Obr. 56. Lebka a mandibula *Sciurotamias davidianus davidianus*; adultní samec z jihovýchodu provincie Šensi, Čína (BMNH 9.1.1.21). Měřítko = 10 mm.

Geographic range (Fig. 57). A significant proportion of the range is to the south of 35° northern longitude, i.e. outside the Palaearctic region as defined for the purposes of our compilation (see Kryštufek & Vohralík 2012). The range extends from the southern Da Hinggan Ling Mts. and the "Shanxi middle high Mt." (Zhang et al. 1997) encircling the Chinese Plain in the east, and the Thibetan Plateau in the west; the northern border is defined by the Songliao plain and the southern border is on the Xi Jiang River; the majority of range, however, is to the north of the Chang Jiang River. The range encompasses the provinces of Hebei, Tianjin, Beijing, Henan, Shanxi, Shaanxi, Ningxia, Gansu, Sichuan, Guizhou, Anhui, and Hubei (Zhang et al.

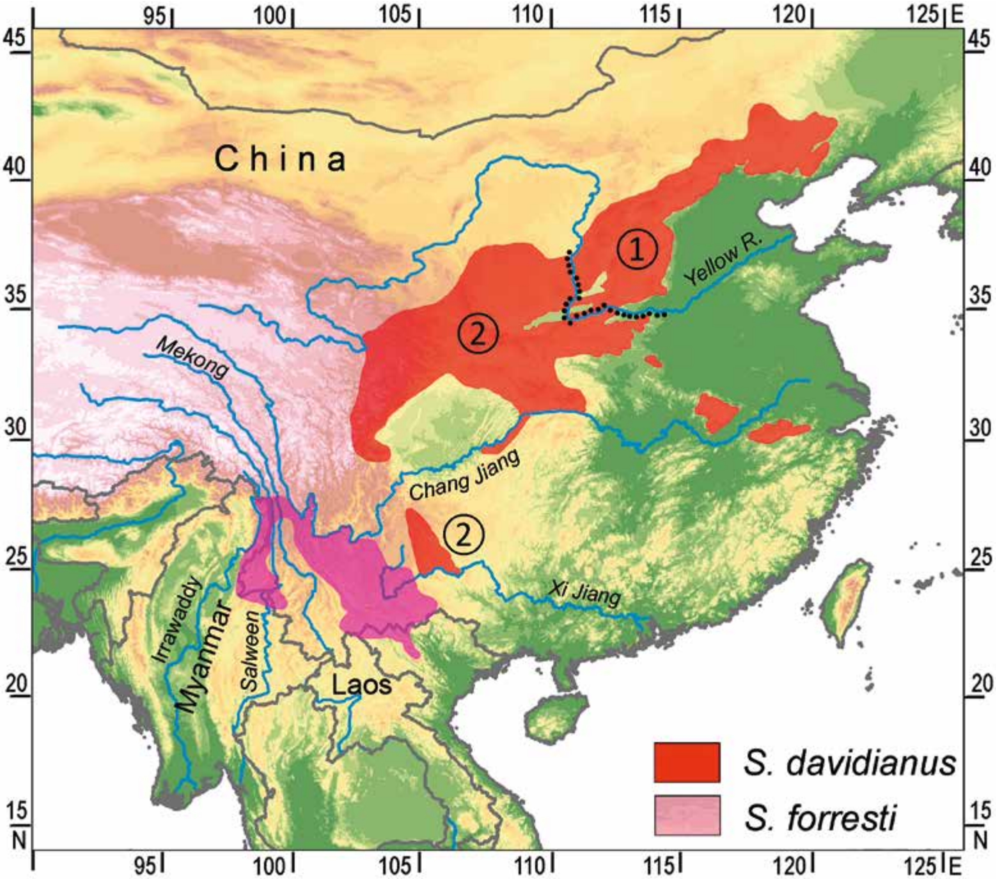


Fig. 57. Distribution of *Sciurotamias davidianus* and *Sciurotamias forresti*. Note that *S. forresti* is entirely Oriental. Compiled from Moore & Tate (1965) and Zhang et al. (1997). Subspecies: 1 – *Sciurotamias davidianus davidianus*; 2 – *S. davidianus consobrinus*.

Obr. 57. Rozšíření *Sciurotamias davidianus a Sciurotamias forresti*. Všimněte si, že *S. forresti* je rozšířem výlučně v orientální oblasti. Zkompilováno podle Moore & Tate (1965) a Zhang et al. (1997). Poddruhy: 1 – *Sciurotamias davidianus davidianus*; 2 – *S. davidianus consobrinus*.

1997). The southern margin is fragmented; two isolates are to the south of the Chang Jian in the Province of Guizhou (in the west) and in the Huaiyang Mts. and in the extreme northern part of the Zheijang-Fujian Mts. (in the east).

Various authors found Père David's rock squirrel to be common or even "extremely plentiful" (e.g. Allen 1940); Andersen who collected in 1908 for the BMNH reported this squirrel as "nowhere common" in Shaanxi and Shanxi (Thomas 1908). Thought its range largely coincides with oak-dominated broad-leaved forests and despite its tree-squirrel external appearance, "*Sciurotamias* is very much a ground squirrel" (Moore & Tate 1965). In Allen's (1940) view it is "the terrestrial derivative" of *Dremomys* (Callosciurini) what is evident, besides others, "from the possession of cheek pouches (so often developed with underground habits in rodents)". Indeed, though *Sciurotamias* is "well able to climb trees, is a rock- and cliff-dwelling animal, making its nests in crevices" (Tate 1947). Typical habitat is on cliffs, in canyons, and on rocky ground where bushes are plentiful and tree growth is thin. Zhang et al. (1997) summarized the habitat as "scrub and farmland in the rocky mountains". In rare occasions of co-occurrence with *Dremomys pernyi* and *D. pyrrhomerus*, *S. davidianus* lives like ground squirrel (Allen 1940, Tate 1947, Moore & Tate 1965). In Sichuan and around, the ranges of *Sciurotamias* and the two *Dremomys* species are nearly perfectly exclusive (Moore & Tate 1965). Altitudinal range is between 1500 and 9000 ft. (= ca. 455–2750 m a. s. l.).

Père David's rock squirrel was reportedly introduced to Dadizele in Flandres, Belgium in 2003 (Bertolino 2009, Grimmberger & Rudloff 2009). As shown by Stuyck et al. (not dated) the introduced squirrels are actually *Callosciurus erythraeus*.

Subspecies. Two groups of populations can be distinguished on the basis of colouration. The subspecific division adopted here follows Moore & Tate (1965). The baculum declines in length and complexity in a north-to-south direction, but the pattern of variation does not support the subspecific division (Callahan & Davis 1982).

Sciurotamias davidianus davidianus (Milne-Edwards, 1867)

Synonym. *latro* (Allen 1940).

Description. Dorsal side lighter (greyish-brown); underparts white and tinted gray but lack extensive buff wash (58a); a whitish post-auricular streak faint, short and tuft-like (Fig. 52a). Hind foot shorter. Dimensions (in mm, sexes pooled): HbL_{33} = 206.6 (179–230), TL_{32} = 138.7 (103–200), HF_{33} = 49.1 (45–55), EL_{31} = 25.3 (20.0–29.5), CbL_{33} = 49.6 (47.2–52.4), ZgB_{42} = 29.7 (28.1–31.0), MxT_{43} = 9.2 (8.4–11.1) (Allen 1940, Moore & Tate 1965, and specimens in BMNH).

Geographic range (Fig. 57). It is in the north-eastern part of the species' area, specifically in northern Shanxi and Hebei.

Sciurotamias davidianus consobrinus (Milne-Edwards, 1868)

Synonyms. *collaris*, *saltitans*, *owstoni*, *thayeri* (Moore & Tate 1965).

Description. Dorsal side darker (dark brownish olivaceous); underparts with a wash of ochraceous buff (Fig. 58b); a smoky white post-auricular streak more prominent and longer (length of up to 30–35 mm; Fig. 52b). Hind foot longer. Dimensions: (in mm, sexes pooled): HbL_{13} = 206.9 (172–235), TL_{13} = 143.0 (120–165), HF_{14} = 54.5 (48–59), EL_{6} = 23.7 (18–28), CbL_{4}

Fig. 58. Skins of the two subspecies of Père David's rock squirrel in ventral view: a – *Sciurotamias davidianus davidianus* from south-eastern Shensi, China (BMNH 10.5.2.19); b – *S. d. consobrinus* from southern Sechuan (BMNH 11.2.1.93). Photo by Boris Kryštufek.
Obr. 58. Balky dvou poddruhů veverky skalní, pohled z břišní strany: a – *Sciurotamias davidianus davidianus* z jihovýchodu provincie Shensi, Čína (BMNH 10.5.2.19); b – *S. d. consobrinus* z jižního Sečuánu (BMNH 11.2.1.93). Foto Boris Kryštufek.

= 49.6 (47.7–51.3), ZgB_{18} = 30.0 (27.9–31.5), MxT_{21} = 9.3 (8.0–10.8) (Allen 1940, Moore & Tate 1965, and specimens in BMNH).

Geographic range (Fig. 57). As stated by Allen (1940: 664) "This richly-colored race is typical of the damp highlands of Szechwan", and occupies also Shansi (= Shanxi) and Shensi (= Shaanxi); population isolated in Kweichow (= Guizhou) province was classified as *consobrinus* (Moore & Tate 1965).

SOUHRN

Předložená práce je pokračováním taxonomické revise palearktických hlodavců, jejíž první díl vyšel v 43. svazku tohoto časopisu (Kryštufek & Vohralík 2012). Způsob zpracování a geografické vymezení studované oblasti zůstaly stejné jako v předchozím díle. Jednotlivé druhy se snažíme definovat na základě jejich morfologie, genetických znaků, rozšíření a biotopových nároků. Jsou zde zpracováni palearktičtí sysli rodu *Urocitellus*, svišti rodu *Marmota* a veverky rodu *Sciurotamias*.

Na základě excerpce stovek literárních pramenů a studia 926 sbírkových exemplářů rozišujeme 12 následujících druhů: sysel dlouhoocasý *Urocitellus undulatus* (se dvěma poddruhy – *undulatus* a *eversmanni*), sysel Parryův *U. parryii* (jeho jediný palearktický poddruh je *leucosticus*), svišť horský *Marmota marmota* (sspp. *marmota* a *latirostris*), svišť stepní *M. bobak*, svišť šedý *M. baibacina*, svišť Kaščenkův *M. kastschenkoi*, svišť sibiřský neboli tarbagan *M. sibirica*, svišť himalájský *M. himalayana*, svišť černohlavý *M. camtschatica* (sspp. *camtschatica*, *bungei* a *doppelmayeri*), svišť dlouhoocasý *M. caudata* (sspp. *caudata*, *aurea a dichrous*), svišť Menzbierův *M. menzbieri* (sspp. *menzbieri* a *zachidovi*) a veverka skalní *Sciurotamias davidianus* (sspp. *davidianus* a *consobrinus*).

Pro uvedené druhy byla shrnuta všechna nám známá jména ze skupiny druhu (celkem 69) a byla přiřazena k příslušným platným jménům jako jejich mladší synonyma. Podle možnosti byly citovány v původním znění všechny typové lokality. Je podán popis validních taxonů a jsou připojeny kresby jejich lebek a fotografie živých jedinců nebo sbírkových exemplářů. Pro všechny druhy a námi rozlišované subspecie byly zpracovány mapy jejich rozšíření.

Taxonomická revise ukázala, že *Arctomys marmota tigrina* Bechstein, 1801 je mladším synonymem sviště stepního *M. bobak* a nikoliv sviště horského *M. marmota*. Bylo znovuobjeveno dříve opomíjené jméno podčeledi Arctomyinae Gray, 1821, které tak nahrazuje dosud běžně používané mladší jméno Marmotinae Pocock, 1923. Stanovili jsme nový subtribus Ammospermophilina, který zahrnuje Nearktické rody *Ammospermophilus* a *Notocitellus* a zaujímá basální pozici ve vývojové linii syslů a svišťů.

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