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Taxonomic revision of the Palaearctic rodents (Rodentia). Sciuridae: Xerinae 1 (*Eutamias* and *Spermophilus*)

Taxonomická revise palearktických hlodavců (Rodentia). Sciuridae: Xerinae 1 (*Eutamias* a *Spermophilus*)

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Abstract. We reviewed the Palaearctic Xerinae (Rodentia: Sciuridae) from the genera *Eutamias* and *Spermophilus*. On the basis of published data and our own examination of >2500 museum vouchers we recognize 12 species and 19 subspecies: *Eutamias sibiricus* (with three subspecies: *senescens* and *barberi* in addition to the nominotypical one), *Spermophilus citellus* (incl. *gradojevici* and *karamani*), *S. taurensis*, *S. xanthoprymnus* (with *gelengius*), *S. suslicus* (*odessanus* is a subspecies), *S. alaschanicus*, *S. dauricus*, *S. pygmaeus* (incl. *musicus* and *planicola*), *S. fulvus*, *S. major*, *S. erythrogenys* (with *heptneri*, *brevicauda* and *pallidicauda*), and *S. relictus* (incl. *nilkaensis*). All species group names (109 in total) are reviewed and linked to senior synonyms. 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. We considered also the Nearctic chipmunk *Tamias striatus* which is feral in one site in western Germany. Introgresive hybridization obscures species limits in *Spermophilus* since it produces paraphyletic or polyphyletic taxa in molecular trees. Hybridization, which is probably facilitated by a general promiscuous multiple paternity in sousliks, is widespread in the genus and has been documented between seven species: *S. major* × *S. fulvus*, *S. major* × *S. pygmaeus*, *S. major* × *S. suslicus*, *S. major* × *S. erythrogenys brevicauda*, *S. erythrogenys pallidicauda* × *S. alaschanicus*, *S. pygmaeus* × *S. suslicus*, and *S. citellus* × *S. suslicus*. Conspecific subspecies are frequently delimited by rivers. Our revision of tribal division of Xerinae resulted in a description of a new tribe Sciurotamiini which includes the genus *Sciurotamias*.

Key words. Species delimitation, taxonomic characters, geographical distribution, identification key, zoological nomenclature, Sciurotamiini new tribe.

INTRODUCTION

Despite of two and a half centuries of continuous research in mammalian taxonomy, the species-accumulation curve for mammals gives no indication of reaching asymptotic value. Over the last two decades this branch of zoology remained to be a dynamic field with 341 species newly named and described between 1992 and 2006. Although the great majority of discoveries came from mega biodiversity hotspots located in the tropics (Reeder et al. 2007), the mammalian species richness remains incompletely characterized also in temperate and boreal regions. The

onset of DNA-sequence data opened a new insight on the historical descent of lineages that is highly informative in species-level taxonomy. In Europe alone, at least seven small terrestrial mammals possibly consist of two or more cryptic species (or "near-species") recognized in molecular studies (Amori et al. 2009). Cases like these need to be integrated into existing taxonomy, with names selected in accordance with the provisions of the International Code of Zoological Nomenclature (ICZN 1999). Despite of comprehensive taxonomic revisions published in recent years (Wilson & Reeder 2005, Pavlinov & Lissovskij 2012), which were accompanied by mapping achievements (IUCN 2012), there is an apparent need of permanent revisionary work at various spatial and taxonomic scales. In this paper we undertook a step towards a review of rodents of the Palaearctic region by focusing on one part of ground squirrels.

Classical taxonomic revisions of Palaearctic mammals date back to the mid-20th century when Ellerman & Morrison Scott (1951) compiled taxonomic names and reorganized taxa into polytypic species. Their work was upgraded by Corbet (1978) who also provided identification keys and distributional maps. We aim in this paper to ensure more comprehensive definitions of Palaearctic mammals by including morphology, genetics, distribution and habitat selection. We hope that mammalogists will find our compilation of help in recognizing species either in the field or in museum collections.

GEOGRAPHIC SCOPE AND TAXONOMIC SETTINGS

In the geographic scope of the Palaearctic region we followed, with slight modifications, Corbet (1978). Therefore, in this paper the Palaearctic realm encompasses northern Africa (to the north of 21°30'N), Europe, and temperate and boreal Asia. In Asia we consider the entire Arabian peninsula; further east the border follows political demarcation between Iran and Afghanistan on one hand, and Pakistan on another; from Afghanistan to China the border is at about 3000 m a. s. l. which leaves alpine zones in the Palaearctic region but excluds lower forested slopes. The boundary in lowland China follows latitude of 35°N and in Japan the latitude is shifted southward to 30°N. For alternative delimitations of biogeographic realms in Asia see Hoffmann (2001). In the Beringia, the division is political with only Russian islands being included into the scope of the Palaearctics. In the Atlantic Ocean, the islands of Spitzbergen, Iceland, Azores, Madeira and the Canary Islands are included.

Similarly as with the geographic scope, we followed Corbet (1978) in criteria by which species and genera have been selected. Only recent species were considered and we mainly focused on their ranges during the 20th century. We did include also introduced exotics which established populations in the wild.

Taxonomic revisions of mammals largely ignore issues of definition and delimitation of species. Corbet (1978) was an exception, and we adopted his definition, by expanding character sets to encompass also genetical evidence: "The recognition of species involves the recognition of those morphological (or other phenotypical) discontinuities that correspond to reproductive incompatibility between populations." Species are "separately evolving metapopulation lineage[s]" (de Queiroz 2007), and the discontinuities between such diverging entities emerge slowly. The continuum of the speciation process causes dissagreements in species delimitation. Confusion is negligible in sympatry, however, the taxonomic decisions become complicated with allopatric and parapatric lineages. Many of such lineages hybridize in nature ower narrow zone but the introgression is ussually limited and assymmetric. Although hybrids are at least partly fertile, their overall fitness is frequently lower than that of their parents (Nevo et al. 2001). In such cases

the arguments over taxonomic status is about two mutually exclusive options, namely whether parapatric lineages represent distinct species or not. A subspecies as an intermediate option is ignored in majority of recent taxonomic revisions. This is understandable, considering that in the past subspecies category was too frequently used for "segments of a species that have no objective boundaries" (Corbet 1978). However, if properly defined, the subspecies may be an appropriate category for well defined lineages which still hybridize and occupy the same ecological niche. Namely, the core issue in species delimitation is whether allopatric populations are sufficiently differentiated to warrant recognition at either species or subspecies level. Lidicker (1962) defined a subspecies as "a relatively homogeneous and genetically distinct portion of a species which represents a separately evolving and, or recently evolved, lineage with its own evolutionary tendencies, inhabits a definite geographic area, is usually at least partially isolated, and may intergrade gradually, although over a fairly narrow zone, with adjacent subspecies." From the current perspective, Lidicker (1962) was talking about phylogeographic lineages (Baker & Bradley 2006), the term coined nearly four decades afterwards (Avise 2000).

Trends in the forthcomming years will show whether the community of mammalogists will choose taxonomic practice with a larger number of monotypic species, or will decide to turn towards a lower number of polytypic species which will be subdivided into subspecies. We adopted in this review the concept of a polytypic species, as it was championed by Mayr (1963), hawing in mind all the undesirable consequences of the current species inflation. Over the last decade many new species have been recognized in the Palaearctic rodents by elevating subspecies to species rank merely on insufficient genetic evidence. In mammal and bird speciation, durations normally entail at least 2 My (Avise et al. 1998, Zink et al. 2004). If this is accepted as a crude yardstick in species delimitation, than majority of parapatric phylogeographic lineages lay within infraspecific variation. We believe that infraspecific taxa which we recognized among the Palaearctic Xerinae have evolutionary meaning and therefore represent units for conservation management. We avoided a traditional practice of recognizing subspecies with no proof of discontinuity and in the absence of sound knowledge on the variation across the species' range.

In our taxonomic arrangement we adopted Wilson & Reeder (2005) as a starting point. The major sources for nomenclature were Palmer (1904), Miller (1912), Allen (1940), Ellerman & Morrison-Scott (1951), Corbet (1978), Ognev (1940, 1947), Moore (1959), Pavlinov & Rossolimo (1987, 1998), Gromov & Baranova (1981), Gromov & Erbajeva (1995), Pavlinov et al. (1995), and Zhang et al. (1997). Whenever possible we consulted original descriptions and quoted type localities as spelled when first reported (emphasized by quotation marks).

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. Our attempt was to base taxonomic conclusions on as wide set of characters as possible. Great attention was paid on museum material and we examined over 2500 voucher specimens in 12 collections, representing all recognized species.

We studied museum vouchers for character states, dimensions and colouration. External measurements (in mm) were scored from specimen tags: HbL – length of head and body; TL – length of tail; HF – length of hind foot; E – length of ear; W – weight (body mass in grams). Three linear measurements are reported for skulls to roughly describe these structures by numerical means, thus allowing further comparisons: CbL – condylobasal length of skull, ZgB – beadth across zygomatic arches, MxT – length of maxillary tooth-row (alveolar). Published data report also other proxies for overall size: HbTL – total length (head

and body plus the tail); PL – profile (or greatest) length of the skull. For detailed definitions see KRYŠTUFEK & VOHRALÍK (2005). Metric data are given as descriptive statistics (mean with a range parenthesized); sample sizes are indicated by numbers in subscript to character abbreviations.

Types of teeth in the heterodont mammalian set are designated by letters. Capitals are used to indicate the maxillary teeth and small 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 1st upper and the 3rd lower molar, respectively. Note that rodents lack canines. Abbreviations are as follows: I/i – upper/lower incisors; P/p – upper/lower premolars; M/m – upper/lower molars.

List of collections (abc):
DZCU – Department of Zoology, Charles University, Prague, Czech Republic;
LBT – Laboratory for Biomonitoring, Academy of Sciencies of Tatarstan Republic, Kazan, Russia;
MNM – Hungarian Natural History Museum, Budapest, Hungary;
NMP – Department of Zoology, National Museum, Prague, Czech Republic;
NMW – Naturhistorisches Museum Wien, Vienna, Austria;
PMBg – Natural History Museum Belgrade, Belgrade, Serbia;
PMS – Natural History Museum of Slovenia, Ljubljana, Slovenia;
SMF – Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt a. M., 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.

Further three museums were visited before the initiation of the revision of the Palaearctic rodents, therefore their resources were not fully utilized with respect to the Palaearctic squirrels: BMNH – Natural History Museum London (formerly British Museum of Natural History), London, UK; FMNH – Field Museum of Natural History, Chicago, USA; NMNH – United States National Museum of Natural History, Washington D.C., USA. Thanks to the courtesy of Jan MATĚJŮ we got at disposal measurements and photographs of ground squirrels' vouchers which he gathered in the collections of NMNH, American Museum of Natural History, New York, USA (AMNH), and Zoological Institute of the Academy of Sciences in Sankt-Peterburg, Russia (ZISP).

TAXONOMIC REVIEW

Family: Sciuridae – Squirrels

1817 Sciuridae Fischer.

REMARK. THORINGTON & HOFFMAN (2005) credit for the family name FISHER DE WALDHEIM; as shown by HUTTERER (2003), FISHER attained his noble title after the publication of 1817 paper (FISCHER 1817).

Squirrels are arboreal (scansorial) or terrestrial rodents, with a densely haired (frequently bushy) tail, dense fur of extremely variable colour and pattern, prominent ears and large eyes. Striped or speckeled pattern is more common than in other rodents. Dental formula: 1/1, 0/0, 1–2/1, 3/3 = 20–22; cheek teeth are rooted, brachyodont or hypsodont; P3 is reduced or absent. Interorbital constriction is not well marked, infraorbital foramen does not transmit masseter muscle; zygomatic plate is broadened and tilted upward (MCLAUGHLIN 1967). The karyotypes

of Sciuridae are highly conservative and close to the ancestral karyotype of rodents (Bekle-misheva et al. 2011).

The family is almost cosmopolitan, being absent only from the Australian region.

Palaearctic squirrels are in 3 subfamilies and in 14 genera (Steppan et al. 2004, Thorington & Hoffmann 2005):

1. Subfamily Sciurinae
   1.1. Tribe Sciurini
      Sciurus (3 native + 1 introduced species)
   1.2. Tribe Pteromyini
      Aeretes (1 species)
      Petaurista (2 species)
      Pteromys (2 species)
      Trogopterus (1 species)
2. Subfamily Callosciurinae
   2.1. Tribe Callosciurini
      Callosciurus (1 introduced species)
      Tamiops (2 species)
   2.2. Tribe Funambulini
      Funambulus (1 species)
3. Subfamily Xerinae
   3.1. Tribe Xerini
      Atlantoxerus (1 species)
      Xerus (1 species)
      Spermophilopsis (1 species)
   3.2. Tribe Marmotini
      3.2.1. Subtribe Tamiina
      Eutamias (1 species)
      Tamias (1 introduced species)
      3.2.2. Subtribe Marmotina
      Spermophilus (11 species)
      Urocitellus (2 species)
      Marmota (8 species)
   3.3. Tribe Sciurotamiini (new tribe)
      Sciurotamias (1 species)

Subfamily: Xerinae

1910 Xerinae Osborn.
1923 Marmotinae Pocock.

Xerinae include the African giant squirrels and the sun squirrels (tribe Protoxerini), the ground squirrels from the tribes Marmotini and Xerini, and the mountain rock squirrels of China for which we establish subsequently a new tribe Sciurotamiini. Xerinae are rarely small (e.g. chipmunks and burunduks), and are mainly medium-sized or large squirrels. They share in common the following traits: the orbit is normally elongate and the interorbital region narrowed, the supraorbital notches are open laterally, the lip of the infraorbital foramen is concave in lateral view, the upper incisors are proodont or opisthodont, and 3rd lower premolar is absent. With some exceptions the sphenopalatine foramen is small and a great majority of genera display 1–3

transbullar septa. Unusual for sciurids, the baculum is minute or entirely absent in some sun squirrels (Moore 1959). Xerinae are in a sister position to Sciurinae (Mercer & Roth 2003).

Xerinae occupy various habitats from deserts and steppes to dry and boreal forests, rocky habitats, Arctic tundra and high altitude pastures throughout the Holarctic and Afrotropic regions; *Sciurotamias* and *Eutamias* marginaly penetrate the Oriental China. While Protoxerini occupy the ecological niche of tree squirrels (i.e. they nest and take refuge primarily above ground in trees, and obtain a substantial proportion of food from the products of the trees) the majority of genera of Marmotini and Xerini are strictly ground dwelling.

Tribe: Marmotini – Ground squirrels

1945 Marmotini Simpson.

Ground squirrels are a monophyletic lineage ranked either as a tribe, or a subfamily Marmotinae (Gromov et al. 1965, Pavlinov & Rossolimo 1987, Pavlinov et al. 1995). The earliest true ground squirrel is *Miospermophilus* from the late Oligocene, which diversified into modern lineages in Miocene (Armitage 2000). Marmotini are endemic to the Holarctic region. In the Palaearctic realm, they are the most diverse and species-rich group of Sciuridae (22 species in 4 genera). In the integrated diversity of the Marmotini, the burunduks (chipmunks), which still exploit terrestrial and arboreal niches, stand sharply apart from the strictly ground-dwelling susliks and marmots. Although the Marmotini show similarities to the Xerini (long orbit, narrow interorbital breadth, small sphenopalatine foramen; Moore 1959), the two tribes are not closely related. Instead, the Marmotini are in a sister position to the African tribe Protoxerini (Steppan et al. 2004). The Marmotini possess in common the following skull characters: (i) 2 transbullar septa per auditory bulla, (ii) long orbit, (iii) supraorbital notches are generally open and trenchant (Moore 1959). Subtribal division, as proposed by Moore (1959), requires modifications. Molecular phylogenetic reconstructions showed that *Spermophilus* (s. lat.) is paraphyletic with respect to *Marmota* (Harrison et al. 2003, Herron et al. 2004). It is therefore not appropriate to keep these two genera in distinct subtribes (Marmotina and Spermophilina, respectively). *Sciurotamias* displays a number of unique properties which justify its allocation in a separate tribe (described in the Taxonomic annex).

Species of the Palaearctic Marmotini are in two subtribes, Tamiina and Marmotina.

Key to Subtribes

1 Back striped, with 5 blackish longitudinal stripes (Fig. 1); tail longer than ½ HbL; baculum tappering gradualy from base to tip; interorbital region wide (about ½ of ZgB). ..... Tamiina

1* Back unmarked, spotted, or flecked, but never stripped; tail shorter than ½ HbL; baculum with a spoon-like expanded distal end; interorbital region narrow (less than ½ of ZgB). ..... Marmotina

Subtribe: Tamiina – Burunduks and Chipmunks

1959 Tamiina Moore.
1963 Tamiini Black.

A predominantly Nearctic group, with only one single representative in the Old World. Burunduks are small ground squirrels, less robust than marmots and sousliks, with longer tail and more prominent ears. The upper incisors tend to be opisthodont, the postorbital processes of frontals

are blunt, and the temporal ridges do not meet to form sagittal crest. Gromov et al. (1965), Pavlinov & Rossolimo (1987), and Pavlinov et al. (1995) ranked burunduks as a tribe.

Eutamias, as the only Palaearctic member, was in the past frequently treated either as a genus on its own right (e.g. Allen 1940, Vinogardov & Gromov 1952), or a subgenus of *Tamias* (e.g. Howell 1929). *Tamias*, *Eutamias* and *Neotamias* diverged earlier than the genera *Marmota* and *Spermophilus* (s. lat.) and therefore merit recognition as distinct genera (Herron et al. 2004).

Key to genera

1 Longitudinal dark stripes equally bold; lateral stripes start behind the ears; pale stripes, which are bordered by dark stripes, are of same width (Fig. 1a); interorbital width < postorbital width; baculum is simple; 5 cheek-teeth in maxilla (Fig. 2a). ..... *Eutamias*

1* Dark medial stripe narrower than the lateral stripes which are shifted backwards behind shoulders; of the two pale stripes, bordered by dark stripes, the medial one is twice as wide as the lateral one (Fig. 1b); interorbital width ≈ postorbital width; baculum with a keel on its ventral tip; 4 cheek-teeth in maxilla (Fig. 2b). ..... *Tamias*

Genus: *Eutamias* – Burunduks

1880. *Eutamias* Trouessart. Type species: *Sciurus striatus asiaticus* Gmelin, 1788.

A predominantly Palaearctic genus, marginally occupying the Oriental China. Contrary to morphological evidence, which placed *Eutamias* closer to Nearctic *Neotamias* (White 1953), a phylogenetic reconstructions based on mitochondrial sequences retrieved its sister position against *Tamias* (Herron et al. 2004, Stepan et al. 2004). The immonological technique of

Fig. 1. Skins of chipmunks in dorsal view. a – *Eutamias sibiricus* (east of the Bajkal Lake, Siberia, Russia; PMS 416/12) (photo by Ciril Mlinar); b – *Tamias striatus* (New Hampshire, USA; ZFMK 92.507).
Obr. 1. Balky burunduka a čipmanka východního (dorsální pohled). a – *Eutamias sibiricus* (východně od jezera Bajkal, Sibiř, Rusko; PMS 416/12; foto Ciril Mlinar); b – *Tamias striatus* (New Hampshire, USA; ZFMK 92.507).

micro-complement fixation indicated the three genera of chipmunks to be distinct since the late Miocene (Ellis & Maxson 1979) and *Eutamias* was present in the latest Miocene faunas in Inner Mongolia, China (Qiu 1991). The only extant species presumably evolved in north--eastern Siberia (Tiunov 1980).

Eutamias sibiricus (Laxmann, 1769) – Siberian chipmunk or burunduk

1769 *Sciurus sibiricus* Laxmann. Type locality: "Barnaul", Altajskij kraj, Siberia, Russia.
1778 *Sciurus striatus* Pallas. Type locality: "Ab uralensi jugo et Kama fl. per omnem Sibiriam sylvosam usque ad sinum Ochotensem et Anadyr fluvium" (= from the Ural Mts. and River Kama through all forests of Siberia up to the Gulf of Ohotsk and River Anadyr). Restricted to "Permskaâ obl. (= oblasť [= Region]) and Tatar Autonomous Republic, r. (= river) Kama", Russia (Pavlinov & Rossolimo 1987). Used in the past as a valid name (e.g. Vinogardov & Gromov 1952); permanently invalid as a secondary homonym of *Sciurus striatus* Linnaeus, 1758 (Obolenskaya et al. 2009).
1788 *Sciurus striatus asiaticus* Gmelin. Type locality: "omni Aſia borealis ad fluvios europaeos Dwina et Kama usque" (= the entire forested Asia till the European rivers Dvina and Kama). Restricted to "Magadanskaâ oblasť, Gižiga", Russia (Pavlinov & Rossolimo 1987).
1811 *Sciurus uthensis* Pallas. Type locality: "regione fl. Uth, in Oceanum orientalem fluentis" (= region of the River Uda, flowing into the Ocean in the East). Restricted to "Habarovskij kr. (= Habarovsk Region), Tuguro-Čumikanskij r-n (= Tugur-Čumikan District), r. (= river) Uda, Udskoe." (Pavlinov & Rossolimo 1987), north-eastern Siberia, Russia.
1824 *Myoxus lineatus* Siebold. Type locality: "Hokkaido, Japan." (Ellerman & Morrison-Scott 1951). Vinogardov & Gromov (1952) quote 1826 as the year of publication.
1859 *Tamias pallasi* Baird. New name to replace *Sciurus striatus* Pallas, 1778.
1898 *Eutamias senescens* Miller. Type locality: "fifteen miles west of Peking (= Beijing), China."
1899 *Tamias orientalis* Bonhote. Type locality: "Sungatscha (= Sungača) River, Upper Ussuri River", Primorskij kraj, Russia.
1908 *Eutamias asiaticus intercessor* Thomas. Type locality: "Ning-wu-fu, Shan-si, China. 6000'."
1908 *Eutamias asiaticus ordinalis* Thomas. Type locality: "Yu-lin-fu, Shen-si, China. 4000'."
1909 *Eutamias albogularis* Allen. Type locality: "Tai-pa-shiang (= Taipai Shan), Shen-si (= Shensi), China."
1912 *Eutamias sibiricus altaicus* Hollister. Type locality: "Topucha, Altai Mountains, Siberia; 6000 feet", according to Pavlinov & Rossolimo (1987): "Topuča (= Tapučaâ), Šebalinskij rajon, Altajskij kraj", Russia.
1927 *Eutamias asiaticus umbrosus* Howel. Type locality: "140 miles south of Lanchowfu, (= vicinity of Archuen, Minshan Mts.), Kansu, China."
1932 *Eutamias asiaticus okadae* Kuroda. Type locality: "Mt. Chachanupuri, Kanushiri Island, South Kurile Islands, Japan."
1935 *Eutamias sibiricus jacutensis* Ognev (in Ognev & Turov). Type locality: "okresnosti g. Âkutska" (Ognev 1940) (= vicinity of Yakutsk), eastern Siberia, Russia.
1955 *Eutamias sibiricus barberi* Johnson et Jones. Type locality: "Central National Forest, near Pup'--yong-ni (37°44'N, 127°12'E), Korea".

Description. The smallest member of Palaearctic marmotine with no special modifications (Fig. 3). Internal cheek-pouches are well developed. Tail is shorter than head and body (63–88% HbL), well haired and flattened. Muzzle is pointed, eyes are large and the prominent ears lack tuft. Limbs are slender, with 4 (fore foot) and 5 (hind foot) long fingers; claws are sharp. Palm is bare, with 5 pads; sole is hairy for the proximal half, from heel to its 4 pads. Hair is short and soft. Along the back are 5 sharply marked black or blackish-brown longitudinal stripes and 4 lighter (buff, greyish or whitish) stripes. Dark stripes are bold and of comparable thickness;

the medial one is the longest and extends from the occipital to near tail base. Lateral stripes start behind the ears and terminate on the rump. Pale stripes are edged with ochraceous in their posterior half. Nape and shoulders are grey with rust tint (Fig. 1). Rump is fawn or rusty, flanks are ochraceous, ventral side is white but mainly clouded with slade underfur. Head is grey-buff to fawn, striped (short line from eye to ear, a second line from base of the whiskers to base of the ear); eyelids are whitish; cheeks are clay coloured. Rims of the ears are whitish. Tail is either grey or of same colour as posterior back; its terminal tuft and sides are margined white. Feet are ochraceous, digits are greyish-white. Females have 4 pairs of nipples (1 pectoral, 2 abdominal, 1 inguinal). Baculum (length about 5 mm) is simple and slender, tappering gradualy from base to the upturned tip (Ognev 1966, Allen 1940).

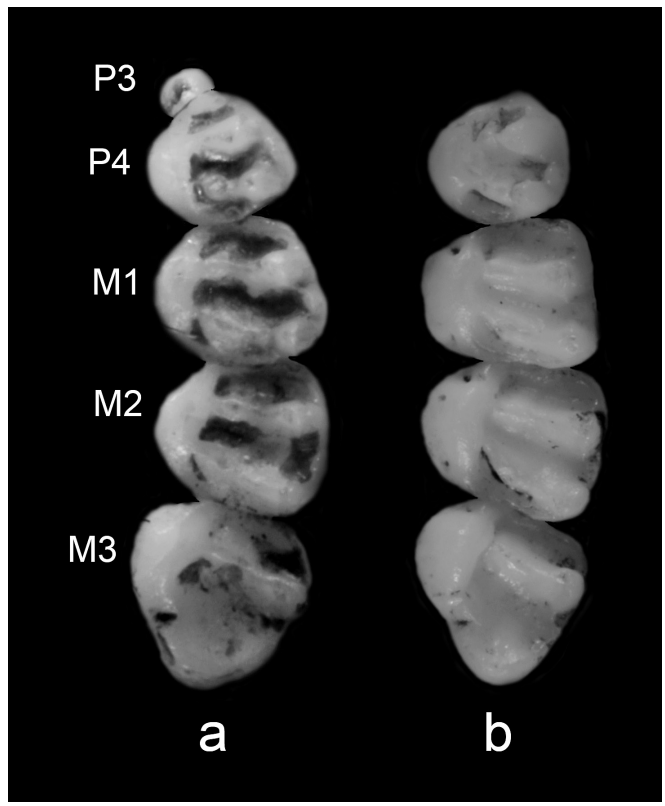


Fig. 2. Maxillary cheek-teeth in chipmunks. a – *Eutamias sibiricus* (Novosibirsk region, Russia; ZFMK 87.785); b – *Tamias striatus* (free-living population at Wuppertal, Germany; ZFMK 89.447). Anterior is at the top, labial is to the right. Not to scale.
Obr. 2. Horní řada zubů burunduka a čipmanka východního. a – *Eutamias sibiricus* (oblast Novosibirska, Rusko; ZFMK 87.785); b – *Tamias striatus* (volně žijící populace, Wuppertal, Německo; ZFMK 89.447). Přední strana je nahoře, lícní strana je vpravo. Zobrazená velikost objektů neodpovídá skutečnosti.

The skull is narrow and flattened dorso-ventrally (Fig. 4). The rostrum is relatively long and tappers gradualy to the tip; interorbital region is flat and wide; braincase is narrower, nasals are longer and infraorbital openings are larger than in ground squirrels. Distema is long (much longer than MxT), incisive foramina minute, rows of cheek-teeth widely appart. Pterygoid region and bullae are without peculiarities. Mandible is shallow, articular process is slender. Dental formula: 1/1, 0/0, 2/1, 3/3 = 22. Upper incisors short, with numerous longitudinal striations. Anterior upper premolar (P3) minute, simple and terete, occassionaly absent (e.g. in 2 out of 41 skulls from Korea; Jones & Johnson 1965); P4 is molariform, M1 and M2 are of sub-equal size; M3 is triangular due to expanded talonid (Fig. 2a). Lower premolar (p4) markedly smaller than remaining cheek-teeth; molars are of about same size. Cheek-teeth display a marmotine general plan of enamel folding. Dimensions (in mm; W in grams): HbL = 120–168, TL = 85–133, HF = 31–40, E = 10–19.5, W = 55–135, CbL = 30.3–41.5, ZgB = 18.5–23.2, MxT = 5.0–7.0. Karyotype: 2n = 38 (Lâpunova & Žolnerovskaâ 1969, Koh 1994, Oshida 2009); morphology of the Y chromosome varies geographicaly, being metacentric or acrocentric (Zima & Král 1984).

Geographic range (Fig. 5). Reviewed and mapped by Obolenskaya (2008): from Archangelsk Region (European Russia) in the west, till the Sea of Okhotsk and Korea in the east. Northern range border posed by the presence of conifers (fir *Abies sibirica* in Europe, larch *Larix sibirica* and *L. daurica* further east); absent from Kamchatka. In the mountainous broad-leaf and mixed forests the range extends into central China (Wang et al. 1992). The south-eastern range border is on the upper flow of the Yellow river. Western border is on the left bank of river Volga (Eu-

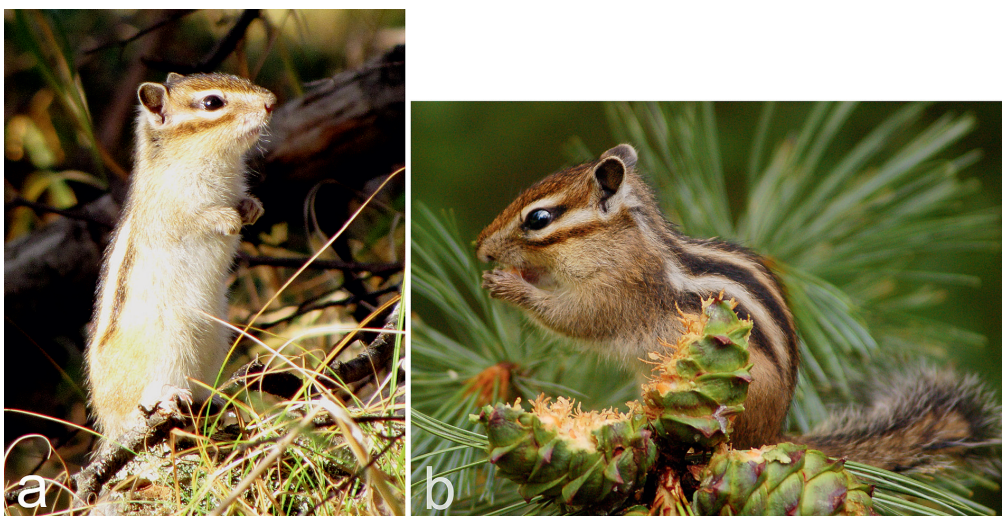


Fig. 3. Siberian chipmunk or burunduk *Eutamias sibiricus*. a – Western Sajan Mts., Hakassiâ, south-eastern Siberia, Russia (photo by Ilya Volodin & Elena Volodina); b – Bureinski Nature Reserve, Far East, Russia (photo by Valdis Pilāts).
Obr. 3. Burunduk *Eutamias sibiricus*. a – Západní Sajany, Chakasie, JV Sibiř, Rusko (foto Ilya Volodin a Elena Volodina); b – Bureinská přírodní reservace, Dálný východ, Rusko (foto Valdis Pilāts).

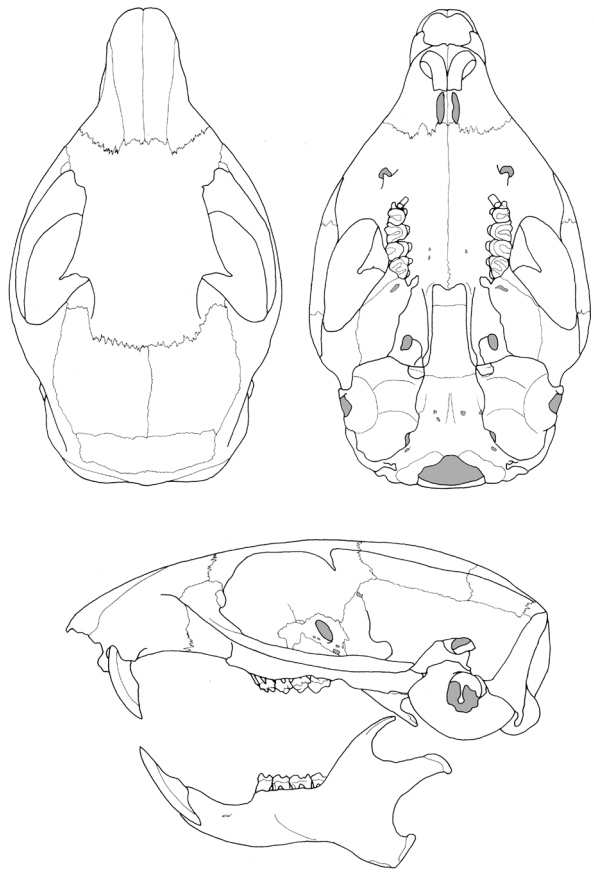


Fig. 4. Skull and mandible of *Eutamias sibiricus* (Jalu, Hingan, China; ZFMK 58.57).
Obr. 4. Lebka a mandibula *Eutamias sibiricus* (Jalu, Chingan, Čína; ZFMK 58.57).

ropean Russia); southern range margin is north of the river Kama, transgresses the Ural Mts. and Čelâbinsk Region; furher east (Omsk, Novosibirsk, Altaj-Sajan) the range border follows the southern margin of woodland. The following islands are occupied in the east: Sakhalin, Hokkaido, Kunashir in the Kuril Islands (record for Iturup is incorrect), four islands offshore the western coast of Hokkaido (Rishiri, Rebun, Teuri, Yagishiri; Oshida 2009), and Bolšoj Šantar (Obolenskaya 2008).

Typical habitat is a coniferous forest with dense understory (Šubin 1991) where dry places are preferred (Kudrâvčeva 1994); also lives in low bushes in semideserts (Allen 1940). Hibernation lasts for about 6 months: from early October to April in north-eastern Europe (Kudrâvčeva 1994), from September to April in western Siberia (Šubin 1991), and from October–early November to late March in Hokkaido, Japan (Kawamichi 1996).

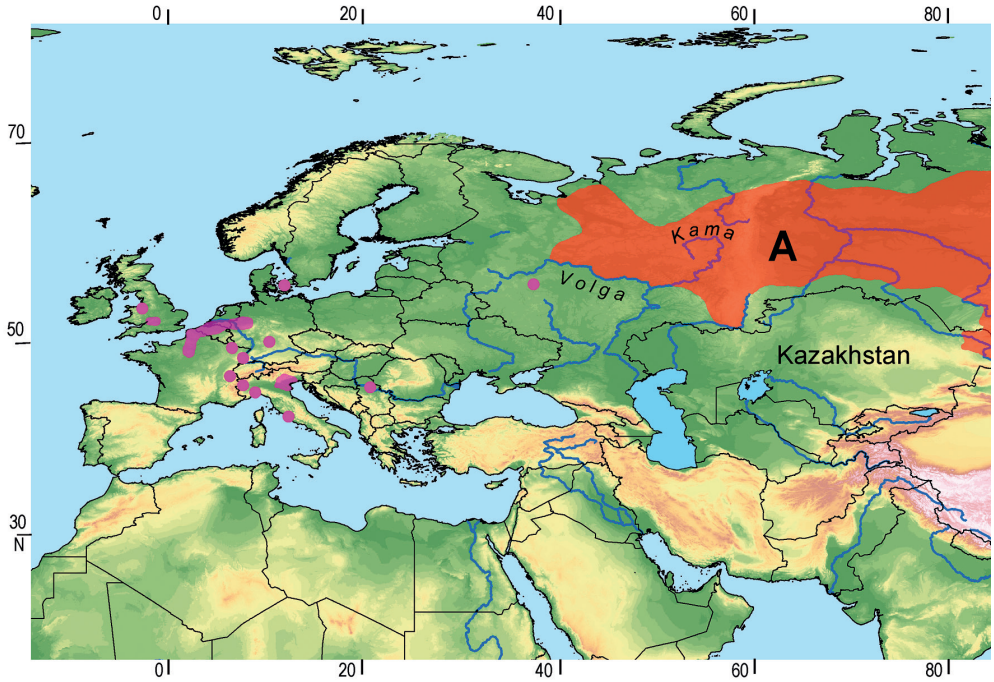
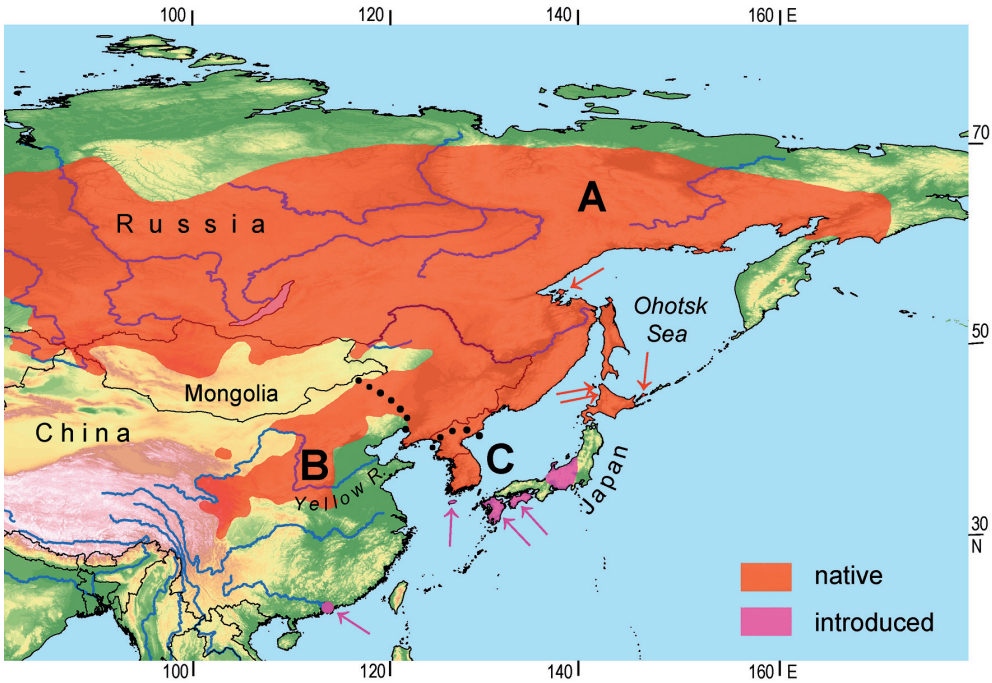


Fig. 5. Native and introduced range of *Eutamias sibiricus*. Red arrows point on autochtonous occurrence on small islands. Recent introductions are shown in violet and majority of those in Asia are emphasized by arrows. Range is compiled from the following sources: the overall range – Obolenskaya (2008); Russia – Popov (1960), Ûdin et al. (1976), Krivošeev (1984); Mongolia – Bannikov (1954); China – Zhang et al. (1997); Japan – Oshida (2009). Introduced populations were largely compiled from Chapuis (2005, 2006) and Bertolino (2009). Subspecies delimitation follows Obolenskaya et al. (2009): A – *E. s. sibiricus*; B – *E. s. senescens*; C – *E. s. barberi*.

Introduced to various European countries since 1970s: Germany, the Netherlands (translocation failed; Bertolino 2009), Belgium, Italy (Amori 1999), France (Chapuis 2005), England (Bertolino 2009), Switzerland (Fernandez 1995), Austria (Krapp 1978a; where no longer present; Spitzenberger 2001), Danmark (Bertolino 2009), and northern Serbia (own data). Free-living populations originate from the releases of pets (available in European pet shops since 1960s; Chapuis 2005), escapes of captive animals and deliberate introductions (Chapius 2006). Geographic origin of translocated animals is the Far East and those in France belong to the Korean subspecies *E. s. barberi* (Pisanu et al. 2012). *E. sibiricus* was introduced also to European Russia (Moscow Region; Obolenskaya 2008), Korea (Island Jeju-do; Bertolino 2009), and Japan: Honshu (probably first to Tiba Prefecture in 1930s; Long 2003), Shikoku and Kyushu (Japan; Bertolino 2009). Rate of successful introductions is high (87% for 38 introductions) and majority of them (71% of all introductions) were followed by a substantial population expansion (Bertolino 2009). Introduced populations occupy urban parks and suburban deciduous woodland.



Obr. 5. Přirozený areál a introdukované populace *Eutamias sibiricus*. Červené šipky ukazují autochtonní výskyt na malých ostrovech. Recentní introdukce jsou zobrazeny fialově a v Asii jsou většinou zdůrazněny šipkou. Rozšíření bylo zkompilováno z následujících pramenů: celkový areál – Obolenskaya (2008); Rusko – Popov (1960), Ûdin et al. (1976), Krivošeev (1984); Mongolsko – Bannikov (1954); Čína – Zhang et al. (1997); Japonsko – Oshida (2009). Introdukované populace byly většinou zkompilovány z Chapuis (2005, 2006) a Bertolino (2009). Ohraničení areálu poddruhů vychází z publikace Obolenskaya et al. (2009): A – *E. s. sibiricus*; B – *E. s. senescens*; C – *E. s. barberi*.

Subspecies were reviewed by Obolenskaya et al. (2009) using molecular and morphological evidence. Divergences between the three recognized subspecies possibly predate Quaternary glaciations and genetic distances between them may be indicative of species recognition (Koh et al. 2010). E.g., the cytocrome *b* sequence variation between ssp. *sibiricus* and ssp. *barberi* (K2P = 11.3%) is within interspecific range for squirrels (Koh et al. 2008, 2010, Lee et al. 2008). Contact zones between subspecies were so far not studied. Thorington et al. (2012) ignored the results of Obolenskaya et al. (2009) and recognized nine subspecies which are based on slight colour differences.

Eutamias sibiricus sibiricus (Laxmann, 1769)

Synonyms. *asiaticus*, *uthensis*, *lineatus*, *pallasi*, *orientalis*, *altaicus*, *okadae*, *jacutensis* (Obolenskaya et al. 2009).

Description. Top of head from snout to between the ears greyish-brown to fulvous-brown, dorsal stripes sharply delimited, light stripes are sandy (medial pair) and sandy grey (lateral pair); rump is brown or ochraceous. Burunduks from the Far East (including Sakhalin and Hokkaido) are brighter with rufous head, ochraceous pale stripes and rusty rump. Post-orbital constriction ≤12.0 mm (Obolenskaya et al. 2009). Dimensions (in mm; W in grams) are fairly stable across the vast distributional range, and display no clear trends. North-eastern European Russia: HbL_{13} = 134.8 (120–145), TL_{13} = 115.9 (85–125), HF_{12} = 34.5 (31–37), E_{11} = 12.5 (10–15), W_{14} = 73.4 (55–96.5), CbL_{11} = 34.2 (30.3–35.5), ZgB_{11} = 20.0 (19.0–22.2), MxT_{11} = 6.0 (5.8–6.6) (Kudrâvčeva 1994b). Southern Altai: HbL_{25} = 144.5 (130–164), TL_{25} = 107.5 (99.5–120), HF_{25} = 35.0 (33.0–38.0), W_{10} = 79.3 (72.0–86.9), CbL_{16} = 35.9 (34.8–37.4), ZgB_{16} = 21.9 (21.1–22.7), MxT_{25} = 6.3 (6.1–6.6) (Sludskij et al. 1977). Far East of Russia: HbL_{325} = 148.6 (135–168), TL_{325} = 111.3 (99–130), HF_{325} = 35.4 (32–40), W_{325} = 87.7 (60–135), CbL_{198} = 35.7 (33.5–38.2), ZgB_{198} = 21.7 (18.5–23.3), MxT_{198} = 6.3 (5.6–7.0) (Krivošeev 1984). Hokkaido (ranges): HbL_{15} = 124–165, TL_{15} = 105–133, HF_{15} = 33–38, E_{15} = 15–17, W_{15} = 71–116 (Oshida 2009). Burunduks introduced to Europe may be larger than in their native range; Germany: HbL_{5} = 148 (145–155), TL_{5} = 110 (107–114), HF_{5} = 36.6 (36–37.5), E_{5} = 15.5 (15–18), W_{3} = 95.8 (67–120), CbL_{5} = 39.9 (38.2–41.5), ZgB_{5} = 22.1 (21.7–22.5), MxT_{5} = 6.5 (6.0–6.7) (Krapp 1978a).

Geographic range (Fig. 5A). Majority of the species' range in Russia, Kazakhstan, Mongolia, Japan, Manchuria (China), and extreme north of Korea; occupy also all of the islands.

Eutamias sibiricus senescens Miller, 1898

Synonyms. *intercessor*, *ordinalis*, *umbrosus*, possibly also *albogularis* (Obolenskaya et al. 2009).

Description. Top of head from snout to between the ears greyish-brown, dark dorsal stripes deep brown with individual light hairs, light stripes are sandy grey (medial pair) and light ash-grey (lateral pair); rump is rufous. Post-orbital constriction ≥ 11.4mm (Obolenskaya et al. 2009). Dimensions (in mm): PL_{17} = 40.2 (38.6–41.5), ZgB_{17} = 22.5 (22.0–23.5), MxT_{17} = 6.6 (5.9–6.9) (Allen 1940).

Geographic range (Fig. 5B). Known from the vicinity of Beijing and provinces of Shanxi and Shaanxi as north as Wawayii Mts. near Qinhuangdao; Obolenskaya et al. 2009). Distributional border against the nominotypical subspecies unresolved.

Remarks. Obolenskaya et al. (2009) suggested that *albogularis* is possibly a junior synonym of *senescens*. This contradicts the conclusion by Allen (1940) that in colouration of the rump, *albogularis* (rump buff olive) more closely resembles the nominotypical subspecies than either *senescens* or *ordinalis*.

Eutamias sibiricus barberi Johnson et Jones, 1955

Description. Top of head from snout to between the ears rusty-brown, dark dorsal stripes nearly black, light stripes are rufous (medial pair) and ochraceous-sandy (lateral pair); bright rufous tint on the rump extends forward till mid-back in some individuals; underparts of tail orange-ochraceous. Post-orbital constriction ≥11.0 mm (Johnson & Jones 1955, Obolenskaya et al. 2009). Dimensions (in mm): $HbTL_{9}$ = 269.8 (258–285), TL_{9} = 117.2 (102–129), HF_{9} = 37.6

(35–40), E_9 = 18.2 (17–19.5), PL_9 = 40.8 (39.9–42.0), ZgB_9 = 22.1 (21.7–22.3), MxT_9 = 6.5 (6.2–6.8) (Johnson & Jones 1955).

Geographic range (Fig. 5C). Korea north to Potaidong, Nongsadong and Musan, at about 40°N latitude; Obolenskaya et al. 2009).

Genus: *Tamias* – Eastern Chipmunks

1811 *Tamias* Illinger. Type species: *Sciurus striatus* Linnaeus, 1758.

If *Neotamias* is generically distinct from *Tamias* and *Eutamias* (cf. arguments under *Eutamias*), than *Tamias* is a monospecific genus, native to the eastern United States and south-eastern Canada.

Tamias striatus (Linnaeus, 1758) – Eastern Chipmunk

1758 *Sciurus striatus* Linnaeus. Type locality: "Habitat in America Septemtrionali" (= lives in Northern America). Restricted to "Upper Savanah River, S.C." (= South Caroline) (Howell 1929), North America.

Remarks. Howell (1929) and Hall & Kelson (1959) listed synonyms.

Description. *T. striatus* superficially resembles *E. sibiricus*, however there are important differences between the two (Fig. 1). The tail is evidently shorter in *T. striatus* (50–66% HbL) and the pattern of longitudinal stripes shows clear peculiarities. Of the five dark-brown or blackish--brown stripes, the medial one is the narrowest and extends from nape to rump; running parallel are two wider stripes which start behind the shoulder. These dark stripes are enclosing 2 paler stripes on either side of the back; the medial stripes (grayish to reddish-orange or brownish) are twice as wide as the lateral ones which are yellowish-white and fade into a yellowish-brown or reddish-brown rump. Head and nape are dark reddish-brown, cheeks and flanks are buff, and belly is white; demarcation along the flanks is abrupt. Tail is grey, with reddish mid-ventral stripe; feet are buff (Fig. 1). Females have 4 pairs of nipples (1 pectoral, 2 abdominal, 1 inguinal). Baculum (length about 4.15 mm) has keel on its ventral tip; os clitoridis accounts for about 60% of length of the baculum (Snyder 1982). The skull is of similar size and shape as in *E. sibiricus* (Fig. 6). The rostrum is more narrowly tiped in *T. striatus*; the interorbital and the postorbital width are subequal (postorbital width is greater than interorbital width in *E. sibiricus*), and bullae are decidedly smaller. Dental formula: 1/1, 0/0, 1/1, 3/3 = 20; the first small premolar (P3) is absent (Fig. 2b). Dimensions (in mm; W in grams) USA (Pennsylvania, North Dakota, New Hampshire, Maine): HbL_7 = 163.9 (154–170), TL_6 = (101.3) 88–110, HF_7 = 33.6 (31.8–35.0), E_7 = 18.2 (17–19.6), W_7 = 116.0 (82–144), CbL_9 = 37.9 (36.2–38,8), ZgB_{10} = 22.6 (21.5–23.0), MxT_{10} = 6.4 (6.2–6.7) (specimens in PMS and ZFMK); Austria (Vienna) and Germany (Wuppertal): HbL_6 = 165.3 (150–180), TL_6 = 93.3 (82–99), HF_6 = 33.6 (32.0–35.2), E_6 = 18.4 (16–21), W_6 = 128.9 (93–144), CbL_4 = 40.6 (39.2–41,5), ZgB_3 = 24.4 (23.6–25.4), MxT_6 = 7.0 (6.4–7.4) (NMW, ZFMK). The karyotype (2n = 38) shows little intraspecific variation (Snyder 1982).

Geographic range. Native to the eastern parts of North America, between the Atlantic coast and Missouri River, from Hudson Bay in the north to Gulf of Mexico in the south. Typical habitat is deciduous woodland, particularly the edges of oak and hickory or beech and maple forest (Whitaker & Hamilton 1998). From late autumn to early spring chipmunks are mainly

underground in "various degrees of torpor", although some remain active throughout the winter (Snyder 1982). Introduced to Europe since the early 20th century, but majority of releases failed: UK (introduced around 1921 or earlier; Long 2003), Austria (several releases since 1957; Krapp 1978b) and Germany (Bertolino 2009). Currently, presence of *T. striatus* is known only for Wuppertal, north of Köln (Germany; Grimmberger & Rudloff 2009), where a small colony persists for about 50 years (R. Hutterer, pers. comm.).

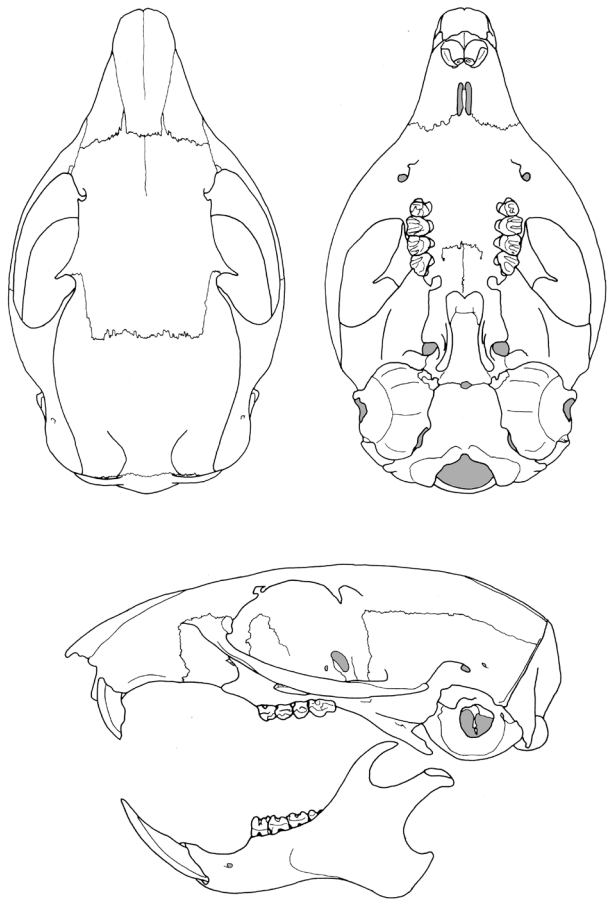


Fig. 6. Skull and mandible of *Tamias striatus* (from a free-living population in Wuppertal, Germany; ZFMK 89.447).
Obr. 6. Lebka a mandibula *Tamias striatus* (z volně žijící populace ve Wuppertalu, Německo; ZFMK 89.447).

Subtribe: Marmotina – marmots and sousliks

1959 Marmotina Moore.
1959 Spermophilina Moore.
1965 Citellini Gromov (in: Gromov et al. 1965).

Moderately large to large ground squirrels with tail normally shorter than half of head and body. Body is round, ears are short and extremities are powerful. Similarly as in Tamiina, the Marmotina have two transbullar septae and lack temporal foramen in the squamoso-parietal suture. They are all strictly terrestrial inhabitants of tree-less grasslands and semideserts where they nest and take refuge when fleeing enemies in burrows in the ground; sousliks and marmots feed on low-growing plants. We recognized 21 species in three genera.

Key to Genera

1. Size large: HbL > 380 mm, W > 1.5 kg, CbL > 70 mm; skull flattened, the point of its greatest elevation is on the rostrum; nasals extend posteriorly beyond the anterior edges of the orbits; paroccipital processes extend beyond the auditory bullae. ..... *Marmota*

1* Size smaller: HbL < 380 mm, W < 1.5kg , CbL < 70 mm; skull is arched and deep, the point of its greatest elevation is on the orbits; nasals do not extend posteriorly beyond the anterior edges of the orbits; paroccipital processes do not extend beyond the auditory bullae. 2

2 Tail longer (> 40% HbL in majority of animals); *processus nasalis ossis premaxillae* wider than the nasal bone (Fig. 7b); P3 relatively larger (Fig. 8c). ..... *Urocitellus*

2* Tail shorter (< 40% HbL in majority of animals); *processus nasalis ossis premaxillae* at most of about same width as the nasal bone (Fig. 7a); P3 relatively smaller (Fig. 8a, b). ..... *Spermophilus*

Genus: *Spermophilus* – Palaearctic sousliks

1816 *Citellus* Oken. Unavailable name (Corbet 1978).
1825 *Spermophilus* Cuvier. Type species: *Mus citellus* Linnaeus, 1766.
1827 *Citillus* Lichtenstein. Based on three distinct species (Pavlinov & Rossolimo 1987).

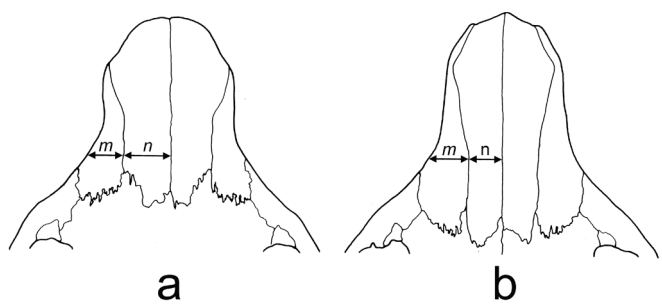


Fig. 7. Rostrum in dorsal view in a – *Spermophilus citellus* (Deliblato Sands, Serbia; PMS 7082) and b – *Urocitellus undulatus* (Gorno Altajsk, Russia; SZM 25494). Note the differences in width of nasals (*n*) against width of *processus nasalis ossis premaxillae* (*m*). Not to scale.
Obr. 7. Rostrum z dorsálního pohledu u a – *Spermophilus citellus* (Deliblatska pescara, Srbsko; PMS 7082) a b – *Urocitellus undulatus* (Gorno Altajsk, Rusko; SZM 25494).Viz rozdíly v šířce nosních kostí (*n*) oproti šířce *processus nasalis ossis premaxillae* (*m*). Zobrazená velikost objektů neodpovídá skutečnosti.

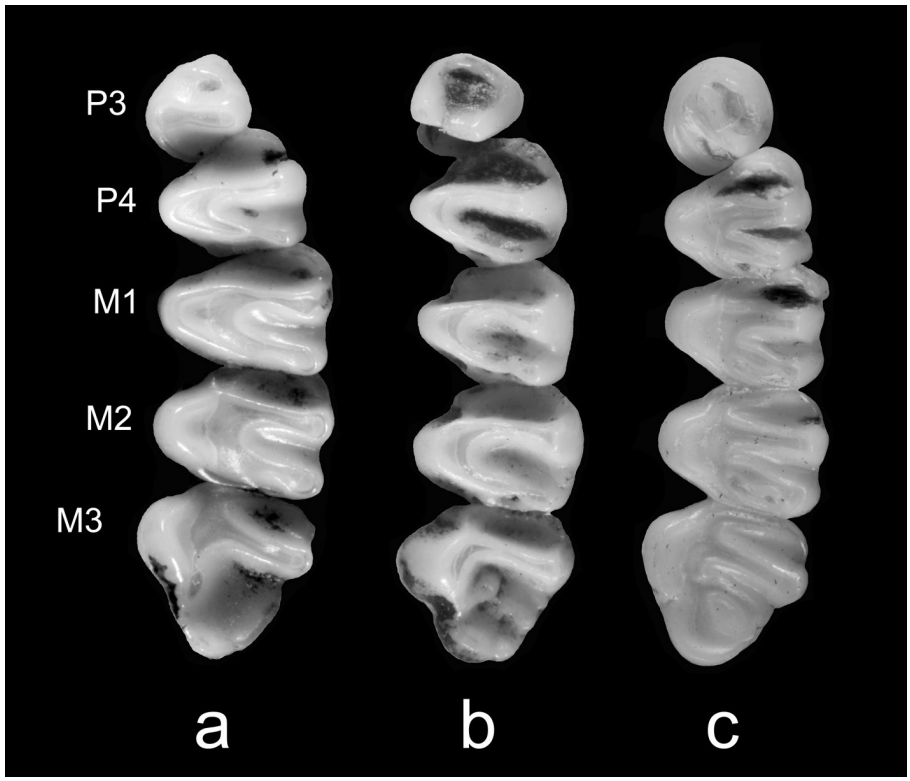


Fig. 8. Maxillary cheek-teeth in Palaearctic ground squirrels. a – *Spermophilus dauricus* (north-eastern China; ZFMK 56.580); b – *S. fulvus* (Afghanistan; ZFMK 92.494); c – *Urocitellus parryii* (Hula-hula River, Alaska, USA; ZFMK 92.502). Anterior is at the top, labial is to the right. Not to scale.
Obr. 8. Horní řady zubů palearktických syslů a – *Spermophilus dauricus* (severovýchodní Čína; ZFMK 56.580); b – *S. fulvus* (Afganistan; ZFMK 92.494); c – *Urocitellus parryii* (řeka Hula-hula, Aljaška, USA; ZFMK 92.502). Přední strana je nahoře, lícní strana je vpravo. Zobrazená velikost objektů neodpovídá skutečnosti.

1830 *Spermatophilus* Wagler. Incorrect spelling of *Spermophilus* (Helgen et al. 2009).
1844 *Colobotis* Brandt. Type species: *Arctomys fulvus* Lichtenstein, 1823.

Throughout the 20th century the Palaearctic sousliks were generically referred to *Citellus* (ruled unavailable by the ICZN 1956, as a non-Linnaean; see Corbet 1978; Helgen et al. 2009). Infrageneric division is either into two subgenera (*Colobotis* vs. *Spermophilus* [*Citellus*]; Gromov et al. 1965, Spiridonova et al. 2006, Tsvirka et al. 2006a) or into three species groups (*fulvus*, *pygmaeus* and *citellus*; Nadler et al. 1982, Pavlinov & Rossolimo 1987, Pavlinov et al. 1995). Interspecific genetic divergence is low in *Spermophilus*, particularly so between *S. fulvus*, *S. major*, and *S. erythrogenys* (Spiridonova et al. 2006). In addition to this, widespread introgressive hybridization obscures species limits since it produces paraphyletic or polyphyletic taxa

in molecular trees (e.g. in *S. major*). Hybridization has been documented so far between seven species: *S. major* × *S. fulvus*, *S. major* × *S. pygmaeus*, *S. major* × *S. suslicus* (Bažanov 1944, Gray 1954, Ermakov et al. 2002, Shmyrov et al. 2012), *S. major* × *S. erythrogenys brevicauda* (Spiridonova et al. 2005, 2006), *S. erythrogenys pallidicauda* × *S. alaschanicus* (Korablev et al. 2006, Tsvirka et al. 2006b), *S. pygmaeus* × *S. suslicus* (Ermakov et al. 2006a), and *S. citellus* × *S. suslicus* (Gromov & Erbajeva 1995). Hybridization is probably facilitated by a general promiscuous multiple paternity in sousliks (Shmyrov 2006).

Chromosomal data were summarized in Vorontsov & Lâpunova (1970) and Zima & Král (1984). Diploid numbers vary between 2n = 34 and 2n = 42, and majority of species display 2n = 36. Variations in diploid number were reported in two species, *S. suslicus* and *S. erythrogenys*, both involving cytotypes 2n = 34 and 36. Alarm call primarily consists of a fundamental frequency alone (additional harmonics in *Urocitellus*); for interspecific differences see Nikol'skij (1979).

We recognize lower number of species in comparison to Thorington & Hoffmann (2005) and Helgen et al. (2009) which makes our taxonomic arrangement closer to the one by Gromov et al. (1965). In our opinion, splitting *S. erythrogenys* and *S. relictus* is poorly supported by the available evidence and we believe it is premature. In phylogenetic reconstructions several species (*S. erythrogenys*, *S. major*, and *S. relictus*) emerged as paraphyletic or polyphyletic groups, most probably a consequence of their widespread past and present interspecific hybridization which twists species limites in molecular trees.

Description. Small to moderately large terrestrial squirrels with round body, short tail and reduced ear. Ears are densely covered with short hairs but there is no tuft. Head is convex in profile, eyes are large and vibrissae are relatively short. Muzzle pad is naked. Cheeck pouches are present. Feet are more robust than in *Eutamias* and claws are less curved. Although the thumb is rudimentary it still bears a nail. There are four large pads on palms and soles. Tail is cylindrical at base; it is densely haired with a short terminal pencil. Fur is short and rough; pelage pattern is unmarked, spotted, or flecked, depending on the species and also on the season. Females have 8–16 nipples (10 in majority of species). The baculum consists of a corpus, a thickened base, and a spoon-like expanded distal spatula which has tooth-like projections (denticles) around the anterior border; denticles, mostly sharply pointed, are directed dorsally. On the ventral side of the distal end of the bone is in majority of species either a median knob-like projection or a keel. The baculum is frequently twisted (Fig. 13). Skull is arched and deeper than in *Eutamias*; the postorbital process is more prominent. The infraorbital foramen passes through the zygomatic plate as a somewhat laterally compressed canal, and opens forward of the plate (Moore 1959). The masseter knob is prominent. Enamel on upper incisors is whitish to pale-yellow. Cheek teeth are relatively hypsodont, with constricted lingual portion in the upper row which gives teeth a triangular appearance. Dental formula: 1/1, 0/0, 2/1, 3/3 = 22.

Geographic range. *Sermophilus* is endemic to the Palaearctic region where occupy belt of steppes (including woodland steppe and semideserts) stretching from east-central Europe (Czech Republic, Austria, Hungary) till the shores of the Bohai Sea (a gulf of theYellow Sea) in China. Distributional borders are frequently posed by large rivers which delimit closely related pairs of species (Vorontsov et al. 1980). As a rule, sousliks are allopatric, although occasionally up to three species may occupy the same region, e.g. *S. major*, *S. pygmaeus* and *S. fulvus* on the eastern bank of the upper flows of the River Ural (Ermakov et al. 2002). Zone of sympatry is broad (200–240 km) between *S. major* and *S. pygmaeus* (Šlâhtin et al. 2009) or narrow between *S. suslicus* and *S. citellus* in Ukraine (Calinescu 1934). In rare occassions two distinct species

form mixed colonies, e.g. *S. major* with *S. suslicus* (Titov 2003, Kuzmin & Titov 2006) and *S. major* with *S. pygmaeus* (Artemev 1965). On the eastern bank of the river Volga, *S. major* occupies mesic places while *S. pygmaeus* prefers higher and xeric sites (Šlâhtin et al. 2009). In Kyrgyzstan, *S. fulvus* and *S. relictus* occur sympatricaly but inhabit different altitudinal zones (Ajzin 1979). Mosaic environment may allow co-existence of two sousliks at low level of hybridization which, in turn, increases promptly in monotonous habitats (Titov et al. 2012).

Key to Species

1. Soles of hind feet hairy from heel to pads; brain-case elongate, longer than wide. 2
1* Soles of hind feet nude throughout, except for heel; brain-case squarish, wider than long (or length ≈ breadth). 7
2 Post-incisive pit absent on praemaxillary; occupy western Palaearctics (west of 50° E latitude). 3
2* Post-incisive pit present on praemaxillary; occupy eastern Palaearctics (east of 90° E latitude). 6
3 Dorsal pelage distinctly spotted (diameter of spots 2–5 mm). ..... *S. suslicus*
3* Dorsal pelage finely speckled (diameter of spots 1–2 mm) or unmarked. 4
4 Tail longer (on average about 30% HbL), with black hairs dorsally; 2n = 40. 5
4* Tail shorter (on average about 20% HbL), with no black hairs dorsally; 2n = 42. ... *S. xanthoprymnus*
5 Back reddish-brown, unspeckled; occupy Asia Minor. ..... *S. taurensis*
5* Back buff, black-white spotted; occupy Europe. ..... *S. citellus*
6 Tail longer (on average 35% HbL); interorbital constriction mainly > 9.0 mm; 2n = 38. ..... *S. alaschanicus*
6* Tail shorter (on average 28% HbL); interorbital constriction mainly < 9.0 mm; 2n = 36. ... *S. dauricus*
7 Back and belly uniformly buff, sandy or yellow; dorsal pelage darkened by distinct black hair; MxT ≥13.0 mm. ..... *S. fulvus*
7* Back and belly of different colour; dorsal pelage speckled with white spots or unmarked; MxT <13.5 mm. 8
8 Reddish spot beneath the eye; zygoma forms nearly right angle at its junction with rostrum. 9
8* No reddish spot beneath the eye; zygoma forms smooth curve at its junction with rostrum. ..... *S. relictus*
9 Distinct rusty spots beneth and above the eye, and around the ear; snout rusty. 10
9* Rusty spot indistinct, frequently restricted to the cheeks; snout buff or greyish. 11
10 Females with 14–16 (rarely 12) nipples; allarm call long (>200 msec). ..... *S. major*
10* Females with 10–12 nipples; allarm call short (<200 msec). ..... *S. erythrogenys erythrogenys*
S. erythrogenys heptneri
11 Size smaller, MxT ≤ 10.2 mm (up to 10.8 mm in ssp. *musicus*); occurs to the west of 70° E latitude. ..... *S. pygmaeus*
11* Size larger, MxT ≥ 10.2 mm; range to the east of 65° E latitude. 12
12 Diploid number of chromosomes 2n = 34. ..... *S. erythrogenys pallidicauda*
12* Diploid number of chromosomes 2n = 36. ..... *S. erythrogenys brevicauda*

Spermophilus citellus (Linnaeus, 1766) – European souslik

1766 *Mus citellus* Linnaeus. Type locality: "Habitat in Austria, Bohemia, Polonia", restricted to "Austria" (Miller 1912), restricted to "Wagram, Austria" (Martino & Martino 1940).

1779 *Mus citillus* Pallas. Unjustified emendation of *Mus citellus* Linnaeus, 1766.

1929 *Citellus citellus gradojevici* Martino et Martino. The authorities for *gradojevici* are "V[ladimir] and E[vgenia] Martino" (Martino & Martino 1929), and not solely "Martino" (cf. Thorington & Hoffmann 2005). Type locality: "Djerdjelija (misspelled, correctly Gevgelija), Macedonia."

1934 *Citellus citellus istricus* Calinescu. Type locality: "Ebene Munteniens" (= lowlands of Muntenia), southeastern Romania.

Fig. 9. Subspecies of *Spermophilus citellus*. a – *S. c. citellus* (Mladá Boleslav, Czech Republic; photo by Alenka Kryštufek); b – *S. c. gradojevici* (Dojran, Macedonia; photo by Tomi Trilar); c – *S. c. karamani* (Gorno Begovo, Mt. Jakupica, Macedonia; photo by Alenka Kryštufek).
Obr. 9. Poddruhy *Spermophilus citellus*. a – *S. c. citellus* (Mladá Boleslav, Česká Republika; foto Alenka Kryštufek); b – *S. c. gradojevici* (Dojran, Makedonie; foto Tomi Trilar); c – *S. c. karamani* (Gorno Begovo, pohoří Jakupica, Makedonie; foto Alenka Kryštufek).

1937 *Citellus citellus karamanni* Martino. Type locality: "na stepskoj visoravni Karađice, iznad 2000 m. nadmorske visine" (= steppic high altitudinal plateau on Mt. Karadžica, above 2000 m of elevation), Macedonia. *Nomen nudum* (variable spelling: also *Citellus citillus karamani*).

1940 *Citellus citellus karamani* Martino et Martino. The authorities for *karamani* are "V[ladimir] & E[vgenia] Martino" (Martino & Martino 1940), and not solely "Martino" (cf. Thorington & Hoffmann 2005). Type locality: "Karadjica (= Karadžica) Mountains, above Patiška, 30 km. S. of Skoplje (= Skopje), South Serbia (= Macedonia). Alt. 2000 m". Misspelled as "*C. c. karemani* Martino (1940)" in Gromov et al. (1965).

1940 *Citellus citellus laskarevi* Martino et Martino. The authorities for *laskarevi* are "V[ladimir] & E[vgenia] Martino" (Martino & Martino 1940), and not solely "Martino" (cf. Thorington & Hoff-

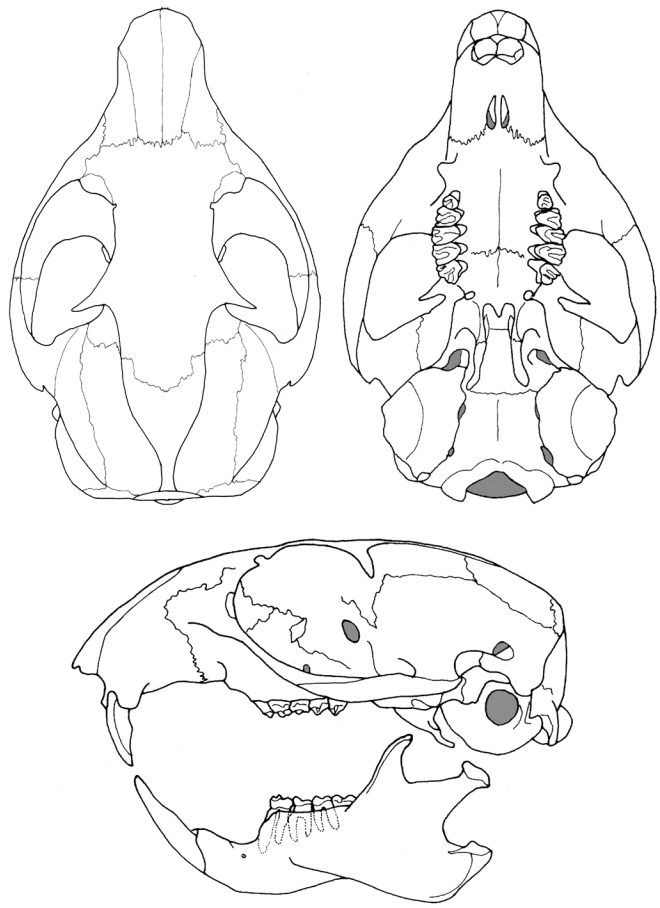


Fig. 10. Skull and mandible of *Spermophilus citellus* (adult male from Karaağaç, Edirne, European Turkey; PMS 11507).
Obr. 10. Lebka a mandibula *Spermophilus citellus* (adultní samec z lokality Karaağaç, Edirne, evropská část Turecka; PMS 11507).

mann 2005). Type locality: "Dolovo, southeastern Banat, Yugoslavia," now Serbia. Occasionally misspelled as *lascaravi* (e.g. Gromov et al. 1965).

1955 *Citellus citellus martinoi* Peshev. Type locality: "Rodopite, okolnostite na v. Kolarov (Belmeken), 2350 m nad morskoto ravniŝe" (= Rhodope Mts., neighbourhoods of the peak Kolarov (= Belmeken), alt. 2,350 m), Bulgaria.

1957 *Citellus citellus balcanicus* Markov. Type locality: "Okolnostite na s. Lokorsko, Sofijsko, na ûg ot Balkana, Blgariâ" (= neighbourhoods of the village Lokorsko, Sofia Region, south to the Balkan Mts., Bulgaria).

1964 *Citellus citellus thracius* Mursaloğlu. Type locality: "A valley-meadow in front of the south-east slope of Murattepe, near Yenibedir, Lüleburgaz, Kirklareli, Turkey in Europe."

1977 *Citellus citellus macedonicus* Fraguedakis-Tsolis. Type locality: "Kozani", Greece.

1985 *Citellus citellus macedonicus* Fraguedakis-Tsolis et Ondrias. Type locality: "Pontokomi, Kozani, western Macedonia, Greece".

Remarks. Syononymy reviewed in Ramos-Lara et al. (in press). *S. citellus* is in a sister position to *S. taurensis* (Gündüz et al., 2007a, Kryštufek et al. 2009). Hybridize with *S. suslicus* in a very restricted zone of sympatry in Ukraine (Gromov & Erbajeva 1995), where the two species are sympatric between the town of Černovci and the river Dniestr (Calinescu 1934).

Description. Medium-sized souslik with moderately long tail (≈22–30% HbL; Fig. 9). Soles are covered with short silvery hairs from heel to pads. Cream-buff back is indistinctly black and white mottled; the speckles are about 1–2 mm in diameter (11–17 speckles per cm^2; Calinescu 1934). Head and cheeks are grizzled; muzzle is rusty shaded; eye ring is whitish to yellowish. Belly is buff washed, feet are yellowish. The upper surface of the tail is grizzled, darker towards the tip, pencil is white margined. Females have 5 pairs of nipples (1 pectoral, 2 abdominal, 2 inguinal). Size and shape of the baculum vary geographically (see under subspecies); length of baculum does not correlate with CbL (Kryštufek & Hrabě 1996). Skull shows no peculiarities; epansion of zygomatic arches is modest (ZyB = 63–72% CbL); supratemporal ridges only exceptionaly converge posteriorly to form a low sagital crest (Fig. 10). Teeth do not deviate from general condition in the genus; P4 is relatively small. Number of roots (maxillary / mandibular): 1, 3, 3, 3, 3 / 2, 4, 4, 4 (Kryštufek & Vohralík 2005). Dimensions (in mm; W in grams): HbL = 168–232, TL = 31–90, HfL = 29.6–43.0, E = 6.0–15.4, W = 131–380, CbL = 38.2–47.7, ZgB = 24.9–31.5, MxT = 8.1–10.7. Males are larger than females and secondary sex dimorphism in cranial size is fairly constant across the species' range (Kryštufek 1996). Karyotype: 2n = 40 (Soldatović et al. 1984).

Geographic range (Fig. 11). The European souslik inhabits the westernmost part of the range of the genus. The first detailed description of its range is by Jacobi (1903). In the 20th century *S. citellus* still populated the area from Bohemia in the west to the Black Sea coast in the east, and from south-eastern Germany and southern Poland (at 52° N) as far south as Thessaloniki and Kozani (Greece), and Thrace. The species' range is disjunct, consisting of two large fragments (the Pannonian and the Balkan) separated by the Carpathians and by the Đerdap Canyon of the Danube. Small isolated populations occur around the periphery in Germany, Poland, Macedonia, Serbia and northern Greece; some of these isolates were exterminated within the last half a century (Kryštufek 1999): by late 1960s in Germany (Saxony; Feiler 1988), by 1983 in Poland (the Silesian Upland, where *S. citellus* was always rare since its first appearance in the early 19th century; Profus 2012; Męczyński 1985) and in Croatia (around Vukovar; Tvrtković 2006). Much of extant range was possibly occupied during a fairly recent expansion which was triggered by changes in land use, particularly a large-scale deforestation; Central Europe was invaded about 700–300 ya (Grulich 1960); first reported presence in "agros Bohemiae" (=

Fig. 11. Distribution of *Spermophilus citellus* in the 20th century when the most extensive. Compiled from the following sources: the overall range – Ružić (1978), Kryštufek (1999), Coroiu et al. (2008); Austria – Spitzenberger & Bauer (2001); Bulgaria – Popov (2007), Koshev (2008); Croatia – Tvrtković (2006); Czech Republic – Matějů et al. (2008), Anděra (2011); Germany – Feiler (1988), Hauer & Feiler (2009); Greece – Fraguedakis-Tsolis & Ondrias (1985); Hungary – Váczi et al. 2007); Macedonia – Kryštufek (1993), Kryštufek et al. (2012); Moldova – Lozan (1970), Savin et al. (2012); Poland – Surdacki (1983a); Romania – Calinescu (1934); Serbia – Ružić-Petrov (1950); Slovakia – Feriancová-Masárová & Hanák (1965), Brtek (1974); Turkey – Kryštufek & Vohralík (2005); Ukraine – Meżżerin (2009a), Zagorodniuk et al. (2010), Muntyanu (not dated). Subspecies are delimited by a dotted line: A – *S. c. citellus*; B – *S. c. gradojevici*; C – *S. c. karamani*. Delimitation line is tentative along the Black Sea coast.
Obr. 11. Rozšíření *Spermophilus citellus* ve 20. stol., v době kdy byl jeho areál nejrozsáhlejší. Zkompilováno z následujících pramenů: celkový areál – Ružić (1978), Kryštufek (1999), Coroiu et al. (2008); Rakousko – Spitzenberger & Bauer (2001); Bulharsko – Popov (2007), Koshev (2008); Chorvatsko– Tvrtković (2006); Česká Republika – Matějů et al. (2008), Anděra (2011); Německo – Feiler (1988), Hauer & Feiler (2009); Řecko – Fraguedakis-Tsolis & Ondrias (1985); Maďarsko – Váczi et al. 2007); Makedonie – Kryštufek (1993), Kryštufek et al. (2012); Moldávie – Lozan (1970), Savin et al. (2012); Polsko – Surdacki (1983a); Rumunsko – Calinescu (1934); Srbsko – Ružić-Petrov (1950); Slovensko – Feriancová-Masárová & Hanák (1965), Brtek (1974); Turecko – Kryštufek & Vohralík (2005); Ukrajina – Meżżerin (2009a), Zagorodniuk et al. (2010), Muntyanu (nedatováno). Rozšíření poddruhů je ohraničeno tečkovanou čarou: A – *S. c. citellus*; B – *S. c. gradojevici*; C – *S. c. karamani*. Hranice areálů poddruhů při černomořském pobřeží je stanovena jen přibližně.

Bohemia) is from 1603 (Profus 2012). The range expansion in marginal populations in Silesia (Poland) still progressed in the 19th century (Brinkmann 1951). In the east, the river Prut was reached only 500–600 ya, and at the beginning of the 20th century sousliks putatively occupied only northern Moldova (Lozan 1970). *S. citellus* gradualy spread southwards along the River Dniester, reaching the village of Vărăncău in 1970s, the village of Sănătăcuca towards the end of 1990s, and Sadova in subsequent years (Savin et al. 2012).

Range was always mosaic, particularly so in a topographically diverse landscape (e.g. the Balkans) and along the periphery. Over the last fifty years populations declined throughout the range (e.g. Ružić 1978, 1979, Ambros 2008, Koshev 2008, Matějů et al. 2008). Fragmentation progressed over last decades through landscape changes; e.g. in Czech Republic, where *S. citellus* was still widespread in early 1950s, only 34 colonies survived untill 2007, but only five of them contained >200 individuals (Matějů et al. 2008, 2010a). In the lack of gene flow the population fragments differentiated genetically and show high level of inbreeding (Hulová & Sedláček 2008). Translocation programmes were initiated 25 ya in Hungary (Tokaji et al. 2012) and were followed up in Czech Republic and Slovakia (Matějů et al. 2010b). In 2000s the extinct Polish population was re-established in the Opolskie and the Dolnośląslie Regions from different source populations (Matějů et al. 2010b).

The European souslik is tied to a short-grass steppe, pastures and meadows on drained soil, both natural and anthropogenic (Kryštufek & Vohralík 2005). Although low vegetation is essential, the animal does not depend on a specific plant or vegetation community (Matějů et al. 2011) and does not require particular soil type (Janderková et al. 2011). Elevational range is from the maritime coast up to 2,500 m. Hibernation lasts 5–5.5 months in the lowlands, 7–7.5 months in the mountains (Ružić 1978).

Subspecies. Phylogenetic reconstruction based on cytochrome *b* gene retrieved three strongly supported lineages (Kryštufek et al. 2009) which we classify as distinct subspecies. Such grouping corresponds with non-metrical cranial divergence (Kryštufek 1990), morphometrics of the postcranial skeleton (pelvis; Kryštufek 1998) and variation in baculum morphology (Kryštufek & Hrabě 1996), but not with the conventional subspecies and the pattern of metric cranial divergence (Kryštufek 1999). The estimated time of divergence for *S. c. gradojevici* is about 0.58 Mya, while the nominotypical subspecies and *S. c. karamani* diverged more recently (c. 0.3 Mya). Major glacial-interglacial refugium for *S. citellus* was presumably along its southern current range, from northern Greece to Turkish Thrace, and further north along the Black Sea coast (Kryštufek et al. 2009).

Spermophilus citellus citellus (Linnaeus, 1766)

Synonyms. *citillus*, *istricus*, *laskarevi*; probably also *martinoi* and *balcanicus*.

Description. Diagnosed primarily by a cytochrome *b* sequence (Kryštufek et al. 2009). Size varies between samples from small to medium. Fur normally lacks buff or ochraceous tint; ventral side of tail greyish (Fig. 9a). Lacrimal bone has a foramen in c. >10% of animals in a population (Kryštufek 1990). Baculum is 2.47–3.66 mm long, 0.87–1.04 mm wide across basal expansion, and 1.22–1.74 mm wide across spatula. A knob like medio-ventral projection on the distal end is small to moderately robust; its appex is frequently blunt. The spatula is margined with a continuous row of 10–16 long and sharp denticles (Fig. 12a; Kryštufek & Hrabě 1996). Dimensions (in mm; W in grams) (Austria) males: HbL_{35} = 204.1 (180–225), TL_{34} = 62.4 (31–90), HfL_{34} = 36.6 (33.7–43.0), E_{27} = 9.9 (6.0–15.4), W_{31} = 238.7 (132–380),

CbL_{30} = 42.3 (40.0–47.7), ZgB_{28} = 28.0 (25.4–31.4), MxT_{32} = 9.1 (8.3–9.8); females: HbL_{37} = 197.0 (174–217), TL_{35} = 61.5 (55–75), HfL_{35} = 35.7 (33.0–41.0), E_{18} = 9.7 (7.5–12.2), W_{32} = 211.2 (152–270), CbL_{38} = 40.8 (38.3–44.3), ZgB_{34} = 27.3 (24.9–29.8), MxT_{38} = 9.0 (8.2–9.7) (Spitzenberger & Bauer 2001). Banat, northern Serbia, males: HbL_{16} = 206.6 (185–220), TL_{16} = 49.1 (33–62), HfL_{16} = 35.0 (29.6–38.7), E_{16} = 9.4 (8.0–11.1), W_{10} = 238.0 (220–280), CbL_{16} = 41.8 (38.2–43.6), ZgB_{16} = 27.8 (25.7–28.7), MxT_{16} = 9.4 (9.0–9.8); females: HbL_{35} = 205.8 (190–218), TL_{29} = 53.3 (44–61), HfL_{35} = 34.5 (30.5–36.9), EL_{35} = 9.2 (8.0–10.3), W_{31} = 212.9 (173–270), CbL_{35} = 40.7 (38.2–42.7), ZgB_{34} = 27.3 (25.9–28.2), MxT_{35} = 9.5 (8.8–10.1) (specimens in BMNH and PMS).

Geographic range (Fig. 11A). Bohemia, the entire Pannonian fragment and majority of the main Balkan fragment, from lowlands to high-elevation meadows; distribution border against ssp. *gradojevici* is not resolved due to insufficient sampling in Bulgaria (see under *gradojevici*). Sousliks from north-eastern part of range in Romania may belong to a distinct sublineage (if formal recognition will prove appropriate, than the name *istricus* is available); further sampling is needed, however.

Spermophilus citellus gradojevici (Martino et Martino, 1929)

Synonyms. *thracius*, *macedonicus*.

Description. Diagnosed primarily by a cytochrome *b* sequence (Kryštufek et al. 2009). Size moderate to large. Fur buff to ochraceous dorsally, belly buffy-tinted; ventral side of tail uniformly

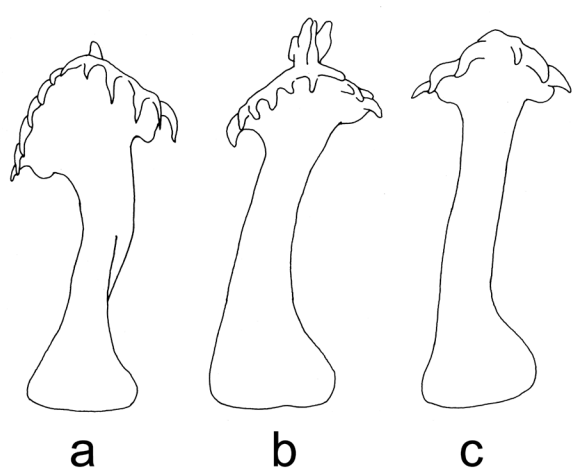


Fig. 12. Baculum in tree subspecies of *Spermophilus citellus*. a – *S. c. citellus* (Banatska Palanka, northern Serbia; PMS 6215); b – *S. c. gradojevici* (Dojran, Macedonia; PMS 7052); c – *S. c. karamani* (Gorno Begovo, Mt. Jakupica, Macedonia; PMS 7077). Scale bar = 1 mm.
Obr. 12. Penisová kost u tří poddruhů *Spermophilus citellus*. a – *S. c. citellus* (Banatska Palanka, severní Srbsko; PMS 6215); b – *S. c. gradojevici* (Dojran, Makedonie; PMS 7052); c – *S. c. karamani* (Gorno Begovo, pohoří Jakupica, Makedonie; PMS 7077). Měřítko = 1 mm.

buff-yellow. The eye ring is whitish (Fig. 9b). Lacrimal bone lacks foramen (Kryštufek 1990). Baculum is 2.70–2.81 mm long, 0.93–1.31 mm wide across basal expansion, and 1.16–1.39 mm wide across spatula. A knob like ventral projection is robust with a crown-like appex. The spatula has 8–12 short and blunt denticles along its anterior margin (Fig. 12b; Kryštufek & Hrabě 1996). Dimensions (in mm; W in grams), Macedonia (topotypes of *gradojevici*), males: HbL_7 = 222.3 (213–232), TL_7 = 57.1 (49–69), HfL_7 = 39.4 (37.5–41.0), E_7 = 9.7 (8.5–10.8), W_6 = 300.0 (290–330), CbL_9 = 45.3 (44.1–46.3), ZgB_8 = 30.7 (29.8–31.5), MxT_{10} = 10.2 (9.8–10.7); females: HbL_{14} = 218.2 (190–230), TL_{14} = 59.6 (51–68), HfL_{15} = 37.5 (35.5–39.7), E_{15} = 9.3 (8.3–10.4), W_{13} = 273.5 (225–325), CbL_{17} = 43.7 (42.2–45.2), ZgB_{16} = 29.5 (28.3–31.1), MxT_{17} = 10.2 (9.8–10.6) (Kryštufek 1993). Thrace (topotypes of *thracius*): males: HbL_{22} = 199.4 (184–228), TL_{28} = 55.8 (49–65), HfL_{11} = 36.5 (34–39), E_{27} = 9.8 (7.5–12), W_{39} = 231.0 (131–340), CbL_{44} = 42.4 (40.4–46.3), ZgB_{44} = 28.4 (25.5–31.0), MxT_{48} = 10.4 (9.0–11.0); females: HbL_{16} = 198.3 (180–214), TL_{21} = 54.4 (48–61), HfL_5 = 35.4 (35–36), E_{24} = 9.5 (8–11), W_{38} = 223.0 (170–353), CbL_{50} = 41.3 (38.6–44.0), ZgB_{48} = 27.6 (25.5–30.4), MxT_{53} = 10.3 (8.8–10.7) (Kryštufek & Vohralík 2005). North-western Greece (Kozani, topotypes of *macedonicus*): males: HbL_{18} = 197.2 (168–217), TL_{18} = 70.2 (56–80), HfL_{18} = 39.3 (37.0–43.0), E_{18} = 10.7 (9.0–12.0), W_{14} = 301.7 (212–378), CbL_{10} = 43.1 (41.4–45.2), ZgB_{10} = 28.1 (26.0–30.6), MxT_{16} = 10.1 (9.4–10.6); females: HbL_{12} = 197.4 (185–214), TL_{12} = 69.2 (60–72), HfL_{12} = 38.9 (37.0–41.0), E_{12} = 11.0 (9–12), W_{10} = 321.0 (282–380), CbL_8 = 42.9 (41.7–43.8), ZgB_8 = 28.3 (26.9–29.2), MxT_{11} = 10.0 (9.5–10.6) (Fraguedakis-Tsolis & Ondrias 1985).

Geographic range (Fig. 11B). Southern part of the Balkan fragment in northern Greece, Macedonia, and Thrace in Greece and Turkey. Range not resolved in Bulgaria. A cytochrome *b* haplotype of ssp. *gradojevici* has been recorded also from the Dobrogea but sampling is insufficient along the entire Black Sea coast to assess the degree of putative overlap with the nominotypical race (Kryštufek et al. 2009). From lowlands along the sea-shore to high-mountain pastures. Recent population decline particularly sharp in north-western Greece (in 2005 we found the isolate in Kozani effectively extinct) and in south-eastern Macedonia.

Spermophilus citellus karamani (Martino et Martino, 1940)

Synonym. *karamanni*.

Description. Diagnosed primarily by a cytochrome *b* sequence (Kryštufek et al. 2009). Size moderate; fur similar to ssp. *gradojevici* but lighter and more grey tinted (Fig. 9c); tail greyish on ventral side. Lacrimals perforated in 41% of cases (Kryštufek 1990). Baculum is 2.70–3.10 mm long, 0.73–0.96 mm wide across basal expansion, and 1.02–1.22 mm wide across spatula. A knob-like ventral projection at the distal end is reduced or absent. The spatula is margined with 8–12 large denticles (Fig. 12c; Kryštufek & Hrabě 1996). Dimensions (in mm; W in grams), males: HbL_{16} = 213.6 (188–230), TL_{15} = 54.9 (45–60), HfL_{16} = 35.4 (30.5–38.5), E_{16} = 9.3 (8.7–10.5), W_{11} = 209.1 (140–250), CbL_{16} = 43.2 (40.6–45.5), ZgB_{15} = 29.4 (27.5–31.2), MxT_{16} = 9.4 (8.8–9.7); females: HbL_{22} = 206.6 (188–225), TL_{20} = 55.8 (47–67), HfL_{22} = 34.6 (32.7–36.1), E_{22} = 9.0 (8.1–10.2), W_{15} = 190.7 (134–235), CbL_{23} = 41.6 (39.4–45.2), ZgB_{22} = 28.4 (27.2–29.5), MxT_{23} = 9.2 (8.1–10.0) (Kryštufek 1993).

Geographic range (Fig. 11C). A small (<2000 adult individuals), relict population restricted to high-altitudinal pastures (1500–2250 m a.s.l.) on Mts. Jakupica-Karadjica in central Macedonia (Kryštufek et al. 2012).

Spermophilus taurensis Gündüz, Jaarola, Tez, Yeniyurt, Polly et Searle, 2007 – Taurus souslik

2007 *Spermophilus taurensis* Gündüz, Jaarola, Yeniyurt, Polly et Searle. Type locality: "Akseki, Yarpuz (37.08° N, 31.53° E) 111 km E of the city of Antalya, Turkey ... Altitude: 1542 m above sea level."

2007 *Spermophilus torosensis* Özkurt, Sözen, Yiğit, Kandemir, Çolak, Gharkheloo et Çolak. Type locality: "Turkey, Antalya, Akseki, Çatılıçukur village, Eşekçukuru area of Salamut Plateau on the Taurus Mts, (36.90823E, 31.96114N, 1879 m)". Predated by *taurensis* (Gündüz et al. 2007b).

Remarks. A multigenic assessment placed *S. taurensis* in a sister position to *S. citellus*; the divergence time estimate between the two species (2.5 Mya; Gündüz *et al*. 2007a) predates the Quaternary glacial dynamics.

Description. A short-eared souslik of about same size and external proportions as *S. citellus*; soles are hairy. Tail is wider and longer as compared to *S. xanthoprymnus*. Dorsum is light reddish brown, grey washed in some individuals, but more reddish than in *S. citellus* or *S. xanthoprymnus*, unspeckled; gray to whitish underside is buff washed. The tail is reddish, paler below than above, and blackish towards the tip (Fig. 13). The overall skull morphology resembles more closely *S. xanthoprymnus* than *S. citellus* (Gündüz et al. 2007a). Rostrum is short, heavy and blunt, nasals are broad, the interpterygoid vacuity is wide, bullae are globular. Supratemporal ridges do not fuse into a crest. Teeth show no peculiarities; number of alveoli same as in *S. citellus* (Özkurt et al. 2007). Dimensions (in mm; W in grams; 3 females): HbL = 201, 194, 200, TL = 64, 62, 65, HfL = 43, 39, 44, E = 6, 7, –, W = 200.7, 260, –, CbL = 44.5, 41.5, –, ZyB = 29.3, 28.5, –, MxT = 9.3, 9.9, – (Gündüz et al. 2007a, Özkurt et al. 2007, PMS specimen). Karyotype: 2n = 40 (Gündüz et al. 2007a, Özkurt et al. 2007, Arslan & Arslan 2010).

Fig. 13. Taurus souslik *Spermophilus taurensis* (near Yarpuz, Akseki, Turkey; photo by Václav Gvoždík).
Obr. 13. Sysel taurský *Spermophilus taurensis* (nedaleko Yarpuz, Akseki, Turecko; foto Václav Gvoždík).

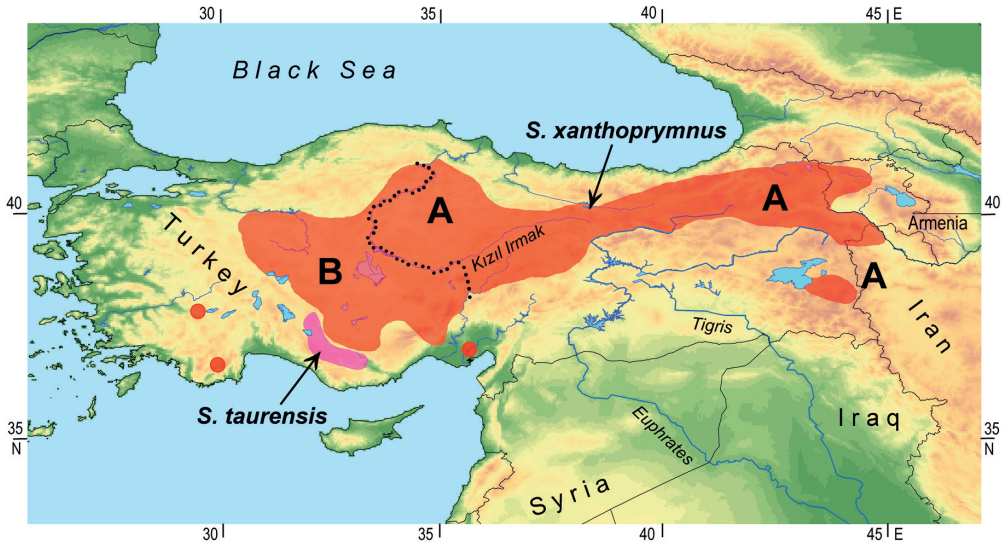


Fig. 14. Ranges of *Spermophilus taurensis* and *S. xanthoprymnus*. Range of *S. taurensis* is based on localities in Gündüz et al. (2007a), Özkurt et al. (2007), and Arslan & Arslan (2010). Distribution of *S. xanthoprymnus* was compiled from Kryštufek & Vohralík (2005), Gündüz et al. (2007a), and Özkurt et al. (2007). Subspecies of *S. xanthoprymnus* are delimited by a dotted line: A – *S. x. xanthorpymnus*; B – *S. x. gelengius*.

Obr. 14. Areály rozšíření *Spermophilus taurensis* a *S. xanthoprymnus*. Areál *S. taurensis* je založen na lokalitách, které publikovali Gündüz et al. (2007a), Özkurt et al. (2007) a Arslan & Arslan (2010). Rozšíření *S. xanthoprymnus* bylo zkompilováno z publikací Kryštufek & Vohralík (2005), Gündüz et al. (2007a) a Özkurt et al. (2007). Areály poddruhů *S. xanthoprymnus* jsou ohraničeny tečkovanou čarou: A – *S. x. xanthorpymnus*; B – *S. x. gelengius*.

Geographic range (Fig. 14) restricted to the Taurus Mts., from Erenkaya (Meram) in the north, to Morca Yaylası (Çukurköy, Akseki) in the south, and from the Salamut Plateau in the west, to Mut (Mersin) in the east. *S. taurensis* is allopatric with respect to *S. xanthoprymnus*. The species inhabits rocky areas with shallow soil layer and sparse vegetation above 1,500 m of elevation (Özkurt et al. 2007).

Subspecies. A monotypic species.

Spermophilus xanthoprymnus (Bennett, 1835) – Anatolian souslik

1835 *Citillus xanthoprymna* Bennett. Type locality: "Erzeroun" (= Erzurum), Turkey.

1908 *Citellus schmidti* Satunin. Type locality: "Digor', Karsskaâ oblast / Digor, Prov. Kars" (Satunin 1908a), Turkey.

1965 *Citellus citellus gelengius* Mursaloğlu. Type locality: "from a mea dow (sic!) extending on and South of a small hill, 5 Km. East of Koçaş, Devlet Üretme Çiftliği, Aksaray, Niğde", Turkey. This name is overlooked in Thorington & Hoffmann (2005).

1965 *C.*[*itellus*]*x.*[*anthoprymnus*] *arzniensis* Gromov et Dahl (in Gromov et al. 1965: 239). Type locality: "pravij bereg r. Zangi u sel. Arzni (Kotajkskij rajon Armjanskoj SSR)" (= right bank of the river Zangi near the village of Arzni [Kotajk District, Armenian Soviet Socialist Republic], Armenia). From the "rannij golocen" (= Early Holocene).

Remarks. Frequently reported in the past as a subspecies of *S. citellus* (e.g. Corbet 1978).

Description. A short-eared souslik with no special modifications. Size as in *S. citellus*, but the tail is shorter (on average about 20% HbL). Back is uniform reddish buff (less redish than in *S. taurensis*); colour varies from nearly greyish to dark brown with hardly any yellowish tinges; back is not speckled. Flanks are cream, whitish or yellow, and the belly is whitish or yellowish. Throat and chin are frequently pure white. The eye ring is whitish (Fig. 15). The tail is of about the same colour as back and lacks dark hairs. Feet are pale, whitish or yellowish. Females have 10 nipples: 1 pectoral, 2 abdominal, and 2 inguinal pairs, respectively (Satunin 1928). Skull is quite angular in dorsal view (Fig. 16). The anterior edges of zygomatic arches frequently form

Fig. 15. Anatolian souslik *Spermophilus xanthoprymnus* (Kayseri, Turkey; photo by Irena Schneiderová).
Obr. 15. Sysel maloasijský *Spermophilus xanthoprymnus* (Kayseri, Turecko; foto Irena Schneiderová).

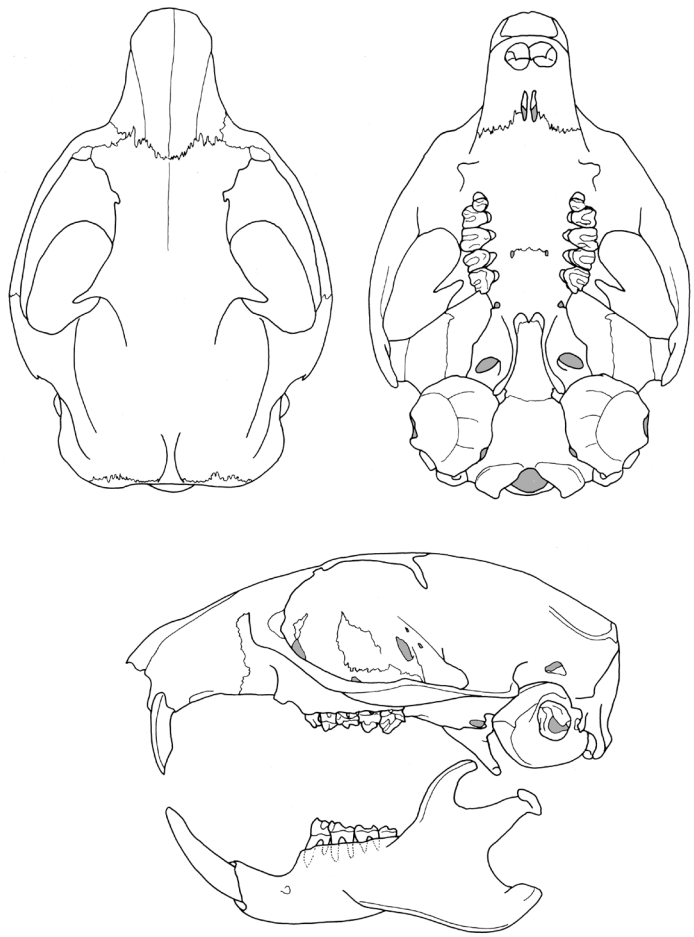


Fig. 16. Skull and mandible of *Spermophilus xanthoprymnus* (adult male from Sivrihisar, Eskişehir, Turkey; PMS 10781).
Obr. 16. Lebka a mandibula *Spermophilus xanthoprymnus* (adultní samec z lokality Sivrihisar, Eskişehir, Turecko; PMS 10781).

an almost right angle at its junction with the rostrum. The interorbital region is slightly broader than in the European souslik (interorbital constriction up to 26% of condylobasal length, as opposed to maximally 22.5% in *S. citellus*). The nasals are blunt at the apex. Bullae are relatively shorter and more rounded than in the European souslik, the upper incisors are weaker, and the nasals are blunt at their apex. Teeth are essentially as in *S. citellus* but the lower premolar retains 3 roots. The baculum is essentially of the same shape and size as in *S. c. citellus* (Kaya & Şimşek 1986). Dimensions (in mm; W in grams): HbL = 170–257, TL = 30–72, HfL = 31–45,

E = 5.5–16, W = 180–325 (before hibernation up to 495), CbL = 36.7–48.6, ZgB = 25.5–33.0, MxT = 8.7–10.7. Karyotype: 2n = 42 (Arslan 2005).

Geographic range (Fig. 14). Nearly endemic to Turkey (Kryštufek & Vohralík 2005), crossing the country borders only slightly in Armenia (Alagez region; Šidlovskij 1976) and extreme north-western Iran (27 km north-west of Makü; Özkurt et al., 2007). The bulk of the range is in central Anatolian highland, with several putative isolates: east of Lake Van and Çukurova plain near Adana (Kryštufek & Vohralík 2005); report for Teke peninsula requires confirmation (Gür & Gür 2010). Most of the records are from elevations above 800–900 m a. s. l. (Kryštufek & Vohralík 2005), and up to 2900 m (Gür & Gür 2010). Regions of Anatolia inhabited by *S. xanthoprymnus* are drier and colder than other parts of Turkey, suggesting that species' distribution is determined, at least partly, by climate, especially summer precipitation (Gür & Gür 2010). *S. xanthoprymnus* was erroneously reported for Syria and Jordan (Thorington & Hoffmann 2005). This statement, which dates back to Tristram (1885), most likely results from confusion with a diurnal *Psamomys obesus* (Kock 1998). During the 20th century, sousliks did not occur south of the Taurus Mts. (Lewis et al. 1967). Range, however, was more extensive during the Early Holocene and encompassed also Mesopotamia (now Iraq); ground squirrels (reported as *S. citellus*) are part of a pre-pottery Neolithic (about 9,500 ya) faunal assemblage of Göbekli Tepe near Şanliurfa (Peters & Schmidt 2004).

Anatolian sousliks inhabit dry stony and degraded short-grass steppes in arid landscape (mainly <500 mm of precipitation annually). In Central Anatolia, they are active from March through August–September, and hibernate during the remaining months (Gür & Gür 2005).

Subspecies. Cytochrome *b* haplotypes of Anatolian sousliks clustered into two deeply divergent allopatric lineages (Gündüz et al. 2007a). These lineages contain 5 phylogroups which are largely sympatric, possibly due to a secondary admixture of allopatrically evolved groups, or to introgresive hybridization, or both. In contrast to phylogroups, the overlap between the two major lineages is very marginal hence we classify them as distinct subspecies. The type locality for the Early Holocene form *arzniensis* is within the current range of the nominotypical subspecies, but we refrain from formally synonymizing the subfossil form.

Spermophilus xanthoprymnus xanthoprymnus (Bennett, 1835)

Synonym. *schmidti*.

Description. Contains cytochrome *b* phylogroups nos. 1, 2, and 3 (sensu Gündüz et al. 2007a). Dimensions (in mm; W in grams): Mt. Erciyes Dağ near Kayseri (central Anatolia), males: HbL_{15} = 201.3 (180–222), TL_{15} = 37.4 (30–50), HfL_{15} = 37.5 (34–41), E_{15} = 13.6 (11–16), CbL_{11} = 41.7 (39.3–43.9), ZgB_{10} = 28.3 (26.8–29.4), MxT_{13} = 9.4 (8.9–10.0); females: HbL_{16} = 193.4 (170–210), TL_{15} = 38.4 (30–50), HfL_{16} = 35.5 (31–40), E_{16} = 12.2 (8–15), CbL_{13} = 39.7 (36.7–41.8), ZgB_{13} = 27.5 (25.5–28.8), MxT_{15} = 9.4 (8.7–10.2) (Kryštufek & Vohralík 2005). Erzurum, males: $HbTL_{13}$ = 273.5 (265–289), TL_{13} = 48.2 (42–52), HfL_{13} = 41.8 (40–43), E_{13} = 10.6 (8–13), CbL_{13} = 47.4 (46.4–48.6), ZgB_{13} = 31.2 (29.2–33.0); females: $HbTL_{18}$ = 255.8 (245–275), TL_{18} = 44.2 (38–50), HfL_{18} = 40.3 (38–42), E_{18} = 10.5 (7–13), CbL_{18} = 42.8 (41.0–44.3), ZgB_{17} = 29.4 (27.3–30.6) (Mursaloğlu 1965).

Geographic range (Fig. 14A). The eastern part of the species' range, to the east of the river Kizil Irmak. Marginal records are (north-to-south): Sungurlu, Kavşat – Çiçekdağ, Kırdök Köyü, Yozgat – Yenifakili, Sivas – Erciyes – Yeşilhisar, Gülbayir, Dörtyol (Gündüz et al. 2007a). Possibly overlaps and intergrades with ssp. *gelengius* between Yeşilhisar and Kayseri.

Spermophilus xanthoprymnus gelengius (Mursaloğlu, 1965)

Description. Contains cytochrome *b* phylogroups nos. 4 and 5 (sensu Gündüz *et al*. 2007a). Dimensions (in mm; W in grams): Niğde (type series), males: $HbTL_{14}$ = 260.4 (248–281), TL_{14} = 46.8 (39–58), HfL_{14} = 40.9 (38–45), E_{14} = 9.4 (7–12), CbL_{13} = 42.6 (40.2–45.0), ZgB_{14} = 29.6 (27.2–31.9); females: $HbTL_{14}$ = 247.0 (231–260), TL_{14} = 41.5 (31–54), HfL_{14} = 39.0 (36–42), E_{14} = 8.4 (6–11), CbL_{14} = 41.3 (36.8–42.7), ZgB_{14} = 28.9 (27.6–29.6) (Mursaloğlu 1965).

Geographic range (Fig. 14B). The western part of the species' range, to the west of the river Kızıl Irmak. Marginal records are (north-to-south): Dede Köyü, Çorum – Akçaali Köyü, Çankırı – Boğazköy – Erkilet – Eğribucak Köyü – Gülşehir, Aksaray – Yeşilhisar, Araplı Köyü, Nevşehir – Edikli – Bereket Köyü – Ulukişla, Maden Köy (Gündüz et al. 2007a).

Spermophilus suslicus (Güldenstaedt, 1770) – Spotted souslik

1770 *Mus suslica* Güldenstaedt. Type locality: "campis vastissimus tanaicensibus precipue urbes Woronesch et Tambov" (= extensive plains, particularly around cities of Voronež and Tambov) (Ognev 1947). "Voronej steppes" (Ellerman & Morrison-Scot 1951); "Voronežskaâ obl." (= Voronež Region) (Pavlinov & Rossolimo 1987), Russia.

1770 *Mus citillus* var. *guttatus* Pallas. Type locality: "Dolina r. P'âny i Sury, Srednee Povolž'e" (= River valleys of P'âna and Sura, middle section of the Volga) (Ognev 1947), "Gor'kovskaâ obl. i Čuvašskaâ ASSR" (= Gor'kij [= today's Nižnij Novgorod] Region and Čuvaš [= Chuvashia] Republic) (Pavlinov & Rossolimo 1987), Russia.

1792 *Arctomys citellus leucopictus* Donndorff. Renaming of *Mus citillus guttatus* Pallas, 1770 (Ellerman & Morrison-Scott 1951).

1842 *Spermophilus citellus* var. *odessana* Nordmann. Type locality: "Odessa, Ukraine" (Ellerman & Morrison-Scot 1951).

1845 *Spermophilus guttulatus* Schinz. New name for *Mus citillus guttatus* Pallas, 1770.

1927 *Citellus suslicus averini* Migulin. Type locality: "Russkaâ Lozovaâ (= Ruska Lozova; misspelled as "Russka Lesonia" in Ellerman & Morrison-Scott 1951), Har'kovskogo okruga (= Harkov Region)" (Ognev 1947), "Russka Lesonia, 18 km north of Kharkov" (Ellerman & Morrison-Scot 1951), Ukraine.

1927 *Citellus suslicus meridio-occidentalis* Migulin. Type locality: "Environs of Odessa" (Ellerman & Morrison-Scott 1951), Ukraine. Incorrectly spelled as "*meridioccidentalis*" (Ellerman & Morrison-Scot 1951) or "*meridiocidentalis*" (Thorington & Hoffmann 2005).

1946 *Citellus suslica volhynensis* Reshetnik. Type locality: "Environs of Olyki, Volhyn region on borders of Polesie and the woodland steppe, between Luck and Rovno, Eastern Poland" (Ellerman & Morrison-Scott 1951). Olyki is now in Volynsk Region, Ukraine.

1946 *Citellus suslica ognevi* Reshetnik. Type locality: "Environs of Kishinev, Rumanian Bessarabia" (Ellerman & Morrison-Scott 1951), now in Moldova.

1958 *Citellus suslica boris thenicus* (sic!) Puzanov. Type locality: "meždureč'e Buga i Dnestra" (= between the rivers Bug and Dniester) in Ukraine.

Remarks. For details on type localities and type specimens see Zagorodniuk & Fedorchenko (1995). *S. suslicus* hybridize with *S. citellus* (Gromov & Erbajeva 1995), *S. major* (Ermakov et al. 2002), and *S. pygmaeus* (Ermakov et al. 2006a). Hybridization is frequent (about half of sousliks being hybrids) in the contact zone with *S. pygmaeus* (Denisov 1961).

Description. Smaller souslik with short tail (15–25% HbL) and distinctly spotted fur pattern (Fig. 17). Soles are hairy from heel to pads. Back is brownish-grey, tawny russet or russet chestnut-brown, clouded by blackish hair tips; sides are pale cream-buff, underside is bright

buff; demarcation along flanks is fairly abrupt. Tail is grizzle of blackish and buff above, russet below, and fringed with cream. Dorsal side from nape to tail base is thickly marked with whitish to buff-white roundish spots (2–5 mm in diameter; 3–5 spots per cm^2; Calinescu 1934). Spots are most sharply defined along the spine, less so along the flanks; head is covered with tiny speckles and flecks. Muzzle, cheeks and feet are cream-buff; eye ring is distinctly cream-whitish and is surrounded with an incomplete rusty ring. Southern populations tend to be paler and northern populations are in general darker. Females have 12–14 nippels (Artemev 1965). Skull and teeth are very similar to *S. citellus* (Fig. 18); zygomatic arches are moderately expanded (ZgB ≈ 67.6% CbL; Ognev 1947); incisive foramens are very short, interpterygoid vacuity is narrow; cheek-teeth are shorter than diastema. Number of roots (maxillary / mandibular): 1, 3, 3, 3, 3 / 3, 4, 4, 4 (Niethammer 1978). Females have 5 pairs of nipples (1 pectoral, 2 abdominal and 2 inguinal; Calinescu 1934). Baculum is on average 2.6 mm long, with small globular ventral medial knob; anterior margin of triangular spatula is edged with 11–12 denticles (Rešetnik & Balahnin 1967). Dimensions (in mm; W in grams): HbL = 170–240 (mainly <220), TL = 25–50, HfL = 27–36, E = 5–10, W = 120–440, CbL = 36.8–44.2, ZgB = 24.6–32.2, MxT = 8.3–11.6. Karyotype is polymorphic: 2n = 34 or 2n = 36; the two cytotypes are separated by the river Dniepr (Korablev 1994, Zagorodniuk & Fedorchenko 1995).

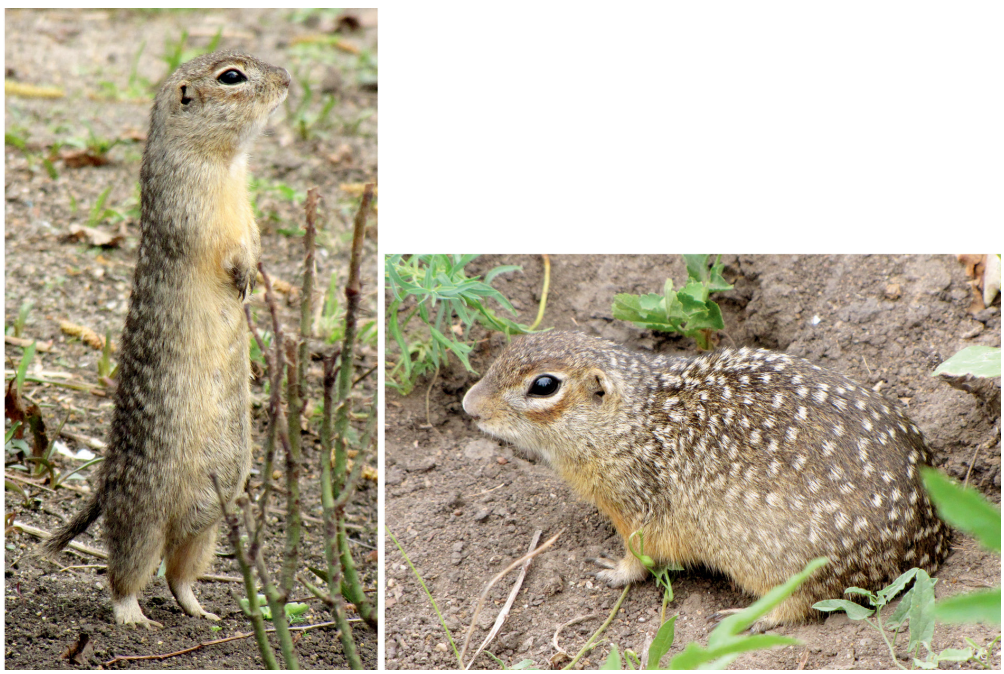


Fig. 17. Spotted souslik *Spermophilus suslicus* (near Lipeck, Russia; photo by Ilya Volodin & Elena Volodina).
Obr. 17. Sysel perličkový *Spermophilus suslicus* (blízko Lipecka, Rusko; foto Ilya Volodin & Elena Volodina).

Geographic range (Fig. 19). Steppes and southern edge of the forest-steppe zone, between the rivers Prut – Dniestr and Volga. The range encompasses Moldova, south-eastern Poland, Belarus, Ukraine and Russia. The range border was dynamic over the last centuries with expansions in the 19th century and a decline in the 20th century. *S. suslicus* occupied the north-eastern part of its range (Tatarstan) in the mid-19th century (Ognev 1947, Gorškov 2006). During the 20th century the northern border of contiguous range followed the line Kazan (where still unknown in the late 19th century; Popov 1960) – river Oka – Brjansk – Chernigov (north of Kiev) – north-west of Czernovits; southern border was on the line Saratov – Lugansk – Kharkov – lower flow of Dniepr – Black Sea coast. During the 20th century, the spotted souslik still occupied some islands on Volga in Tatarstan (Ognev 1963) where now extinct (I. Askeev, in litt.). Currently, the spotted souslik does not approach closely the right bank of the river Volga, and majority of the esternmost records are to the west of river Svijlaga (Titov 2001). The past range was more extensive also in the west, and during the Holocene *S. suslicus* still occupied Romania where now absent (Lozan 1971). Several isolates occur along the western margin of distribution in Ukraine (Volynsk highland; Biedrzycka & Radwan 2008, Meżżerin 2009b), Belarus (during 1950s still present between the Baranoviči and Sluck Regions, to the nort of the river Pripât; Seržanin 1961, Savickij et al. 2005), and Poland (Lublin Upland; Surdacki 1983b, Próchnicki 2008). A human caused shrink in distributional range started in 1940s and 1950s throughout the entire range (e.g. Lozan 1970, Surdacki 1963, Titov 2001). From 1950s to 1970s the southern border shifted northwards due to range expansion of ecologically more plastic *S. pygmaeus*; the two species are strictly allopatric (Popov 1960, Denisov 1961, Šlâhtin et al. 2009). Population decline was most sharp in 1980s; e.g. in western Ukraine populations declined by about 30% in the early 1990s. Although population crash primarily resulted from direct persecution and

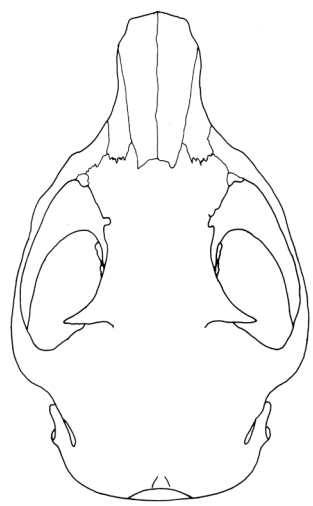


Fig. 18. Skull (dorsal view) of *Spermophilus suslicus* (adult female from Lublin district, Poland; NMW 38487).
Obr. 18. Lebka (dorsalní pohled) *Spermophilus suslicus* (adultní samice z vojvodství Lublin, Polsko; NMW 38487).

Fig. 19. Distribution of *Spermophilus suslicus* in the 20th century when the most extensive. Compiled from the following sources: the overall range – Ognev (1947), Zagorodnyuk et al. (2008), Titov & Ermakov (not dated); Belarus – Seržanin (1961), Savickij et al. (2005); Moldova – Calinescu (1934), Savin et al. (2012); Poland – Surdacki (1983b); Russia – Popov (1960), Denisov (1961), Titov (2001), Večkanov et al. (2004), Šlâhtin et al. (2009); Ukraine – Zagorodniuk & Fedorchenko (1995), Biedrzycka & Konopiński (2008), Meždžerin (2009b). Subspecies are delimited by a dotted line: A – *S. s. suslicus*; B – *S. s. odessanus*.
Obr. 19. Rozšíření *Spermophilus suslicus* ve 20. stol., v době kdy byl jeho areál nejrozsáhlejší. Zkompilováno z následujících pramenů: celkový areál – Ognev (1947), Zagorodnyuk et al. (2008), Titov & Ermakov (nedatováno); Bělorusko – Seržanin (1961), Savickij et al. (2005); Moldávie – Calinescu (1934), Savin et al. (2012); Polsko – Surdacki (1983b); Rusko – Popov (1960), Denisov (1961), Titov (2001), Večkanov et al. (2004), Šlâhtin et al. (2009); Ukrajina – Zagorodniuk & Fedorchenko (1995), Biedrzycka & Konopiński (2008), Meždžerin (2009b). Areály poddruhů jsou ohraničeny tečkovanou čarou: A – *S. s. suslicus*; B – *S. s. odessanus*.

landscape transformation, climate change might also contributed (Lobkov 2006). Despite of some recovery in recent years, the range remains to be fragmented and the colonies are mainly small and widely apart (Titov 2001, Shekarova et al. 2008). In any case, habitat loss depleted the genetic diversity in the western part of range (Biedrzycka & Konopiński 2008).

In early 20th century, *S. suslicus* was parapatric with *S. citellus* in a triangle Zastavna – Cozmeni – Boian between the rivers Prut and Dniestr (Calinescu 1934). Afterwards, *S. citellus* putatively competitively excluded the spotted souslik and expanded soutward (Lozan 1970). Despite this, *S. suslicus* is still widespread in Moldova (Savin et al. 2012). Zone of sympatry (over 100 km wide) with *S. major* emerged in 1990s on the western bank of Volga. The two sousliks are distributed in a mosaic way, with *S. major* preferring arid habitats and *S. suslicus* preferring mesic sites (Titov 2000). Ranges of *S. suslicus* and *S. pygmaeus* are mutually exclusive and *S. pygmaeus*

outcompet the spotted souslik (Denisov 1961). *S. suslicus* possibly invaded the current range in the east during the Holocene. In the Late Pleistocene the area was occupied by the extinct *S. severskensis* (Gromov, 1965) (in Gromov et al. 1965)which is not a likely ancestor to *S. suslicus* (Popova 2010). On the other hand, the spotted souslik was abundant in Ukraine already in the Middle Pleistocene (Krohmal' & Rekovec 2010) and continuously occupied Moldova during the Upper Pleistocene (Lozan 1971).

S. suslicus inhabits grasslands with low vegetation, pastures, fallow fields and other poorly harnessed land, preferably on chernozem clayey or loamy subsoil (Petrovsky 1961, Ognev 1963), invariably at low elevations (<500 m). Hibernates from September – early October to late January – mid-April (Seržanin 1961); locally sousliks aestivate during peak summer drought (e.g. Popov 1960). In Russia, the active period is 70–130 days annualy (Artemev 1965).

Spotted sousliks from Ukraine were translocated to the Caucasus, where a colony was present in 1969 on the eastern slopes of Mt. Elbruz at the elevation of 3000 m (Knorre 1977, Korablev et al. 1991).

Subspecies. Two subspecies were traditionally recognized on the basis of colour: the northern *S. s. guttatus* (darker) and the southern *S. c. suslicus* (paler); for differences see colour plate next to page 160 in Ognev (1947). The reality of these two subspecies was repeatedly questioned (e.g. Popov 1960) and they doubtfuly represent distinct phylogenetic lineages; Titov (2001) plotted the border between them on the line: river Medvedica – Penza (about 45° E longitude).

The two chromosomal forms, separated by the river Dniepr, are treated as distinct species by some authors (e.g. Zagorodnyuk & Fedorchenko 1995, Tsvirka et al. 2003). Allozyme divergence between these two cytotypes (Nei D = 0.115) is below the threshold normally observed between species of *Spermophilus* and only two loci of total 25 were discriminative (Frisman et al. 1999, Frisman 2008). We rank these lineages as distinct subspecies (cf. also Grimmbergerer & Rudloff 2009).

Spermophilus suslicus suslicus (Güldenstaedt, 1779)

Synonyms. *guttatus*, *guttulatus*, *averini*.

Description. 2n = 34; fundamental number of autosomal arms (NFa) varies and the two cytotypes which differ in this trait, were classified as distinct subspecies NFa = 68 (ssp. *averini*) and NFa = 64 (ssp. *guttatus*; Vorontsov & Lâpunova 1969). Cheek-teeth on average longer (MxT_{21} = 9.93 mm ± 0.34 standard deviation; Zagorodniuk 2004); fur tends to be darker with more distinct spots (Zagorodniuk & Fedorchenko 1995). Dimensions (in mm; W in grams) (Tatarstan, Russia), males: HbL_{39} = 223 (190–260), TL_{39} = 35.5 (28–47), HfL_{39} = 34.2 (31–37), W_{39} = 269 (161–440); females: HbL_{60} = 215 (180–245), TL_{60} = 34.8 (25–45), HfL_{60} = 33.7 (30–38), W_{60} = 229 (138–340); (sexes pooled in cranial dimensions): CbL_{109} = 39.9 (38.7–41.3), ZgB_{109} = 26.9 (25.6–28.3), MxT_{109} = 9.6 (9.0–9.9) (Popov 1960).

Geographic range (Fig. 19A). Eastern portion of the range (to the east of the river Dniepr) in eastern Ukraine and Russia (Zagorodniuk & Fedorchenko 1995, Zagorodniuk 2002).

Spermophilus suslicus odessanus Nordmann, 1842

Synonyms. *meridiooccidentalis*, *volhynensis*, *ognevi*, *boristhenicus*.

Description. 2n = 36. Cheek-teeth on average shorter (MxT_{81} = 9.21 mm ± 0.34 standard deviation; Zagorodniuk 2004); fur tends to be paler with smaller spots (Zagorodniuk & Fe-

DORCHENKO 1995). Dimensions (in mm; W in grams) (Moldova and Poland), males: HbL_{90} = 201.9 (170–226), TL_{90} = 42.2 (29–54), HfL_{90} = 33.4 (30–39.5), E_7 = 7.6 (6.5–9), W_{82} = 248.5 (170–367), CbL_{32} = 42.7 (39.2–45.0), ZgB_{33} = 28.1 (25.2–30.6), MxT_9 = 8.6 (8.2–9.2); females: HbL_{82} = 199.1 (163–220), TL_{82} = 41.8 (29–53), HfL_{82} = 32.7 (28–37), E_4 = 7.3 (7–7.5), W_{78} = 231.7 (165–315), CbL_{35} = 41.2 (35.0–43.0), ZgB_{35} = 27.3 (22.8–29.1), MxT_7 = 8.3 (7.7–8.8) (CALINESCU 1934, SURDACKI 1958).

GEOGRAPHIC RANGE (Fig. 19B). Western portion of the range (to the west of river Dniepr) in Moldova, Poland, Belarus and western Ukraine (ZAGORODNIUK & FEDORCHENKO 1995, ZAGORODNIUK 2002).

Spermophilus alaschanicus Büchner, 1888 – Alashan souslik

1888 *Spermophilus alaschanicus* Büchner. The name of the authority was originally printed in Cyrillic characters (Бихнер) which transliterates to "Bichner" (e.g. OGNEV 1947, GROMOV et al. 1965, BARANOVA & GROMOV 2003), but "Büchner", also used in the original paper (BICHNER 1888), is quoted in the West (e.g. THORINGTON & HOFFMANN 2005). Type locality: "southern Alashan, Mongolia" (ALLEN 1940, ELLERMAN & MORRISON-SCOTT 1951). Southern Alashan is located in Nei Mongol, China.

1888 *Spermophilus obscurus* Büchner. For proper spelling of the authority name cf. the above comment under *Spermophilus alaschanicus*. Type locality: "north of Tschagryn-gol" (ALLEN 1925), Kansu, China.

1929 *Citellus alaschanicus dilutus* Formozov. Type locality: "Ihè-Bogdo, Mongol'skij Altaj" (OGNEV 1947); "Ihe Bogdo, Mongolian Altai" (ELLERMAN & MORRISON-SCOTT 1951), Mongolia.

Fig. 20. Skins (in dorsal view) of: a – *Spermophilus alaschanicus* (Qinghai Province, China; SMG M7833); and b – *S. dauricus* (near Bayan-Onjuul, Mongolia; SMG M6705).
Obr. 20. Balky (dorsální pohled): a – *Spermophilus alaschanicus* (provincie Qinghai, Čína; SMG M7833); b – *S. dauricus* (nedaleko Bayan-Onjuul, Mongolsko; SMG M6705).

Fig. 21. Alashan souslik *Spermophilus alaschanicus* (Mongolia; photo by Michael & Anne Stubbe).
Obr. 21. Sysel alašanský *Spermophilus alaschanicus* (Mongolsko; foto Michael a Anne Stubbeovi).

Remarks. Occassionaly synonymized with *dauricus* (e.g. Allen 1940, Zhang et al. 1997), but mainly considered to be a species on its own right (e.g. Obolensky 1927). Hybridize with *S. erythrogenys pallidicauda*; hybrids are fertile and capable of backcrossing (Korablev et al. 2006, Tsvirka et al. 2006b).

Description. A small souslik with a tail of moderate length (29.5–41.6% HbL, mean = 35%) and with hairy soles of hind foot. Dorsal fur is pinkish-buff to dark sandy in colour, occassionally with a grey, wood-brown or sandy-yellow tinge. Although slightly darkened by black hair tips, pelage is not speckled (Figs. 20a, 21). Head of same colour as back, snout is occasionally rusty, eye ring is white or light greyish, fairly indistinct; there is a light rusty spot below the eye; cheecks and flanks are lighter, pale buffy-white, olive-buff, rusty yellow or pinkish cinnamon; chin and throat are whitish in some populations. Belly is light yellowish to ochraceous, clouded with grey underfur. Paws are yellowish white to buff grey. Proximal tail is like back, distal part is more pinkish-cinnamon, with blackish-brown subterminal band; tail tip is margined with yellow-whitish hairs. Ventrally the tail is cinnamon-buff, pinkish-cinnamon, or distinctly rusty. Females have 8 (exceptionally 9) nipples (Stroganova & Chu-Tsing 1961). Skull is narrow (ZgB = 64.1–67.9% CbL; mean = 66.0%), the anterior edge of the zygoma forms a smooth curve. Interorbital region is wide (mean = 9.4 mm), postorbital processes are weak; supratemporat ridges do not form saggital crest. Skull is evenly convex in profile, except for the nasal region which is lifted upward. Bullae are elongate, longer than wide. Upper premolars are relatively large for the genus (Fig. 22). Dimensions (in mm; W in grams; sexes pooled): HbL_{27} = 197.7 (174–233), TL_{28} = 67.7 (55–87), HfL_{27} = 36.8 (30–43), E_{25} = 8.1 (6–12), W_{13} = 204.2, (162–370), CbL_{29} = 44.1 (39,6–45.6), ZgB_{36} = 27.9 (25.5–30.1), MxT_{36} = 10.2 (9.2–11.0) (Allen 1940, Ognev 1963, Stroganova & Chu-Tsing 1961, Tinnin et al. 2002, specimens in AMNH, ZISP, SMG, and ZMB). Karyotype: 2n = 38 (Orlov et al. 1978, Tsvirka et al. 2006b).

Geographic range (Fig. 23) is in two fragments: the north-eastern edge of Gobi Altai Mountain Range in Mongolia (Bannikov 1954, Sokolov & Orlov 1980) and Ala-Shan Mts. and Nan--Shan Mts. in north-central China (Tinnin et al. 2002). Zhang et al. (1997) did not distinguish between *dauricus* and *alaschanicus* and distributional details were never revised in China.

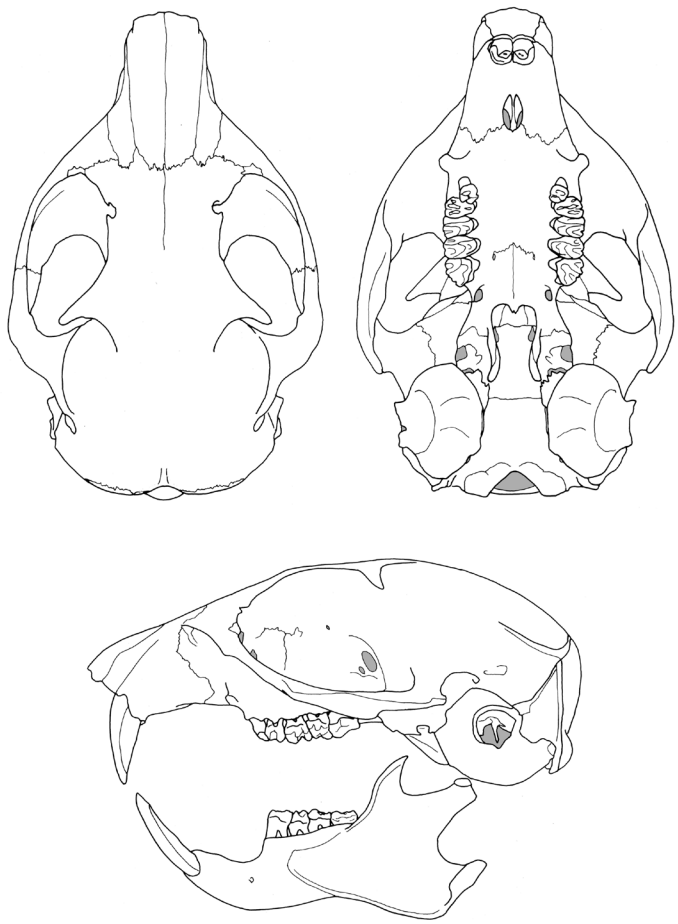


Fig. 22. Skull and mandible of *Spermophilus alashanicus* (adult female from Ich Bogd, Mongolia; ZMB 62177).
Obr. 22. Lebka a mandibula *Spermophilus alashanicus* (adultní samice z lokality Ich Bogd, Mongolsko; ZMB 62177).

Maps by Smith & Xie (2008) presume a wide sympatry of these two sousliks and are evidently erroneous. Although there seems to be some overlap in Shaanxi and Shanxi (Bannikov 1954), Ningxia and Gansu are reportedly inhabited only by *S. alaschanicus* (Xu 1997). Panteleyev (1998) mapped ranges of these two sousliks as separated by the Yellow River, which we follow.

In Mongolia, typical habitats are slopy steppes with *Stipa* and *Artemisia* at high altitude (c. 3100–3200 m a. s. l.) (Bannikov 1954); in China (Ala-Shan Mts. and Nan-Shan Mts.) reported from the mountain steppes till the altitude 3500–3800 m (Gromov et al. 1965).

Fig. 23. Ranges of *Spermophilus alaschanicus* and *S. dauricus*. Range of *S. alaschanicus* was compiled from the following sources: overall range – Panteleyev (1998); China – Zhang et al. (1997); Mongolia – Bannikov (1954), Sokolov & Orlov (1980). Distribution of *S. dauricus* is based on: overall range – Panteleyev (1998); China – Zhang et al. (1997); Mongolia – Bannikov (1954); specimens in SMG; Russia – Flint et al. (1965).
Obr. 23. Areály rozšíření *Spermophilus alaschanicus* a *S. dauricus*. Areál *S. alaschanicus* byl zkompilován z následujících pramenů: celkový areál – Panteleyev (1998); Čína – Zhang et al. (1997); Mongolsko – Bannikov (1954), Sokolov & Orlov (1980). Rozšíření *S. dauricus* je založeno na pramenech: celkový areál – Panteleyev (1998); Čína – Zhang et al. (1997); Mongolsko – Bannikov (1954), exempláře v SMG; Rusko – Flint et al. (1965).

Subspecies. Allen (1940) recognized two subspecies, *alaschanicus* and *obscurus* (with *dilutes* as a junior synonym) on basis of colour. There is no evidence of discontinuity and geographic variation was never comprehensively assessed. Sousliks from desert regions tend to be paler.

Spermophilus dauricus Brandt, 1844 – Daurian souslik

1844 *Spermophilus dauricus* Brandt. Type locality: "Circa Torei lacum exciccatum Dawuriae et ad Onon Bursa rivum" (Ognev 1947); "based on Pallas's account of a specimen taken near [Lake] Tarei-Nor in northern Mongolia" (Allen 1940), i.e. "ca. 250 miles east of Lake Baikal" (Ellerman & Morrison-Scott 1951). Type locality reported as "Torejskie ozera (= Torei Lakes), reki (rivers) Onon i Borzâ, Čitinskaâ oblast" (Baranova & Gromov 2003), Russia. With 1844 as the year of publication, we follow Ellerman & Morrison-Scott (1951) and Pavlinov & Rossolimo

(1987); 1843 is quoted in Ognev (1947), Vinogardov & Gromov (1952), Gromov et al. (1965) and Thorington & Hoffmann (2005).

1867 *Spermophilus mongolicus* Milne-Edwards. Type is from "la Mongolie chinoise et dans le voisinage de Pèkin" (Allen 1940); Thomas (1908) restricted type locality to "Suen-hwa-fu" (= Suanhwafu, Hopei [= Chihli]), China.

1908 *Citellus mongolicus umbratus* Thomas. Type locality: "Taboul (= Tabool), about 100 miles N.W. of Kalgan (today Zhangjiakou), Alt. 5000'." China.

1909 *Citellus mongolicus ramosus* Thomas. Type locality not specified, specimens were collected at "Chu Chia Tai" and "Fan Chia Tun", both in Kirin (= Jilin) Province, now Chang Chun Province, China. Ellerman & Morrison-Scott (1951) selected "Fan Chia Tun" as the type locality.

1925 *Citellus obscurus siccus* Allen. Type locality: "ten miles west of Taiyuanfu, Shansi, China". Synonymized with *S. alaschanicus* by Ognev (1947) and Thorington & Hoffmann (2005).

1939 *Citellus dauricus yamashinai* Kuroda. Type locality: "Jalamute, east of Hai-la-erh, Northern Manchuria" (= Nei Mongol, China) (Ellerman & Morrison-Scott 1951). Spelled as *yamashinae* in Thorington & Hoffmann (2005).

Remarks. Although merged with *S. alaschanicus* (Allen 1940, Corbet 1978, Zhang et al. (997), *S. dauricus* was in the past frequently considered to be species on its own (e.g. Obolensky 1927, Ognev 1947).

Fig. 24. Daurian souslik *Spermophilus dauricus* (Nei Mongol, China; photo by Wu Xiaodong).
Obr. 24. Sysel daurský *Spermophilus dauricus* (Vnitřní Mongolsko, Čína; foto Wu Xiaodong).

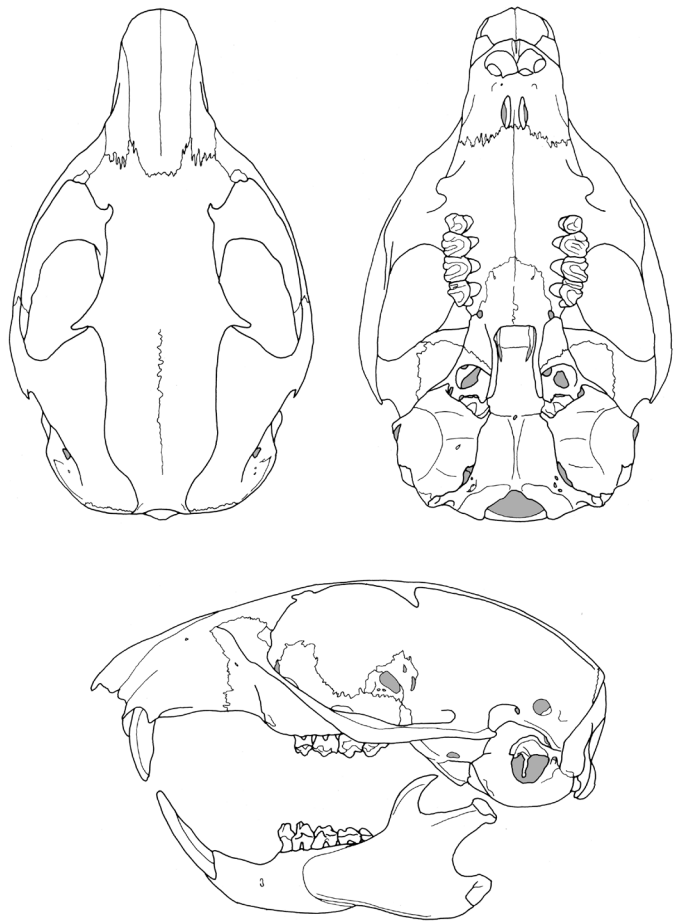


Fig. 25. Skull and mandible of *Spermophilus dauricus* (adult male from Thalai Nor, Nei Mongol, China; ZMB 1023).
Obr. 25. Lebka a mandibula *Spermophilus dauricus* (adultní samec z lokality Thalai Nor, Vnitřní Mongolsko, Čína; ZMB 1023).

Description. A small souslik with short to moderately long tail (13–40% HbL; mean = 28.6%). Soles of hind foot sparsely hairy, with indistinct, naked stripe along outer margin. Pelage is plian light brown olive, not speckled although with a greater admixture of black or black-tipped hairs. Head of same colour as back, more tawny-olive in some individuals; eye ring is pale and a whitish line extends from muzzle towards the ear. Cheeks are buffy-grey, nose is cinnamon. Ventral side is cream buff to pinkish buff, shaded by grey undercoat; chin and throat are whitish with buff tints. Flanks are yellowish-grey; paws are cinnamon buff to cream buff. Tail is of same colour as back, with more black hairs; there is a blackish subterminal band and the tip is margined whitish (Figs. 20b, 24). Summer fur is short (6–9 mm) and rather soft; winter fur is

longer (11–13 mm), softer (Ognev 1963) and lighter, pale buff dorsally, nearly white ventrally (Allen 1940). Skull without peculiarities, narrow (ZgB = 62.6–71.5% CbL; mean = 66.5%), with the zygomata sloping gradualy backward. Interorbital constriction is narrow (mean = 8.8 mm); bullae are elongate, longer than wide (Fig. 25). Cheek-teeth are rather hypsodont. Dimensions (in mm; W in grams), males: HbL_{23} = 197.0 (174–260), TL_{23} = 57.6 (35–75), HfL_{23} = 35.0 (30–38), E_{14} = 7.6 (5.0–9.0), W_5 = 202.4 (159–275), CbL_{26} = 41.7 (38.6–46.2), ZgB_{26} = 27.4 (25.6–31.1), MxT_{28} = 9.8 (8.3–10.6); females: HbL_{30} = 199.7 (178–260), TL_{30} = 59.1 (38–85), HfL_{30} = 34.0 (30.0–40.0), E_{20} = 8.2 (7.0–11.0), W_{16} = 199.8 (134–315), CbL_{34} = 40.8 (38.1–43.5), ZgB_{29} = 27.1 (25.4–29.2), MxT_{34} = 9.9 (9.1–10.7) (specimens in SZM, AMNH, NMNH, ZISP, SMG, ZMB, NMP, SMF, ZFMK); body mass is up to 425 g (Bannikov 1954). Karyotype: 2n = 36 (Liapunova & Vorontsov 1970, Voroncov & L'apunova 1974a, Li et al. 1985).

Geographic range (Fig. 23) covers eastern Mongolia (Bannikov 1954), adjacent Russia (Čitinskaâ Oblast in south-eastern Transbaikalia, southward and eastward of the River Onon; Borisova et al. 2001) and north-eastern China in Heilongjiang, eastern Nei Mongol, western Jilin, western Liaoning, Beijing, Tianjin, Hebei, and marginally Shandong, Shanxi, and possibly also Shaanxi (Zhang et al. 1997). South-western border is poorly resolved (see account on *S. alaschanicus*); SMG specimens extend range in Mongolia as west as Bayan-Onjuul. The south-eastern border is roughly on the river Hunhe. This is common rodent in noth-eastern China since the Middle Pleistocene (Zhang et al. 2010).

Daurian souslik is inhabitant of steppes with *Artemisia* and *Tanacetum* and is particularly abundant on overgrazed pastures around settlements (Bannikov 1954). Hibernation lasts seven (females) or eight months (males); active season is from end of March – mid April till late July – early September (Bannikov 1954).

Subspecies. Variation in size, colour and relative length of tail resulted in description of five subspecies; Gromov et al. (1965) recognized three of them (*dauricus*, *mongolicus*, *ramosus*) to be valid. There is no evidence of discontinuity and geographic variation was never comprehensively assessed.

Spermophilus pygmaeus (Pallas, 1779) – Little souslik

1779 *Mus citillus* (sic!) varietas *pygmea* (sic!) Pallas. Type locality: "in deſerto limoſo circa oppidum Iaïcense" (Pallas 1779: 223) (= in a muddy desert around the town of Yaitsk [= Uralsk in Russian, Oral in Kazakh]), Orenburg Region, Russia. Ognev (1947) claimed that the type (most probably a neotype) is from "Indersk" (= Inderborskij), therefore the type locality was given as ,"Inderskij rajon, Gur'evskaâ oblast', Kazahstan" by Pavlinov & Rossolimo (1987), or "Indersk" by Thorington & Hoffmann (2005). Ellerman & Morrison-Scott (1951) and Corbet (1978) reported the type locality as "Between Emba and Ural River, north-east of Caspian Sea". The year of publication is given as 1778 in Vinogradov & Gromov (1952) and Gromov et al. (1965).

1779 *Mus citellus flavescens* Pallas. Type locality not known (Ellerman & Morrison-Scott 1951); *nomen dubium* (Pavlinov & Rossolimo 1987).

1823 *Arctomys mugosaricus* Lichtenstein. Type locality: "Mugodžarskie gori" (Ognev 1947) (= Mugodžary Mts.; Mugodshary Mts. in Ellerman & Morrison-Scott 1951), Aktûbinsk Region, Kazakhstan (Pavlinov & Rossolimo 1987), not "Kirghizia" (Ellerman & Morrison-Scott 1951).

1832 *Spermophilus musicus* Ménétries. Type locality: "il habite le Caucase sur les montagnes le plus élevées et non loin des neiges éternelles" (= occupy high Caucasian mountains not far from permanent snow; Ognev 1947). According to Ognev (1947) type specimens originated from Karačaj, … around the villages of Učkulan, Hurzuk, and Kart-Džurt. Restricted to "Foot of Elbruz Mountain, Caucasus" (Ellerman & Morrison-Scott 1951). Pavlinov & Rossolimo (1987) restricted the

type locality to "Stavropolskij kr., Karačaevo- Čerkesskaâ AO, Karačaevskij r-n, Učkulan" (= Stavropol' Region, Karačaevo-Čerkeskaâ Autonomous Region, Karačaevsk District, Učkulan).

1908 *Citellus musicus typicus* Satunin. (Pavlinov & Rossolimo 1987).

1909 *Citellus musicus planicola* Satunin. Syntypes were from two localities in Russia (Satunin 1908b): "Karanogajskaâ step' / Karanogai Steppe" (= Karanogajskaâ steppe, between Terek and Kuma rivers, Republic of Kalmykia), and "Novočerkassk', Donskaâ oblast" (= ca. 25 km north-east of Rostov na Donu). In compliance with Articles 73.2.3 and 76.1 of the ICZN, the type locality encompasses the places of origin of all of syntypes. Ognev (1947) restricted the type locality to "Karanogajskaâ step" which was reported as "Karanogai steppes, Kizljar, Caucasus" by Ellerman & Morrison-Scott (1951). The year of publication given as 1908 in Ellerman (1940), Ellerman & Morrison-Scott (1951), and Pavlinov & Lissovskij (2012), but the majority of authors quote 1909 (Ognev 1947, Vinogardov & Gromov 1952, Gromov et al. 1965).

1910 *Citellus* (*Citellus*) *citellus pygmaeus* Trouessart. Emendation of *Mus citillus* varietas *pygmea* Pallas, 1779.

1915 *Citellus mugosaricus* n. *herbidus* Martino. *Nomen nudum* (Pavlinov & Rossolimo 1987). The new name appears on p. 197 in Martino (1915), and not on pp. 5–6 (cf. Ognev 1947, Pavlinov & Rossolimo 1987).

1917 *Citellus mugosaricus* natio *herbicola* Martino et Martino. Syntypes were from "Ak'-Tûbe" (= Aktûbinsk in Russian, Aktobe in Kazakh), and "Džurun" (= Žuryn in Russian, Dzhurun in Kazakh), both localities are in Aktûbinsk (= Aktobe) Region, Kazakhstan. In compliance with Articles 73.2.3 and 76.1 of the ICZN, the type locality encompasses the places of origin of all of syntypes. Location of the type locality as "Orenburgskaâ obl." (= Orenburg Region; Pavlinov & Rossolimo 1987) is erroneous. The year of publication quoted as 1914 (Vinogradov & Gromov 1952, Gromov et al. 1965).

1917 *Citellus* (*Colobotis*) *musicus brauneri* Martino et Martino. Type locality: "Igren', b. (= byvšego [former]) Novomoskovskogo uezda b. Ekaterinoslavskoj gubernii" (Ognev 1947); "Igren district, Ecaterinoslav Govt., Crimea" (Ellerman & Morrison-Scott 1951). Baranova & Gromov (2003) quoted a lectotype from "Igren', Novomoskovskij uezd, Ekaterinoslavskaâ guberniâ (Dnepropetrovskaâ oblast, Ukraina)". The year of publication is quoted as 1916 (Vinogardov & Gromov 1952, Gromov et al. 1965) and 1920 (Baranova & Gromov 2003). There are differences between the sources regarding the correct year of publication; e.g. 1914 in Thorington & Hoffmann (2005); 1916 (Vinogradov & Gromov 1952, Gromov et al. 1965); 1917 (Ognev 1947, Ellerman & Morrison-Scott 1951, Pavlinov & Rossolimo 1987); and 1920 (Ellerman 1940, Baranova & Gromov 2003).

1922 *Citellus satunini* Sviridenko. Type locality: "Okresnosti Temir-Han-Šuri" (= vicinity of Temir-Han-Šura) (Ognev 1947), "Daghestan, 2,000 ft. environs of Temir Khan Sura, about 42°50'N., 47° E., Caucasus" in Ellerman & Morrison-Scott (1951), Dagestan, Russia.

1927 *Citellus pygmaeus* var. *atricapilla* Orlov. Type locality: "Kujbyševskaâ obl. (= Kujbyšev [now Samara] Region), Bezenčukskij r-n (= Bezenčuk District), Pokrovskoe" (Pavlinov & Rossolimo 1987), Russia. *Nomen nudum* in the conclusion by Geptner (1948), because the name was proposed for an "aberration of *C. pygmaeus* Pall." (cf. Pavlinov & Lissovskij 2012).

1927 *Citellus pygmaeus pallidus* Orlov et Fenyuk. Type locality: "Uročiše Ulan Hol (stavka Èrket-Ulusa), b. (= byvšaâ [former]) Kalmyckaâ oblast" (Ognev 1947) (= lonely house Ulan Hol [belongs to estate Èrket-Ulus]), Republic of Kalmykia, Russia. Vinogardov & Gromov (1952) and Gromov et al. (1965) quote Orlov as the authority.

1927 *Citellus pygmaeus septentrionalis* Obolensky (quoted also as Obolenskiy or Obolenskij). Type locality: "selo Ferapontovka, b. (= byvšij [former]) Buzulukskij uezd b. (= byvšej [former]) Samarskoj gubernii" (= village Ferapontovka, former Buzuluk region, former Samara Governate) (Ognev 1947), Orenburg Region, Russia.

1932 *Citellus pygmaeus boehmii* Krassovsky. Type locality: "Nižnie-Acylyk" (= "Nižnie Ačaluki", Ognev 1947; "Nishnie Ataluki", Ellerman & Morrison-Scott 1951), Nazranovsk District, Čečen-Inguš Republic, Russia (Pavlinov & Rossolimo 1987). Misspelled as *boehmi* (Vinogardov & Gromov 1952) or as *bohemi* in Gromov et al. (1965).

1934 *Citellus pygmaeus nikolskii* Heptner. Type locality: "40 km k severo-vostoku ot g. Aral'ska, na severnom beregu Aral'skogo morja" (= 40 km north-east of Aralsk, northern side of the Aral Sea) (Ognev 1947), Kazakhstan.

1935 *Citellus pygmaeus pallidus arenicola* Rall'. Type locality: "Kazahstan, Gur'evskaâ obl. (= Gur'evsk Region), Čučaki" (Pavlinov & Rossolimo 1987).

1935 *Citellus pygmaeus kazakstanicus* Goodwin. Type locality: "Tuz Bulak, one hundred and fifty miles north of Kizil Orda (= Kzyl-Orda) (Perovsk), Kazakhstan, Central Asia, altitude 600 feet." Misspelled as *kasachstanicus* in Gromov et al. (1965: 263).

1937 *Citellus* (*Colobotis*) *pygmaeus kalabuchovi* Ognev. Type locality: "okrestnosti sela Fedoseevki Zavetčinskogo rajona Sal'skogo okruga Severo-Kavkazskogo kraâ (dolina r. Sala)" (= vicinity of the village Fedoseevka, Zavetčinskij rajon, Salsk district, north-Caucasian area (valley of the river Sal)) (Ognev 1947), Rostov Region, Russia.

1940 [*Citellus*] *binominatus* Ellerman (in a footnote on p. 442). New replacement name for *Citellus pygmaeus* var. *atricapilla* Orlov, 1927, which was at the time considerd to be congeneric with, and therefore preoccupied by the Nearctic *Spermophilus grammurus atricapillus* Bryant, 1889 (now *Otospermophilus atricapillus*; Helgen et al. 2009). Ellerman's (1940) *binominatus* is regarded *nomen nudum* by Pavlinov & Rossolimo (1987), evidently on grounds of an earlier invalidation of *atricapilla* Orlov, 1927 by Geptner (1948).

1940 *Citellus pygameus orlovi* Ellerman. New replacement name for *Citellus pygmaeus pallidus* Orlov et Fenyuk, 1927, which was at the time considered to be congeneric with, and therefore preoccupied by the Nearctic *Spermophilus tridecemlineatus* var. *pallidus* J. A. Allen, 1874 (now *Ictidomys tridecemlineatus pallidus*; Helgen et al. 2009). Ellerman's (1940) name is preoccupied by *Citellus* (*Colobotis*) *fulvus orlovi* Ognev, 1937.

1944 *Citellus pygmaeus ellermani* Harris. New replacement name for *Citellus pygmaeus pallidus* Orlov et Fenyuk, 1927; cf. comments under *Citellus pygameus orlovi* Ellerman, 1940.

1947 *Citellus* (*Colobotis*) *pygmaeus musicus* natio *saturatus* Ognev. Type locality: "Okresnosti aula Orzakovskogo, verhov'e r. Baksana (b. Nal'čikskogo okruga) na vysote 4500' – 6000'." (= vicinity of aul Orzakovskij, upper reaches of the Baksan River (former Nalčik district), at the elevation of 4500' – 6000'), Kabardino-Balkarian Republic, Russia. *Nomen nudum* (Pavlinov & Lissovskij 2012).

1948 *Citellus pygmaeus magistri* Geptner. The name of the authority was originally printed in Cyrillic characters (Гептнер; Geptner 1948: 710) which transliterate to "Geptner" and not "Heptner" (e.g. Pavlinov & Lissovskij 2012). New replacement name for *Citellus* (*Colobotis*) *pygmaeus musicus saturatus* Ognev, 1947, which was at the time considered to be congeneric with, and therefore preoccupied by the Nearctic *Tamias lateralis saturatus* Rhoads, 1895 (*Spermophilus saturatus* in Hall & Kelson 1959; now *Callospermophilus saturatus*; Helgen et al. 2009). *Nomen nudum* (Pavlinov & Lissovskij 2012); cf. the above remark under *saturatus* Ognev, 1947. Misspeled as *magisteri* by Thorington & Hoffmann (2005).

1948 *Citellus pygameus ralli* Geptner. The name of the authority was originally printed in Cyrillic characters (Гептнер; Geptner 1948: 710) which transliterare to "Geptner" and not "Heptner" (e.g. Pavlinov & Rossolimo 1987, Pavlinov & Lissovskij 2012). New name for *Citellus pygmaeus pallidus arenicola* Rall', 1935, which was at the time considered to be congeneric with, and therefore preoccupied by the Nearctic *Citellus tridecemlineatus arenicola* A. H. Howell, 1928 (now *Ictidomys tridecemlineatus arenicola*; Helgen et al. 2009).

1965 *C.*[*itellus*] *p.*[*ygmaeus*] *jigulensis* Gromov (in: Gromov et al. 1965:266). Type locality: "Žiguli, sel. (= village) Širâevo", Russia. The type is from the Early Holocene ("rannij golocen").

Remarks. Four junior synonyms of *S. pygmaeus* (*atricapilla*, *pallidus*, *arenicola*, *saturatus*) were in the past homonymous of various Nearctic ground squirrels, which are now in genera other than *Spermophilus* (i.e. *Ictidomys*, *Callospermophilus* and *Otospermophilus*; Helgen et 2009). The above names for the Palaearctic *S. pygmaeus* are therefore no longer preoccupied.

See comments under *Citellus binominatus* Ellerman, 1940, *Citellus pygameus orlovi* Ellerman, 1940, *Citellus pygmaeus magistri* Geptner, 1948, and *Citellus pygameus ralli* Geptner, 1948.

Sousliks from the Greater Caucasus Range were so far considered as specifically distinct (as *S. musicus*) from *S. pygmaeus* (Pavlinov et al. 1995, Thorington & Hoffmann 2005, Pavlinov & Lissovskij 2012); Gromov et al. (1965) even placed these two taxa into distinct subgenera: *S. musicus* into a subgenus *Citellus*, and *S. pygmaeus* into *Colobotis*. Such an arrangement is not supported in phylogenetic reconstructions based on allozymes (Frisman 2008) and on mitochondrial and nuclear DNA markers (Ermakov et al. 2006b). Tsvirka et al. (2003) reported genetic divergence between *S. musicus* and *S. pygmaeus* to be lower than between two subspecies of *S. suslicus* (see under that species). *S. musicus* and *S. pygmaeus* also display very similar alarm calls (Nikolskij 1969). The Caucasian population presumably diverged from *S. pygmaeus* less than 4000 ya (Ermakov et al. 2006b) but this estimate is not congruent with the interpretation of paleontological evidence; I. Gromov (in: Gromov et al. 1965: 252) described a subspecies *C.*[*itellus*] *m.*[*usicus*] *sviridenkoi* from the end of Middle Pleistocene – beginning of Late Pleistocene which suggests more ancient roots of *musicus*; the type locality of *sviridenkoi* is "hrebet Aziš-Tau (1400–1500 m nad ur. m.) na vostočnoj okraine Lagonakskogo plato v meždureč'e r. Beloj i ee levogo pritoka r. Kurdžips." (= ridge of Aziš-Tau [1400–1500 m a. s. l.] on the eastern border of the Lagonakskoe Plateau between the river Belaâ and its left tributary Kurdžips). Similarly to some earlier authors (e.g. Ognev 1947, Vinogradov & Gromov 1952, Tembotov 1972) we keep *musicus* as a subspecies of *S. pygmaeus*.

Recently, Pavlinov & Lissovskij (2012) split pygmy sousliks, other than *musicus*, into two species, *S. pygmaeus* and *S. planicola*. Titov et al. (2003) suggested that geographic boundary posed by the river Volga facilitated their prolonged separation with subsequent differentiation in their gene sequences, acoustics, and shape of the baculum. We treat these two allopatric groups of populations as distinct subspecies.

Fig. 26. Little souslik *Spermophilus pygmaeus planicola* (Oiyl, Aktobe [= Aktjubinsk] district, Kazakhstan; photo by Sergey Titov).
Obr. 26. Sysel malý *Spermophilus pygmaeus planicola* (Oijl, Akťubinská oblast, Kazachstán; foto Sergey Titov).

On the western bank of Volga *S. pygmaeus* occasionally hybridize with *S. suslicus* (Denisov 1961); on the eastern bank (Denisov 1963, Ermakov 2002, 2006a) and in Kazakhstan (Ermakov et al. 2006c) *S. pygmaeus* hybridize with *S. major* but less than 1% of individuals are hybrids (Šlâhtin et al. 2009).

The small souslik is possibly in a sister position against all the remaining species of *Spermophilus* (Harrison et al. 2003).

Description. A small souslik (HbL mainly < 220 mm) with a short tail (about 12–25% HbL; mean ≈ 19%) and bare soles. Colour varies between populations from light grey-yellow, sand yellow or pinkish-buff to dark greyish-brown. Pelage pattern is unmarked or speckled, and the

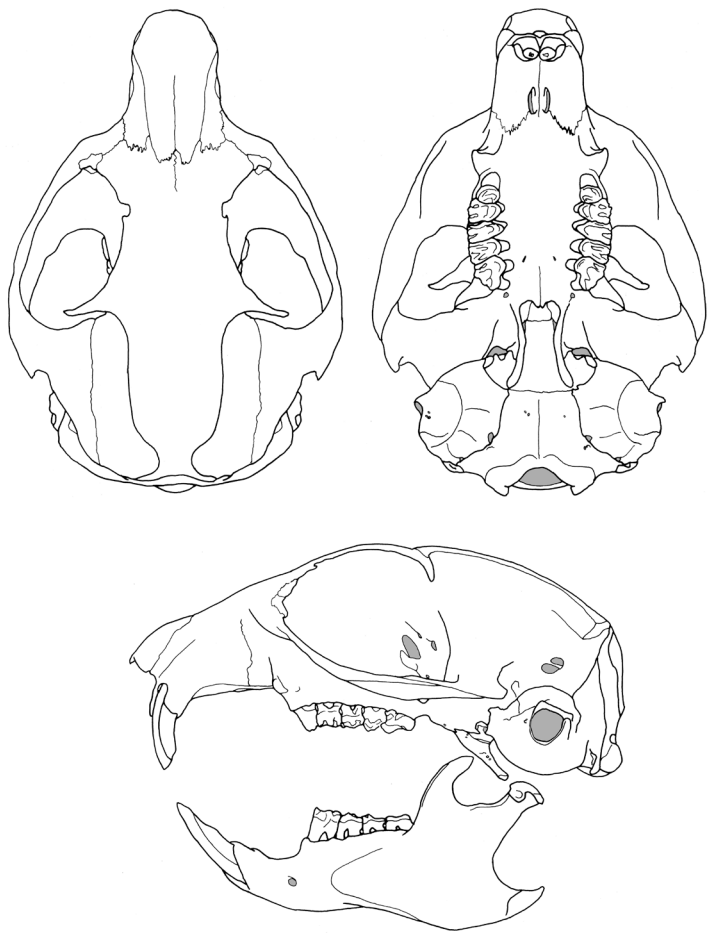


Fig. 27. Skull and mandible of *Spermophilus pygmaeus planicola* (Rostov-na-Done, Russia; SMF 47.916).
Obr. 27. Lebka a mandibula *Spermophilus pygmaeus planicola* (Rostov na Donu, Rusko; SMF 47.916).

Fig. 28. Skin of *Spermophilus pygmaeus musicus* (NMNH; photo by Jan Matějů).
Obr. 28. Balk *Spermophilus pygmaeus musicus* (NMNH; foto Jan Matějů).

two extremes intergrade. Top of head often contrasts colour of the back, being darker, or ochraceous (Figs. 26, 28). Underside is whitish, frequently washed yellowish or buff, and invariably clouded by slate underfur. Throat and chin are nearly white; eye ring is cream-whitish. Tip of the tail is margined white; blackish subterminal ring is evident in dark individuals. Juveniles are more distinctly spotted, particularly on the posterior half of the back. Baculum (mean length

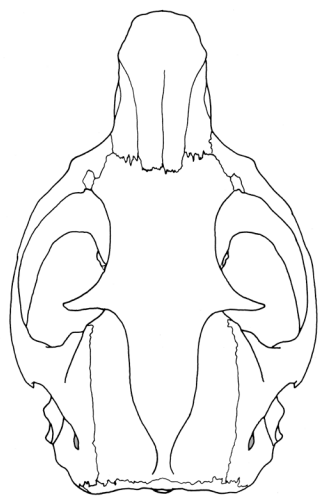


Fig. 29. Skull of *Spermophilus pygmaeus musicus* in dorsal view (Nalčik district, Kabardino-Balkar Republic, Russia; MNM 3453).
Obr. 29. Lebka *Spermophilus pygmaeus musicus* z dorsálního pohledu (oblast Nalčiku, Kabardino-Balkarská republika, Rusko; MNM 3453).

= 2.7 mm; Rešetnik & Balahnin 1967) is of similar shape as in *S. citellus*. Females have 10 –12 nippels (Artemev 1965). Skull shows no peculiarities; zygomatic arches are moderately expanded (ZgB = 65–75% CbL); the zygomata bow abruptly outwards; supratemporal ridges exceptionaly converge posteriorly to form a low and short sagital crest (Figs. 27, 29). Teeth do not differ appreciably from those of *S. citellus*, except for larger P4 and M3. Dimensions (in mm; W in grams): HbL = 172–260, TL = 23–60, HfL = 24.0–40.0, E = 5.0–10.0, W = 122–497, CbL = 35.2–45.5, ZgB = 22.1–30.8, MxT = 8.5–11.0. Males are larger than females. Although the diploid number is stable (2n = 36), position of centromere in various autosomes and the sex chromosomes varies between populations (Voroncov & L'apunova 1974a, Zima & Král 1984) and some of these differences might be associated with subspecific differentiation. Location and quantity of the nuclear organizer varies even within the same population in *S. p. musicus* (Tsvirka et al. 2003).

Geographic range (Fig. 30) extends from the river Dnieper to western Betpak-Dala desert and covers Ukraine, Russia, Uzbekistan and Kazakhstan; putative marginal occurrence in Georgia (at the springs of river Terek) remains unconfirmed (Bukhnikashvili 2004). Nothern border is posed by the line Dniepropetrovsk (Zolotnoska) – Harkov – south of Voronež – Saratov – Buzuluk steppes – Birsk (the northern-most extension) – Troick – Omsk region. Southern margin follows north-western shores of the Black Sea (including Crimea and Kerč), encompasses Kuban steppes and mountains of the Central Caucasus, northern Dagestan, northern shores of the Caspian Sea, further east to the Aral Sea and the south-west part of Betpak-Dala. There is an isolate in Daghestan (between Mahačkala and Bujnaksk) and further small isolated colonies (occupying areas of up to 400 ha each) along the southern border in the Terek area (Ognev 1947). Range expansion westward of the river Don was presumably a fairly recent event, although it was present in Ukraine already in the Middle Pleistocene (Krohmal' & Rekovec 2010). Range expansion documented since 1920s in various parts of the range, e.g. north of the Caucasus (Tembotov 1972), in the regions of Stavropol and river Don, and on the western bank of the river Volga (Denisov 1961); range shifted up to 2.5–3 km year^{-1} (Gromov et al. 1965). Along the expanding northern range border *S. pygmaeus* outcompete *S. suslicus* (Denisov 1961). *S. pygmaeus* inhabits grassy (*Stipa*, *Festuca*, *Poa*, etc.) and sagebrush steppes on chernozem and hard clay soils, semideserts on compact loamy soil, saline plains and mountain pastures. Preferred are habitats with sparse and low vegetation, a semi-desert rather than a steppe (e.g. Rogovin 2007); numbers declined and range shrank in 1980s in the Saratov region when humidity increased (Šlâhtin et al. 2009); overall decline also reported during the 20th century in dry steppes of the trans-Volga region (Oparin 2005). Populations from sand deserts are the more prone to drastic declines in western Kazakhstan (Okulova et al. 2006). Elevational range is from the lowlands till 3100 m in the Caucasus. Hibernates from early August (the Caucasus) till late February – early April; in arid regions sousliks may start aestivation in late July and continue into hibernation (Ognev 1947).

Subspecies. Phylogenetic assessments based on allozymes and various DNA markers retrieved three major lineages (Ermakov et al. 2006b, Frisman 2008) which we interpret as distinct subspecies. Diagnostic characters involve also differences in karyotype (see above Remarks for references). Of the junior synonyms listed above, *Mus citellus flavescens* (Pallas, 1779) was not assign to any of the recognized subspecies. The type locality for the Early Holocene form *jigulensis* is on the right bank of river Volga, i.e. within the current range of *S. pygmaeus planicola*, but we refrain from formally synonymizing the subfossil form. Gromov et al. (1965) stress that *jigulensis* is smaller if compared to *septentrionalis*.

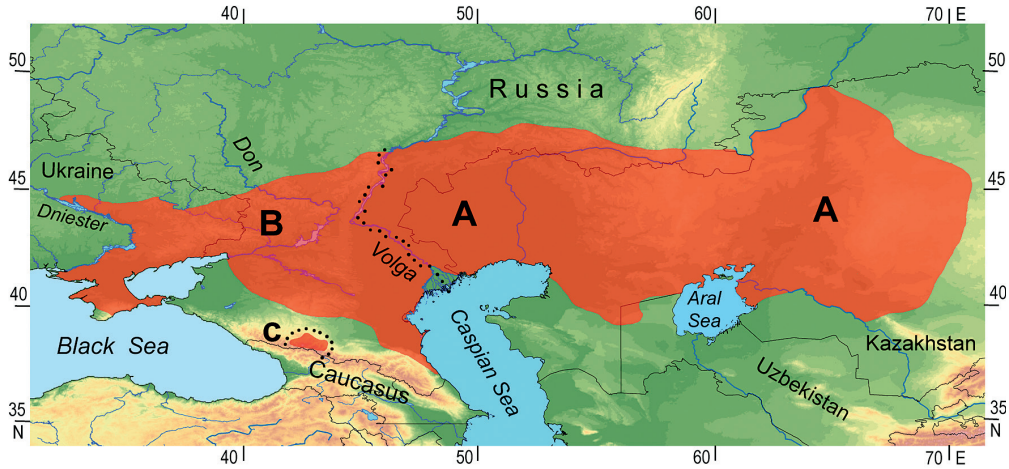


Fig. 30. Distribution of *Spermophilus pygmaeus* in the 20th century at its most extensive. Compiled from the following sources: the overall range – Ognev (1947), Tsytsulina et al. (2008b); Russia – Popov (1960), Denisov (1961), Tembotov (1972), Šidlovskij (1976), Šlâhtin et al. (2009); Kazakhstan – Afanas'ev et al. (1953), Sludskij et al. (1969). Subspecies are delimited by a dotted line: A – *S. p. pygmaeus*; B – *S. p. planicola*; C – *S. p. musicus*.

Obr. 30. Rozšíření *Spermophilus pygmaeus* ve 20. stol., v době kdy byl jeho areál nejrozsáhlejší. Zkompilováno z následujících pramenů: celkový areál – Ognev (1947), Tsytsulina et al. (2008b); Rusko – Popov (1960), Denisov (1961), Tembotov (1972), Šidlovskij (1976), Šlâhtin et al. (2009); Kazachstán – Afanas'ev et al. (1953), Sludskij et al. (1969). Areály poddruhů jsou ohraničeny tečkovanou čarou: A – *S. p. pygmaeus*; B – *S. p. planicola*; C – *S. p. musicus*.

Spermophilus pygmaeus pygmaeus (Pallas, 1779)

Synonyms. *mugosaricus*, *herbicola*, *herbidus*, *atricapilla*, *septentrionalis*, *nikolskii*, *arenicola*, *kazakstanicus*, *binominatus*, *ralli*.

Description. Diagnosis is based on DNA sequences (Ermakov et al. 2006b) and on Nei genetic distances derived from allozyme polymorphism (Frisman 2008). Differs from ssp. *planicola* in karyometric peculiarities (Zima & Král 1984). Tends to be paler than *musicus* and *planicola*, and less distinctly speckled than the latter (Fig. 26). Baculum (mean ± standard deviation) is 2.63±0.073 mm long, 0.84±0.031 mm wide across basal expansion, and 1.25±0.037 mm wide across spatula. Number of alarm calls in a series is 5.577±0.419 (Titov et al. 2003). Dimensions (in mm; W in grams) (Andreevka in Samara region; Artemev 1965), males: HbL_{50} = 202 (180–226), TL_{50} = 32 (27–37), HfL_{50} = 33 (31–35), CbL_{30} = 40.2 (38.1–44.2), ZgB_{30} = 28.1 (26.5–30.0); females: HbL_{50} = 200 (185–221), TL_{50} = 31 (25–40), HfL_{50} = 32 (29–34), CbL_{30} = 39.0 (37.7–40.4), ZgB_{30} = 27.0 (26.3–29.2); pooled samples from throughout the range (Ognev 1947): males: HbL_{12} = 205.1 (193–225), TL_{12} = 31.9 (25–35), HfL_{12} = 32.4 (30–35), E_8 = 8.3 (7.3–10), CbL_{13} = 38.6 (36.7–41.5), ZgB_{14} = 27.5 (26.0–29.3), MxT_{14} = 9.3 (8.3–10.0); females: HbL_5 = 192.6 (172–211), TL_5 = 33.4 (26–45), HfL_5 = 31.2 (30–32), E_1 = 9.0, CbL_7 = 37.9 (36.1–40.1), ZgB_8 = 27.1 (25.2–29.5), MxT_8 = 9.4 (9.1–10.2).

Geographic range (Fig. 30A) is to the east of Volga in Russia and Kazakhstan. Typical inhabitant of plains at low elevation; never occurs >600 m in Kazakhstan (Afanas'ev et al. 1953). On the eastern bank of Volga the active period lasts 70–115 days annualy (Artemev 1965).

Spermophilus pygmaeus musicus Ménétriès, 1832

Synonyms. *typicus*, *boehmii*, *saturatus*, *magistri*.

Remarks. *S. p. musicus* is frequently regarded to be species on its own right (Tsvirka et al. 2003, Thorington & Hoffmann 2005, Pavlinov & Lissovskij 2012).

Description. A single locus of total 24 discriminates *musicus* from *planicola* (Frisman 2008). *S. p. musicus* differs from the remainig subspecies in distribution of C-heterochromatin, by the presence of telomeric bands on 6 chromosomes (Zima & Král 1984), and by 16 pairs of metacentric autosomes (18 metacentrics in the remainder *S. pygmaeus* populations; Voroncov & L'apunova 1974a). A large race with dark pelage (back is wood-brown to buffy-brown) and faded speckleness (Fig. 28). Dimensions (in mm; W in grams), males: HbL_{16} = 217.3 (177–250), TL_{16} = 42.4 (33–52), HfL_{16} = 36.1 (31–40), E_3 = 6.5 (5.0–9.0), W_{11} = 305.8 (181–497), CbL_{16} = 42.6 (39.7–44.9), ZgB_{15} = 29.0 (27.6–30.3), MxT_{16} = 10.2 (9.5–10.8); females: HbL_{14} = 214.8 (194–240), TL_{14} = 42.0 (30–48), HfL_{14} = 34.6 (32–38), E_3 = 6.2 (4.6–7.5), W_9 = 248.3 (208–340), CbL_{15} = 40.9 (38.7–43.2), ZgB_{13} = 28.2 (27.1–28.9), MxT_{15} = 10.2 (9.7–10.7) (ZISP).

Geographic range (Fig. 30C) is in small isolates (areas of 10–100 ha) on the slopes of Mt. Elbrus and the Balkarian Mts. (the main Caucasus range), i.e. in the upper reaches of the rivers Kuban and Terek; putative presence in Georgia was not confirmed (Bukhnikashvili 2004). The gap separating ranges of *musicus* and *planicola* was 50 km prior to 1970s but shrank subsequently to 25 km at its narrowest (Tembotov 1972). Inhabited are high mountain pastures at elevations 1050–3200 m (Gromov & Erbajeva 1995) where sousliks hibernate for 210–233 days per year; this period is prolonged by 22–32 days in the subalpine zone (Lysikova not dated). Sousliks resembling the recent *S. p. musicus* occupied the Causus already in the Middle Pleistocene (Baryshnikov 2002).

Spermophilus pygmaeus planicola (Satunin, 1908)

Synonyms. *brauneri*, *satunini*, *pallidus*, *kalabuchovi*, *orlovi*, *ellermani*.

Remark. Pavlinov & Lissovskij (2012) regard *S. p. planicola* as a species on its own right.

Description. Sspp. *planicola* and *musicus* differ in karyometric peculiarities (Zima & Král 1984) and in a single locus of a total 24 studied by Frisman (2008). The ssp. *planicola* tends to be darker than the nominotypical subspecies and *musicus*, and more distinctly speckled than the former. Southern populations from semideserts are pale, however. Baculum (mean ± standard deviation) is 2.66±0.023 mm long, 0.96±0.014 mm wide across basal expansion, and 1.25±0.023 mm wide across spatula. Number of alarm calls in a series is 8.786±0.873 (Titov et al. 2003). Dimensions (in mm; W in grams) (Rostov on Don, Russia), males: HbL_{15} = 208.9 (180–235), TL_{15} = 34.8 (28–41), HfL_{15} = 33.6 (32–36), E_{13} = 7.3 (5.0–9.5), W_{11} = 213.6 (158–299), CbL_{15} = 40.9 (38.2–44.1), ZgB_{14} = 28.5 (26.1–30.7), MxT_{15} = 9.8 (9.5–10.4); females: HbL_{14} = 198.1 (175–215), TL_{14} = 36.1 (25–46), HfL_{14} = 31.3 (27.0–33.8), E_{12} = 7.4 (5.0–8.7), W_5 = 200.5 (126–259), CbL_{14} = 39.6 (38.0–41.2), ZgB_{12} = 28.0 (27.0–29.9), MxT_{14} = 9.9 (9.4–10.2) (ZISP).

Geographic range. It includes Ukraine and western Russia; the eastern border is on the right bank of Volga (Fig. 30B).

Spermophilus fulvus (Lichtenstein, 1823) – Yellow souslik

1779 *Mus citellus maximus* Pallas. Type locality: "inferiorem Iaïcum" (= Lower Yaik; now river Ural). *Nomen oblitum* (Corbet 1978). With 1779 as the year of publication, we follow Pavlinov & Rossolimo (1987) and Pavlinov & Lissovskij (2012); Vinogardov & Gromov (1952), Gromov et al. (1965) and Thorington & Hoffmann (2005) quote 1778.

1823 *Arctomys fulvus* Lichtenstein. Type locality: "River Kuwandzaliur (= Kuvandžur in Ognev 1947), east of Mugodshary Mountains (= Mogudžarskie Mts., Ognev 1947), North of Sea of Aral, Kirghizia." (sic !) (Ellerman & Morrison-Scott 1951). According to Pavlinov & Rossolimo (1987): River Kuvandžur, Aktûbinskaâ oblast, Kazakhstan.

1829 *Arctomys concolor* Fischer.

1829 *Arctomys concolor* var. *giganteus* Fischer.

1829 *Arctomys concolor* var. *nanus* Fischer.

1831 *Spermophilus concolor* Geoffroy. Type locality: "Sultenia, near Kazvin, North-Western Persia" (Ellerman & Morrison-Scott 1951), Iran.

1909 *Cynomys concolor hypoleucos* Satunin. Type locality: "Kutschan, Northern Persia" (Ellerman & Morrison-Scott 1951), Iran.

1915 *Citellus fulvus parthianus* Thomas. Type locality: "Meshed, alt. 3000'." north-eastern Iran.

1915 *Citellus fulvus oxianus* Thomas. Type locality: "50 miles S.W. of Bokhara (= Bukhara), Alt. 600'." Uzbekistan.

1937 *Citellus* (*Colobotis*) *fulvus orlovi* Ognev. Type locality: "Nižnevolžskij kraj, levyj bereg Volgi protiv Vol'ska" (Ognev 1947), (= Lower Volga, left bank, towards Vol'sk), Russia. This name is overlooked in Thorington & Hoffmann (2005).

1942 *Citellus fulvus nigrimontanus* Antipin. Type locality: "Kazahstan, Čikmentskaâ obl. (= Čikment Region), sev.-vost. sklon hr. (= north-eastern slope of the ridge of) Karatau, Mynželke" (Pavlinov & Rossolimo 1987).

Remarks. About 2–3% of individuals are phenotypic hybrids in the zone of sympatry of *S. fulvus* and *S. major* (Šlâhtin et al. 2009), but this proportion is much higher (58% of hybrids) in a recently established contact zone (Shmyrov et al. 2012). Hybrids are fertile but *S. major* predominantly participate in backcrosses (Ermakov et al. 2002, 2006a).

Description. A large souslik (HbL up to 395 mm; Gromov & Erbajeva 1995) with short ears (5–9 mm), moderately long tail (24–35% HbL), bare palms and soles, and small cheek pouches. A rusty yellowish to dull buff-grey summer pelage is darkened by brownish-black hair tips. Head is cinnamon-buff, a narrow eye ring is light yellowish, and the area behind the ears is greyish. Flanks are light greyish-ochraceous, limbs are yellowish ochraceous; belly is pinkish buff, shaded grey by slate hair bases; throat and chin are whitish. Tail is of same colour as the back, below it is cinnamon-buff, with a black subterminal ring which is edged with white hair tips (Fig. 31). Yellow sousliks are the darkest in the north-western part of their range, i.e. on the eastern banks of Volga. Palest sousliks (e.g. from southern Kyzylkum) have sandy yellow back, occasionally shaded rusty; head is paler. Winter pelage is longer, softer, denser and darker. Females normaly have 6 pairs of nipples (1 pectoral, 3 abdominal, 2 inguinal), but the number varies from 10 to 14 (Ognev 1963). Baculum is about 4 mm long with a pronouncedly twisted triangular distal spatula, which is edged by blunt denticles (Didier 1952). Skull is robust and shallow, with well pronounced sagittal and lambdoidal crests in adults. Zygomatic arches are widely expanded (ZgB = 71–77% CbL); the zygomata bow abruptly outwards; interorbital region

Fig. 31. Yellow souslik *Spermophilus fulvus* (Dâkonovka, Saratov Region, Russia). Note that back and belly are uniformly buff (photo by Sergey Cherenkov).
Obr. 31. Sysel žlutý *Spermophilus fulvus* (Djakonovka, Saratovská oblast, Rusko). Hřbet i břicho jsou uniformě žlutohnědé (foto Sergey Cherenkov).

is broad (10.2–16.2 mm), postorbital processes are prominent. The skull is less evenly convex in profile view than in remaining *Spermophilus* species, with a protruding supra-orbital region. Rows of cheek-teeth are widely apart; braincase is rather short and broadly oval (Fig. 32). Teeth show no peculiarities: P3 is relatively large; P4 and M1–2 are less compressed in majority of yellow sousliks. Number of roots for cheek-teeth (maxillar / mandibular): 1, 3, 3, 3, 3 / 2, 4, 4, 4 (Özkurt et al. 2007). Dimensions (in mm; W in grams) (north-western Turkmenistan), males: HbL_{50} = 290 (240–360), TL_{50} = 82.4 (60–125), HfL_{50} = 47.5 (35–65), W_{50} = 756 (460–1486), CbL_{30} = 55.1 (53.3–56.9), ZgB_{30} = 40.7 (39.2–43.4), MxT_{30} = 14.1 (13.2–14.9); females: HbL_{70} = 255.5 (220–283), TL_{70} = 80.2 (68–100), HfL_{70} = 46.1 (38–74), W_{70} = 684 (418–1174), CbL_{30} = 52.4 (48.5–55.0), ZgB_{30} = 39.0 (37.0–41.6), MxT_{30} = 14.0 (13.0–18.8) (Efimov 2005). Vasileva et al. (2009) report body mass to reach 2 kg. Karyotype: 2n = 36 (Voroncov & L'apunova 1974a, Özkurt et al. 2007).

Geographic range (Fig. 33) in the former Soviet Union reviewed by Kucheruk (1998). Range extends from the estern bank of river Volga and the eastern shores of the Caspian Sea, to Almaty and river Ili, south of Lake Balkaš. Northern range border at about 52°N latitude is posed by the coniferous forest zone; along the Volga the northern record (at 51°21' N latitude) is near Saratov (Šlâhtin et al. 2009). Southern margin is in northern Kyrgyzstan, north-western Tajikistan, Afghanistan, northern Iran, and south-eastern Turkmenistan. Populations along the southern distributional border are isolates, particularly so in south-eastern Afghanistan (Katawaz plain;

Niethammer 1965, Habibi 2004), north-western Afghanistan (Herat and Obeh; Niethammer 1965, Habibi 2004) and adjacent north-eastern Iran (Khorassan province between 150 km north-west and 290 km south of Mashad; Lay 1967, Darvish 2002), and in north-western Iran (marginal records: Hamadan–Bijar–Zanjan–Qazvin; Misonne 1959, Lay 1967). *S. fulvus* is absent from Kyzylkum and Karakum sandy deserts of Turkmenistan and Uzbekistan. Occurrence in "Chinese Turkestan" (i.e. Kashgar in western Xinjang; Ellerman & Morrison-Scott 1951), still accepted by Tsytsulina et al. (2008a), is probably erroneous (cf. Zhang et al. 1997).

During the Early Holocene, *S. fulvus* was still present between the rivers Volga and Don (Gromov et al. 1965). Retreat of the western border towards east for 250–300 km "during the last 30 years" (Gromov et al. 1965) and small scale range changes were observed in Turkme-

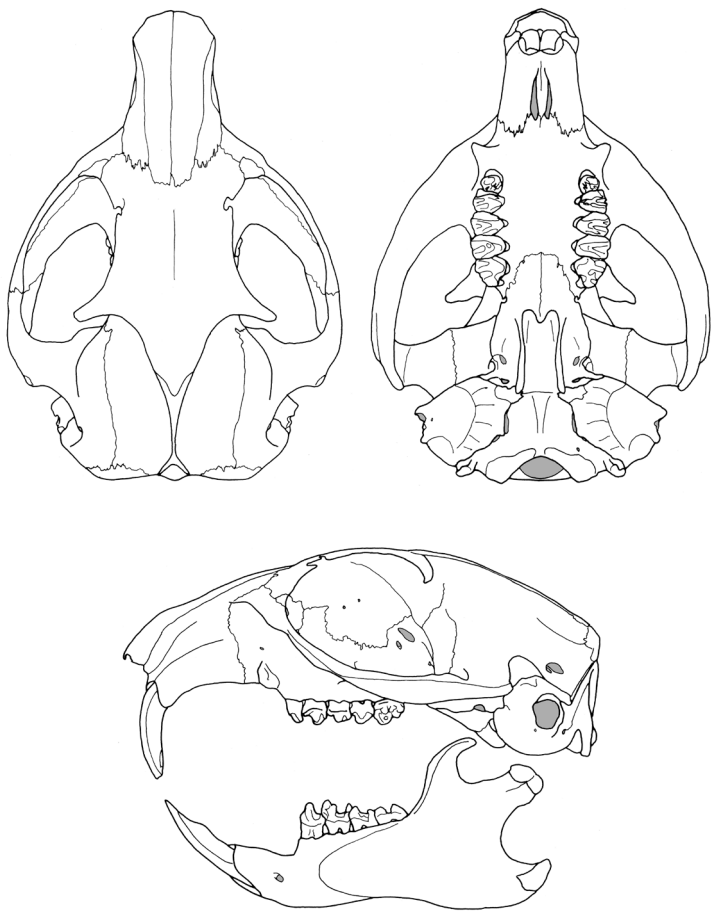


Fig. 32. Skull and mandible of *Spermophilus fulvus* (Afghanistan; ZFMK 92.494).
Obr. 32. Lebka a mandibula *Spermophilus fulvus* (Afganistan; ZFMK 92.494).

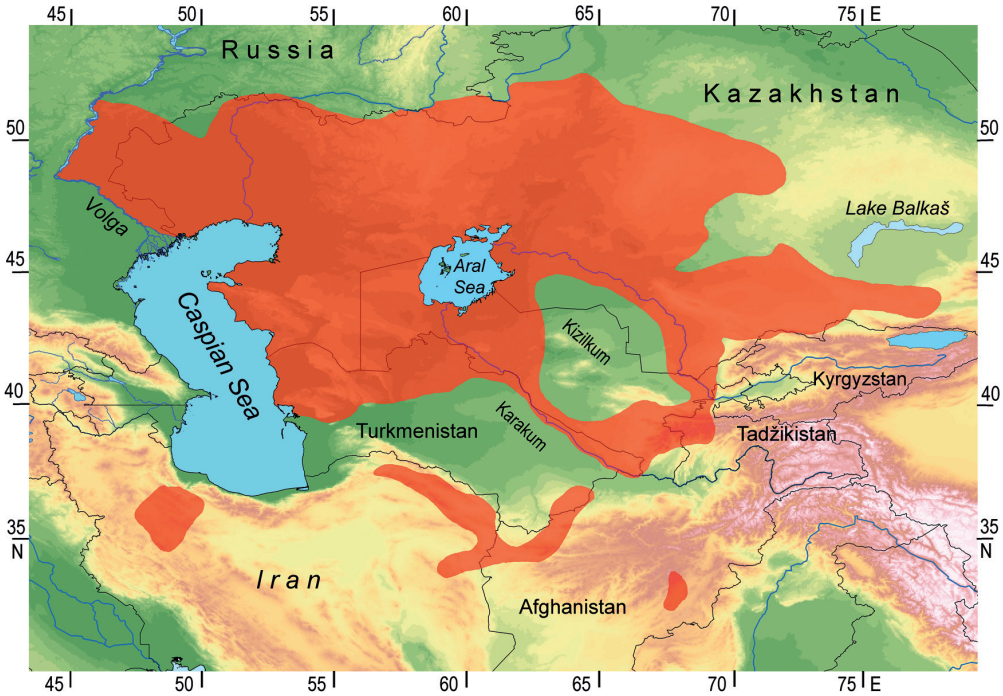


Fig. 33. Distribution of *Spermophilus fulvus*. Compiled from the following sources: the overall range – Ognev (1947,1963), Kucheruk (1998); Russia – Popov (1960), Ermakov et al. (2006b), Šlâhtin et al. (2009); Kazakhstan – Sludskij et al. (1969); Turkmenistan – Efimov (2005); Iran – Lay (1967), Darvish (2006), Gharkeloo et al. (2007), Özkurt et al. (2007); Afghanistan – Niethammer (1965), Habibi (2003), and voucher specimens in ZFMK; Tajikistan – Davydov (1964).
Obr. 33. Rozšíření *Spermophilus fulvus*. Zkompilováno z následujících pramenů: celkový areál – Ognev (1947,1963), Kucheruk (1998); Rusko – Popov (1960), Ermakov et al. (2006b), Šlâhtin et al. (2009); Kazachstan – Sludskij et al. (1969); Turkmenistan – Efimov (2005); Irán – Lay (1967), Darvish (2006), Gharkeloo et al. (2007), Özkurt et al. (2007); Afghanistan – Niethammer (1965), Habibi (2003) a dokladové exempláře v ZFMK; Tadžikistan – Davydov (1964).

nistan since 1950s (Efimov 2005). Populations were stable during the 20th century in dry steppes of the trans-Volga region (Oparin 2005). During 1929–1931 several thousand yellow sousliks were introduced to two islands in the Sea of Aral: Barsa-Kel'mes (Ismagilov 1952) and Kug--aral (Afanas'ev et al. 1953); another contemporary introduction was to the eastern Karaganda region of Kazakhstan (Kiris 1973).

Typical habitat includes steppes and semideserts, preferably on loamy sand or clay; saline soils are tolerated, but moving sands are avoided. Altitudinally the range extends up to 1600 m in Tajikistan (Davydov 1974), 1700 m in Kyrgyzstan (Ajzin 1979), and 3200 m in Afghanistan (Habibi 2004). The activity season is as short as 3 month in Russia (Vasilieva et al. 2009). In Iran sousliks become lethargic for 6.8 (males) to 7.3 (females) months already in May–July (Misonne 1959); hibernation lasts 7.5–8 months in Tajikistan (Davydov 1974) and about 8.5

months in Turkmenistan (Efimov 2005). Drought in late summer further truncates the active period (Neronov & Shilova 2012).

Subspecies. Not comprehensively reviewed; Thorington & Hoffmann (2005) recognize three subspecies (*fulvus*, *hypoleucos*, *oxianus*). Fur colouration and size (the main diagnostic characters) intergrade which prevents clear demarcation of subspecies (Ognev 1947). Between the lower reaches of rivers Volga and Ural, yellow sousliks decreased in size from the Upper Pleistocene to Holocene (Dmitriev 1981).

Spermophilus major (Pallas, 1779) – Russet souslik

1779 *Mus citellus* var. *major* Pallas. Type locality: "campis herbidis circa Samaram" (= grassy plain (steppe) around Samara), therefore: Samara, Russia. Note that Samara was named Kujbyšev in 1935–1991, therefore the type locality was given as "Kujbyšev Region, left bank of River Volga" (Pavlinov & Rossolimo 1987). With 1779 as the year of publication we follow Ellerman & Morrison-Scott (1951), Pavlinov & Rossolimo (1987), and Pavlinov & Lissovskij (2012); Vinogardov & Gromov (1952), Gromov et al. (1965) and Thorington & Hoffmann (2005) quote 1778.

1840 *Spermophilus rufescens* Keyserling et Blasius. Type locality: "Im Orenburgischen und Kasanschen vom 50sten bis 56sten Breitengrade." Type locality interpreted either as "Ural Mountains, Russia" (Ellerman & Morrison-Scott 1951) or, more narrowly, as "Orenburgskaâ oblast" (Orenburg Region) (Vasil'eva 1968).

1947 *Citellus major* rassa oecologica *argiropuloi* (sic!) Bažanov (spelled as Bajanov by Gromov et al. 1965). Type locality: "Kazakhstan, Gur'evskaâ obl. (= Gur'evsk Region), Kzylkoginskij r-n (= Kzylkoginsk District), r. Uil (= river Uil), peski (= sands) Bijrûk" (Pavlinov & Rossolimo 1987).

1952 *C.*[*itellus*] *m.*[*ajor*] *argyropuloi* Vinogradov et Gromov, 1952. Emendation of *Citellus major argiropuloi* Bažanov, 1947 (Vinogradov & Gromov1952: 122).

Remarks. *S. major* hybridize with at least 4 species: *S. fulvus*, *S. pygmaeus*, *S. suslicus* (Ermakov et al. 2002, 2006a, c), and *S. erythrogenys heptneri* (Spiridonova et al. 2005, 2006). Introgressive hybridization with *S. fulvus* and *S. pgymaeus* is common in the Volga region for mitochondrial genes, but less so for the Y-chromosome genes (Ermakov et al. 2006a). Noteworthy, alien mitochondrial haplotypes of *S. fulvus* and *S. pygmaeus* were found in *S. major* also outside zones of sympatry, evidently a consequence of an ancient introgression. Hybridization with *S. suslicus* is believed to be sporadic (Ermakov et al. 2002). See also remarks under *S. fulvus*.

Description. A large souslik (HbL up to 340 mm), with moderately long tail (20–44% HbL; mean ≈ 28%) and bare soles. Back is fairly dark yellow-rusty, shaded silver-grey, and speckled with white hair tips. Speckles are distinct in some populations, faded in others. Head is ash-grey to silver-grey, black and white mottled; muzzle is rusty, cheeks and eye ring are pinkish buff to cinnamon buff. There is bright spot beneath the eye, a rusty stripe above the eye and an extensive rusty spot below the eye. The area around the ear is also rusty (Fig. 34). Belly is whitish-yellow to cinnamon-buff and grey tinted; flanks are rusty shaded and black and white mottled. Tail above of same colour as back, below rusty; tip is darker and white margined, but lacks a clear subterminal dark ring. Winter pelage is more dense and greyer. Females have 12–16 nipples (Afanas'ev et al. 1953). Skull shows no peculiarities; zygomatic arches are moderately expanded (ZgB = 66–75% CbL); the zygomata bow abruptly outwards; interorbital region is relatively narrow (interorbital width <11 mm); auditory bullae broader than long (Fig. 35). Maxillary cheek teeth are shorter than diastema; margin of hard palate shifted well behind M3; nasals expand backward to the maxillary-frontal suture; messopterygoid fossa is wide. Teeth do not deviate from general condition in the genus; P4 is relatively small. Dimensions (in mm; W

Fig. 34. Russet souslik *Spermophilus major* (Sarabikulovo, Tatarstan, Russia; photo by Alenka Kryštufek).
Obr. 34. Sysel velký *Spermophilus major* (Sarabikulovo, Tatarstan, Rusko; foto Alenka Kryštufek).

in grams): HbL = 246–340, TL = 55–134, HfL = 33.0–56.0, E = 4.5–10.0, W = 287–570 (before hibernation up to 1106 g and 1386 g, respectively in females and males; Popov 1960), CbL = 47.6–59.8, ZgB = 32.3–40.1, MxT = 11.3–13.5. Males are larger than females (sample from Andreevka in Samara Region, Russia): HbL_{50} = 292 (253–314), TL_{50} = 73 (57–88), HfL_{50} = 48 (43–52), CbL_{30} = 54.3 (50.3–57.0), ZgB_{30} = 39.0 (36.0–41.5); females: HbL_{50} = 280 (243–316), TL_{50} = 66 (53–81), HfL_{50} = 45 (32–48), CbL_{30} = 51.9 (50.0–54.3), ZgB_{30} = 37.5 (36.0–39.4) (Artemev 1965). Karyotype 2n = 36 (Voroncov & L'apunova 1974a).

Geographic range (Fig. 36) extends between the river Volga and the upper flows of Išim; northern range border mainly follows river Belaja; further east the range margin is on the line Čeljabinsk – watershed of Tobol and Išim (left tributaries of Irtyš) in central Kazakhstan. Species is rare in the north and colonies are widely apart (Popov 1960). Southern range border is at 51°24' N latitude on Volga (Šlâhtin et al. 2009), at 50° N latitude on the river Ural and at 48° N latitude on the river Emba. A record from north-eastern Xinjiang (Zhang et al. 1997) seems more likely to be based upon misidentified *S. erythrogenys*. During the 10th–11th centuries *S. major* still occupied western banks of the river Don (Gromov et al. 1965) and possibly survived in Ukraine until the 19th century (Sokur 1961). Populations which are currently present on the western bank of Volga may be relicts from that period, however, it is much more likely that *S. major* re-appeared on the western bank in the last decades (Ermakov & Titov 2000). Presence

opposite to Samara dates back to 1951 (Popov 1960), south-west of Ulânovsk to 1950s (possibly a translocation; Titov 2000), and in Verhneuslonskij region north of Kazan to 2000 (Volga was presumably crossed by a bridge; Askeev et al. 2002). Presence in the district of Penza is due to translocation in 1988 (Il'in et al. 2006). Sousliks continue to expand their territory at an average velocity of 4 km per year (Šlâhtin et al. 2009).

S. major spontaneously expanded its range southwards along the Volga from 52° N latitude at the beginning of the 20th century to 51°22' N in 1960s (Šlâhtin et al. 2009) and to 51° N in 1990s; the average gain of new territory was 3.3 km per year (Ermakov & Titov 2000).

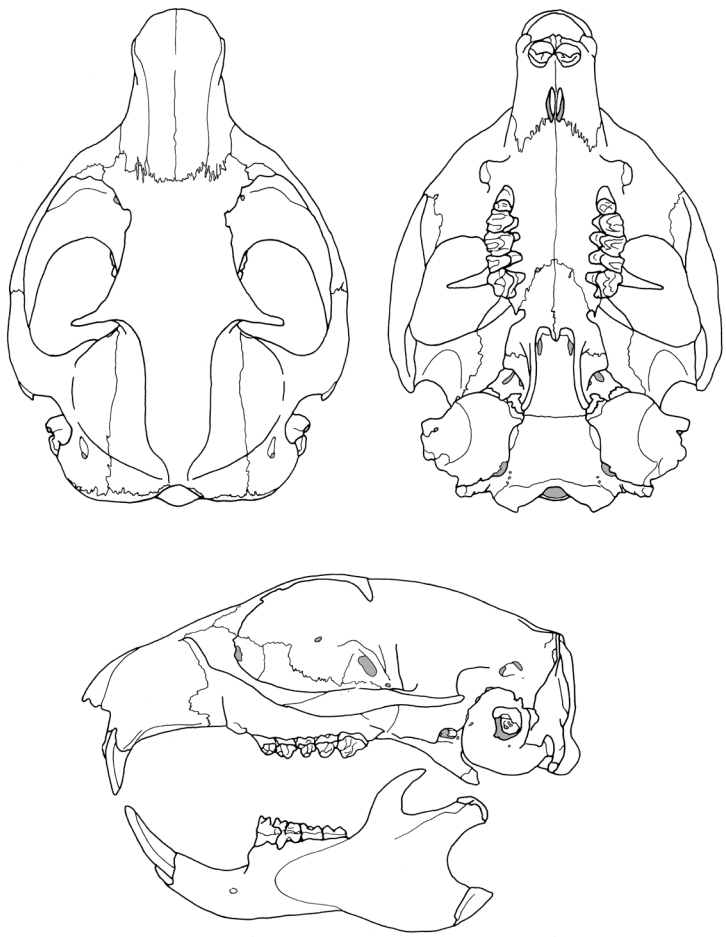


Fig. 35. Skull and mandible of *Spermophilus major* (adult female from the Samara steppe, southern Ural, Russia; ZMB 23131).
Obr. 35. Lebka a mandibula *Spermophilus major* (adultní samice ze Samarské stepi, jižní Ural, Rusko; ZMB 23131).

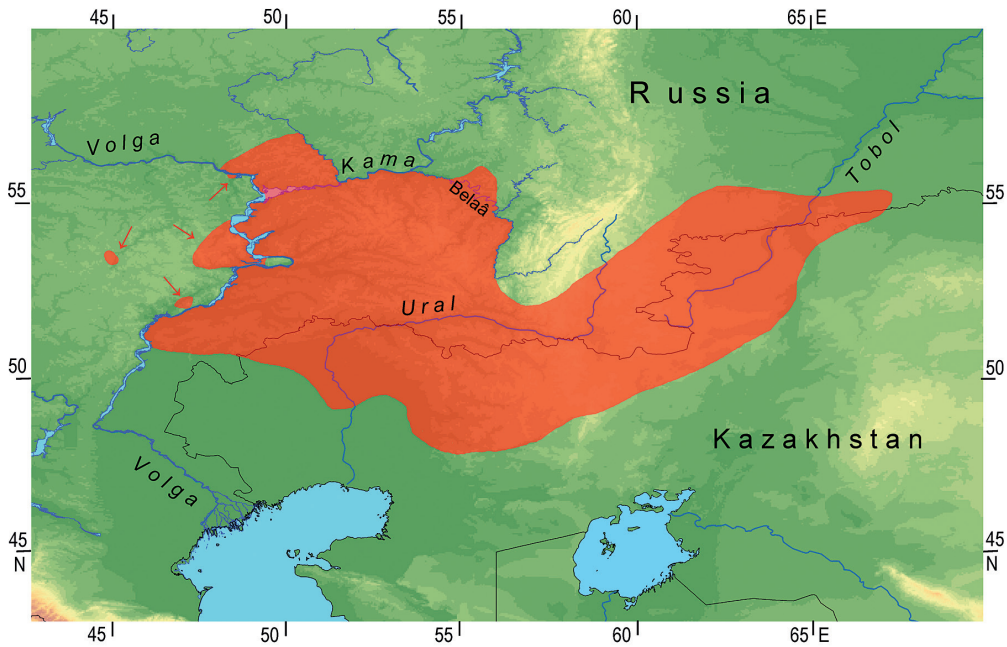


Fig. 36. Distribution of *Spermophilus major*. Compiled from the following sources: the overall range – Popov (1960), Ognev (1947, 1963), Titov (2001), Ermakov et al. (2002), Spiridonova et al. (2005), Tsvirka et al. (2006a), Šlâhtin et al. (2009); Kazakhstan – Sludskij et al. (1969), Nikolskii (1984); range on the western bank of River Volga (indicated by arrows) – Ermakov & Titov (2000), Il'in et al. (2006), Askeev et al. (2002).

Obr. 36. Rošíření *Spermophilus major*. Zkompilováno z následujících pramenů: celkový areál – Popov (1960), Ognev (1947, 1963), Titov (2001), Ermakov et al. (2002), Spiridonova et al. (2005), Tsvirka et al. (2006a), Šlâhtin et al. (2009); Kazachstán – Sludskij et al. (1969), Nikolskii (1984); areál na západním břehu Volhy (označeno šipkami) – Ermakov & Titov (2000), Il'in et al. (2006) a Askeev et al. (2002).

During the 20th century *S. major* became more abundant (shift from "rare" to "common") in dry steppes of the trans-Volga region (Oparin 2005). Resons for expansion are not known but global climate change ensures higher survival and better reproduction, while the expanded road network facilitates spreading along enbankments (Ermakov & Titov 2000).

Since 1960s, some populations got isolated on the islands created by the Volgograd water tank (Šlâhtin et al. 2009). In 1930s and 1950s *S. major* was introduced to the Caucasus (Bertolino 2009).

S. major is a lowland species, with the highest elevational records at 500–600 m. Inhabits steppes (preferably on loamy soils) and fallow land, marginally also semideserts; rarely found on edges of deciduous forests or even within them. Hibernates between late August – early September and April (Tatarstan; Popov 1960); active period is shorter than in smaller species of sousliks and lasts 50–110 days per year in the Volga-Kama region (Artemev 1965).

Subspecies. Darker and larger (mean CbL = 54.1 mm) in mesic habitats along Volga and Kama; paler and smaller (mean CbL = 49.7 mm) under more arid conditions in Orenburg area (Popov 1960). No evidence on discrete evolutionary lineages.

Spermophilus erythrogenys Brandt, 1841 – Red-cheeked souslik

1841 *Spermophilus erythrogenys* Brandt. Type locality: "okresnosti Barnaula" (= vicinity of Barnaul), Russia (Ognev 1947). Vasil'eva (1968) gives the year of publication as 1842; 1843 in Vinogradov & Gromov (1952: 122) is a typographical error (1841 is quoted on p. 123).

1844 *Spermophilus brevicauda* Brandt. Type locality: "in provincis Altaicis australioribus versus lacum Balchasch" (= in the Russian province of Atlai, towards the Lake Balkaš; Ognev 1947). Restricted to "Kazahstan, vostočno-Kazahstanskaâ obl. (= East Kazakhstan Region), oz. (= Lake) Zajsan." (Pavlinov & Rossolimo 1987). Vinogradov & Gromov (1952) quote 1841 as the year of publication.

1844 *Spermophilus intermedius* Brandt. Type locality: "Ad. lac. Balchasch" (Baranova & Gromov 2003), "Lake Balkash" (Ellerman & Morrison-Scott 1951), Burlûtobinsk District, Taldy-Kurgan Region, Kazakhstan (Pavlinov & Rossolimo 1987).

1903 *Spermophilus pallidicauda* Satunin. Type loc.: "See Chulmu-Noor (6800' hoch), Gobi-Altai" (= Lake Chulmu Nor, Gobi Altai), Mongolia. Vasil'eva (1968) gives 1902 as the year of publication.

1912 *Citellus carruthersi* Thomas. Type locality: "Barlik Mts., S. side, N-W Dzungaria, 5000–7000'.", northern Chinese Turkestan.

1923 *Citellus erythrogenys ungae* Martino et Martino. The authorities for *ungae* are "V[ladimir] et E[vgenia] Martino" (Ognev 1947: 74), and not solely "Martino" (cf. Thorington & Hoffmann 2005, Pavlinov & Lissovskij 2012). Type locality: "Okresnosti Omska" (Ognev 1947, Baranova & Gromov 2003) (= near Omsk, Russia); right bank of the river Irtyš (Gromov et al. 1965).

1937 *Citellus erythrogeny saryarka* Selevin. Type locality: "Kazahstan, Pavlodarskaâ obl." (= Pavlodar Region); *nomen nudum* (Pavlinov & Rossolimo 1987).

1941 *Citellus erythrogenys selevini* Argiropulo (in Vinogradov & Argiropulo 1941). Type locality: "Kazakhstan, Džezkazganskaâ obl., Šetskij r-n, Dar'inskij (= Dar'â)" (Pavlinov & Rossolimo 1987), i.e. between Karaganda and Lake Balkaš, north-eastern Betpak-Dala. Synonymized with *S. major* in Thorington & Hoffmann (2005); we follow Pavlinov & Rossolimo (1987) who placed *selevini* into *S. erythrogenys*.

1945 *Citellus pygmaeus iliensis* Belyaev ("Belâev" in Gromov et al. 1965). Type locality: "Kazahstan, Alma-Atinskaâ obl. (= Almaty Region), Čilik" (Pavlinov & Rossolimo 1987). Misspeled as "*ilensis*" in Thorington & Hoffmann (2005).

1954 *Citellus erythrogenys brunnescens* Belyaev ("Belâev" in Gromov et al. 1965). Type locality: "Kazahstan, Pavlodarskaâ obl. (= Pavlodar Region), Èkibastuzskij r-n (= Ekibastuz District), r. (= river) Čidèrty" (Pavlinov & Rossolimo 1987). Vasileva (1968) gives the year of publication as 1955.

1964 *Citellus major heptneri* Vasil'eva (in Vasil'eva 1964a) (spelled as Vasiljeva by Gromov et al. 1965 and Thorington & Hoffmann 2005)). Type locality: "Kazahstan, Pavlodarskaâ obl. (= Pavlodar Region), Irtyšskij r-n (= Irtyšsk District), pravoberež'e r. Irtyš (= right bank of river Irtyš)" (Pavlinov & Rossolimo 1987).

Remarks. Taxonomic scope of *S. erythrogenys* is not satisfactorily defined and the arrangement proposed here is provisional. Uncretain is already delimitation between *S. erythrogenys* and *S. major* and these two sousliks were treated as conspecific in some earlier revisions (e.g. Ellerman & Morrison-Scott 1951). *S. erythrogenys* and *S. major* are at least partly sympatric between the rivers Išim and Tobol where they hybridize (Spiridonova et al. 2005, Tsvirka 2006a). In this zone the two sousliks differ, among others, in their alarm calls (Nikol'skii 1984). Note that vocal repertoires are remarkably similar between species in *Spermophilus*, while the alarm

calls tend to be species-specific (Matrosova et al. 2012). Next uncertainty concerns the eastern distributional border of *S. major*. Vasil'eva (1968) regarded *heptneri* as part of *S. major* and therefore placed the range border of the latter on the river Irtyš. By synonymizing *ungae* with *S. majori*, Vinogradov & Gromov (1952) shifted the eastern range of *S. majori* even further east of Irtyš. The taxonomic position of *heptneri* is puzzling: while it resembles *S. major* in colour, genetic evidence placed it into *S. erythrogenys* (Spiridonova et al. 2005).

Recently, Thorington & Hoffmann (2005) separated *brevicauda* and *pallidicauda* from the scope of *S. erythrogenys* and treated both of them as species on their own right. This steams from interpretation of the results by Harrison et al. (2003) whose study was not intended to delimit species. Such an arrangement, however, is not a novel one since diverse taxonomic solutions for the *erythrogenys* group were discussed in the past. E.g. *erythrogenys*, *brevicauda* and *pallidicauda* were treated as conspecific by Gromov et al. (1965), Pavlinov et al. (1995) and Zhang et al. (1997), but *brevicauda* was treated a species on its own right by Ognev (1947) and Sludskij et al. (1969; as *intermedius*). Ellerman & Morrison-Scott (1951), on the other hand, synonymyzed *brevicauda* and *intermedius* with *S. pygmaeus*. Similarly unstable was

Fig. 37. Red-cheeked souslik *Spermophilus erythrogenys erythrogenys* (region of Altai, Russia; photo by Yuriy Danilov).
Obr. 37. Sysel rudolící *Spermophilus erythrogenys erythrogenys* (oblast Altaje, Rusko; foto Yuriy Danilov).

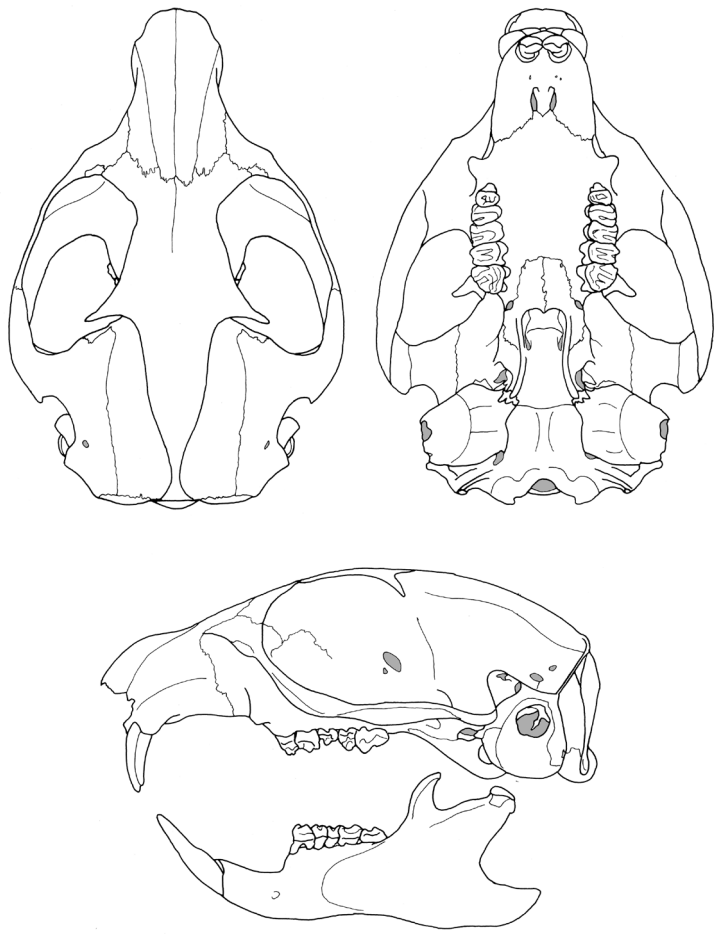


Fig. 38. Skull and mandible of *Spermophilus erythrogenys erythrogenys* (adult female collected north of Kiselevo, Novosibirsk Region, Russia; ZFMK 87.787).
Obr. 38. Lebka a mandibula *Spermophilus erythrogenys erythrogenys* (adultní samice ulovená severně od Kiseleva, Novosibirská oblast, Rusko; ZFMK 87.787).

position of *pallidicauda*; if not synonymized with *erythrogenys*, *pallidicauda* was either treated a subspecies of *S. brevicauda* (e.g. Ognev 1947), or a species on its own right (Allen 1940). Recently, Nikol'skii & Rumyantsev (2004) recognized three species (*erythrogenis*, *carruthersi* and *brevicauda*) on grounds of variability of the alarm call.

Spiridonova et al. (2005, 2006) reported low pairwise genetic distances between *erythrogenys*, *pallidicauda*, *heptneri* and *brevicauda*, and argued against taxonomic splitting. *S. brevicauda* is very similar to *S. erythrogenys*, and the two have the alarm call of about same duration (Nikol'skii 1979). Variation in morphometric data and transferrin alelles retrieved a cline between

erythrogenys and *brevicauda*, and the divergence between the two is estimated at only 10–11 kya (Vorontsov et al. 1980). *S. pallidicauda* differs from *erythrogenys* (incl. *brevicauda*) in diploid chromosomal count (cf. below). Genetic divergences separating *erythrogenys*, *brevicauda* and *pallidicauda* are of about same magnitude (Spiridonova et al. 2005, Tsvirka et al. 2006a); Frisman & Korablev (2007) did not find a single locus with a fixed allele which would unambigously differentiate between *brevicauda* and *pallidicauda*. Hence, we see no reason to separate *pallidicauda* from the scope of *erythrogenys*.

The taxonomic scope of *S. erythrogenys* is evident from the list of synonyms. We recognize subsequently four subspecies. Similar was the conclusion by Gromov et al. (1965), who however, synonymized *heptneri* with *S. major*. Vasil'eva (1968), who recognized seven subspecies (*erythrogenys*, *ungae*, *brevicauda*, *intermedius*, *carruthersi*, *iliensis*, and *pallidicauda*), similarly regarded *heptneri* as part of *S. major*. In retaining *heptneri* in *S. erythrogenys* we follow Spiridonova et al. (2005, 2006) and Tsvirka et al. (2006a).

S. erythrogenys brevicauda hybridize with *S. fulvus* (Afanasyev et al. 1953); *S. e. heptneri* hybridize with *S. major* (Spiridonova et al. 2005) and *S. e. pallidicauda* hybridize with *S. alaschanicus* (Korablev et al. 2006, Tsvirka et al. 2006b).

Description. Medium sized souslik with a short tail (13–26% HbL, mean = 19%) and naked soles of hind feet. Dorsal fur is light sand, yellow buff, rusty yellow or cinnamon, mottled with

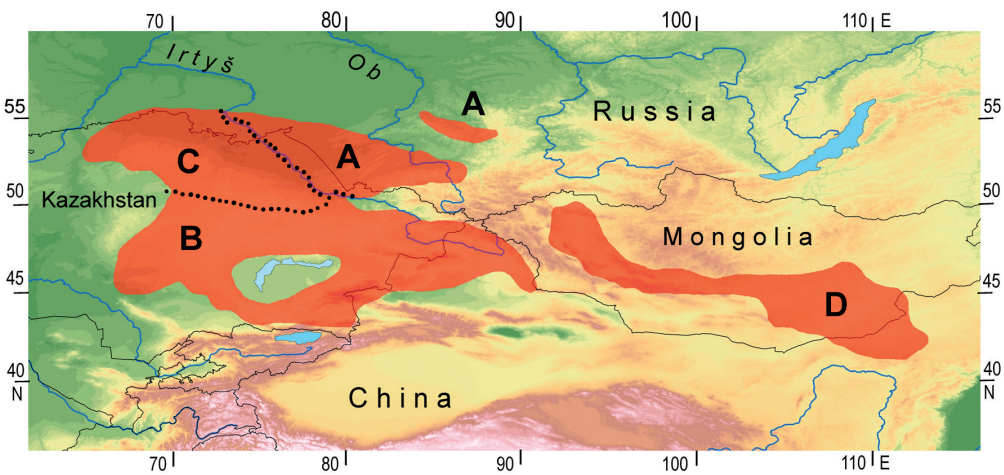


Fig. 39. Distribution of *Spermophilus erythrogenys*. Compiled from the following sources: Russia – Ognev (1947, 1963), Vasileva (1968), Spiridonova et al. (2005), Tsvirka et al. (2006a); Kazakhstan – Sludskij et al. (1969), Ismagilov (1961); Mongolia – Bannikov (1954); China – Zhang et al. (1997). Subspecies are delimited by a dotted line: A – *S. e. erythrogenys*; B – *S. e. brevicauda*; C – *S. e. heptneri*; D – *S. e. pallidicauda*.

Obr. 39. Rozšíření *Spermophilus erythrogenys*. Zkompilováno z následujících pramenů: Rusko – Ognev (1947, 1963), Vasil'eva (1968), Spiridonova et al. (2005), Tsvirka et al. (2006a); Kazachstan – Sludskij et al. (1969), Ismagilov (1961); Mongolsko – Bannikov (1954); Čína – Zhang et al. (1997). Areály poddruhů jsou ohraničeny tečkovanou čarou: A – *S. e. erythrogenys*; B – *S. e. brevicauda*; C – *S. e. heptneri*; D – *S. e. pallidicauda*.

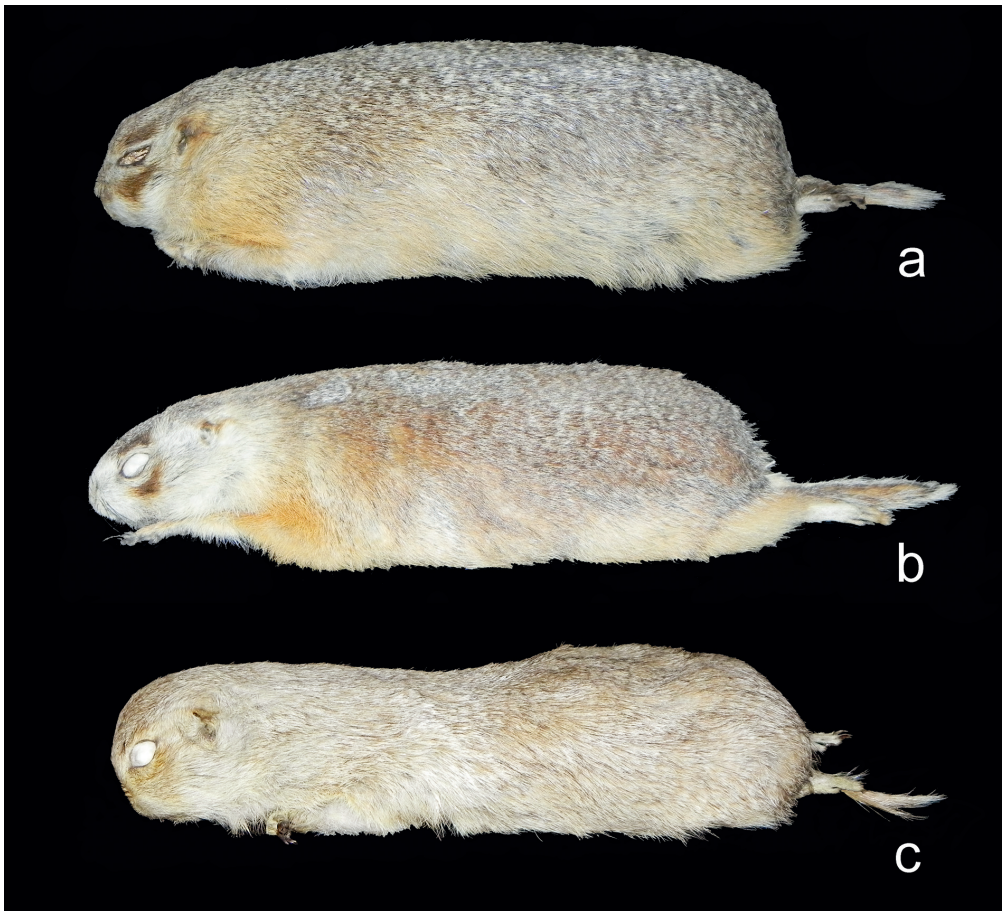


Fig. 40. Skins (in semilateral view) in three subspecies of *Spermophilus erythrogenys*. a – *S. e. erythrogenys* (vicinity of Novosibirsk, Russia; SZM 18939); b – *S. e. heptneri* (Sargatskoe, Omsk Region, Russia; SZM 9885); and c – *S. e. brevicauda* (Almaty Region, Kazakhstan; SZM 57052; photo by Boris Kryštufek).
Obr. 40. Balky (v semilaterálním pohledu) tří subspecií *Spermophilus erythrogenys*. a – *S. e. erythrogenys* (okolí Novosibirska, Rusko; SZM 18939); b – *S. e. heptneri* (Sargatskoe, Omská oblast, Rusko; SZM 9885); c – *S. e. brevicauda* (Almatinská oblast, Kazachstan; SZM 57052; foto Boris Kryštufek).

whitish-yellowish speckles, or unspeckled. The head is of same colour as back, albeit frequently darker, the snout is rusty; characteristic is a rusty-brown spot below and above the eye; eye ring is whitish to light buff. The ear is grey or rusty. Cheeks are white or cream, chin and throat are whitish, belly is pale yellowish-buff, occassionally with rusty shades; flanks are pinkish-buff to pinkish-cinnamon (Figs. 37, 40, 41). Tail at base of same colour as back, pronouncedly rusty in the distal portin, without a blackish-brown subterminal band; the tip is whitish or yellowish edged in dark animals. Skull very similar to *S. major* (Figs. 38, 42), with widely expanded

zygomatic arches (ZgB = 70–76% CbL), a narrow and depressed interorbital region (width of interorbital constriction <10 mm), posteriorly shifted margin of hard palate, and broad auditory bullae. Interpterygoid vacuity widely expanded; posterior margin of hard palate with a distinct denticle. Maxillary tooth-row distinctly longer than diastema. Dimensions (in mm; W in grams): HbL = 195–283, TL = 30–75, HfL = 32–49, EL = 3–10, W = 120–870, CbL = 34.3–51.2, ZgB = 27.8–38.1, MxT = 10.2–12.8. Karyotype: 2n = 34 (*pallidicauda* Tsvirka et al. 2006b), 2n = 36 (the remaining subspecies; Voroncov & Lâpunova 1969, Frisman & Korablev 2007).

Fig. 41. Two subspecies of *Spermophilus erythrogenys*: *a – S. e. brevicauda* (Bedpak-Dala desert, Kazakhstan; photo by Nedko Nedyalkov); b – *S. e. pallidicauda* (Mongolia; photo by Michael & Anne Stubbe).
Obr. 41. Dvě subspecie *Spermophilus erythrogenys*: *a – S. e. brevicauda* (poušť Bedpak-Dala, Kazachstan; foto Nedko Nedyalkov); b – *S. e. pallidicauda* (Mongolsko; foto Michael a Anne Stubbeovi).

Geographic range (Fig. 39). From the upper reaches of river Ob and its tributaries (Išim and Irtyš), to central Nei Mongol in China. Northern range is on the line Omsk – Novossibirsk – Kemerovo, south to Lake Zaisan and north-eastern Xinjiang (Bannikov 1954, Zhang et al. 1997); western border is between rivers Tobol and Išim, and in Betpak-Dala; for further details see subspecies. Occupy forest steppe in the north, *Stipa* steppes and semideserts in the south. Digs burrows in sandy or loamy substrate, clay and saline soils, from flat country up to 2100 m of altitude; habitats with tall vegetation are avoided (Gromov et al. 1965, Šubin 1991).

Subspecies. Despite the inconclusive results of the phylogenetic reconstructions, the recognition of four subspecies seems well founded.

Spermophilus erytrogenys erythrogenys Brandt, 1841

Synonyms. *ungae*, *brunnescens*.

Remark. Identity of *ungae* is uncertain (Gromov et al. 1965); we list it under the nominotypical subspecies on the basis of geographic position of the type locality (right bank of river Irtyš). Afanas'ev et al. (1953) classified *erythrogenys* as a subspecies of *S. major*.

Description. A large and short-tailed subspecies (TL equals 13–26% of HbL; 20% on average). Dorsal pelage is speckled, light yellowish-grey, shaded rusty; flanks pinkish buff or warm buff; ventral side light ochraceous, occassionally rusty tinged, chin and throat white. Rusty patch on the snout present. Head yellowish-grey; a chestnut-brown stripe on the nose and behind the ear; eye ring light-grey to white, rusty patch below the eye contrasts white cheeks. Tail yellowish--grey with rusty tints (Figs. 37, 40a). Females have 12 nipples (Afanas'ev et al. 1953). Skull with moderately expanded zygomatic arches, relatively long nasals, and narrow interorbital region (Fig. 38). Dimensions (in mm; W in grams) (neighbourhoods of Novosibirsk), males: HbL_{54} = 251.3 (200–283), TL_{54} = 48.9 (40–65), HfL_{50} = 39.2 (32–43), E_{15} = 7.3 (5–9), W_{47} = 484.4 (195–870), CbL_{46} = 48.1 (41.9–50.6), ZgB_{45} = 34.8 (31.7–36.5), MxT_{47} = 11.3 (10.7–12.2); females: HbL_{44} = 237.0 (210–265), TL_{44} = 46.9 (40–57), HfL_{44} = 38.2 (34–42), E_{12} = 6.7 (6–7), W_{42} = 385.5 (215–852), CbL_{32} = 45.9 (42.5–48.2), ZgB_{30} = 33.0 (29.9–34.8), MxT_{32} = 11.2 (10.4–11.8) (ZISP, SZM). Karyotype: 2n = 36 (Voroncov & Lâpunova 1969).

Geographic range (Fig. 39A) is in Russia and adjacent north-eastern Kazakhstan, mainly between the rivers Irtyš and Ob, and to the north of about 50° N; population at Kemerovo (to the east of Ob) is an isolate (Gromov et al. 1965). Inhabits flat steppes (frequently on saline soils) and avoids foothills. Hibernates from the beginning of August or first half of September utill the end of March–April (Ognev 1947).

Spermophilus erytrogenys heptneri (Vasil'eva, 1964)

Description. Closely resembles *S. major*, although slightly smaller (Fig. 40b). Tail relatively longer than in other subspecies of *S. erythrogenys* (mean is 26% of HbL). Dorsal pelage fairly dull yellow-rusty, shaded grey, and speckled with white hair tips; flanks are light yellowish, throat and cheeks are whitsh, reddish spots on cheeks and above the eyes well defined; rusty patch on the snout is frequently absent; head is washed grey, but less distinctly than in *S. major*. Tail of same colour as back, terminal hairs are whitish. Skull as in *S. major*. Dimensions (in mm; sexes pooled): HbL_{18} = 249.6 (222–275), TL_{17} = 64.0 (49–76), HfL_{8} = 43.7 (38.5–48.2), E_{3} = 7.0, 7.5, 8.4, W_{3} = 468, 493, 578, CbL_{37} = 46.7 (39.4–51.1), ZgB_{6} = 36.5 (34.8–37.5), MxT_{37} = 11.5 (10.5–12.3) (Vasil'eva 1968; SZM).

Geographic range (Fig. 39C) is predominantly in Kazakhstan, to the west of Irtyš and to the north of about 50° N.

Spermophilus erytrogenys brevicauda Brandt, 1844

Synonyms. *intermedius*, *carruthersi*, *saryarka*, *selevini*, *iliensis*.

Description. A short tailed subspecies (TL equals 15–19% HbL; 17.3% on average); tail of about the same length as hind foot. Size varies, being small in the south (mean CbL = 40.0 mm) and large in the north (= 47.9 mm; Ognev 1947). Dorsal pelage is speckled; colour varies from pinkish-buff to greyish-buff or reddish-brown. Tail is pinkish buff to light rusty with pronounced rusty tints, and without subterminal dark band. Reddish spots on cheeks and above eyes rather well defined; rusty patch on the snout is frequently absent (Figs. 40c, 41a). Females have 10 or 12 nipples (Afanas'ev et al. 1953). Skull as in the nominotypical subspecies, but with more bowed zygomata and shorter nasals (Fig. 42a). Dimensions (in mm; W in grams; sexes pooled): HbL_8 = 226.8 (195–256), TL_8 = 40.0 (30–54), HfL_8 = 37.0 (32–42), E_8 = 5.3 (3–10), W_6 = 352.3 (282–447), CbL_{16} = 44.8 (38.4–51.0), ZgB_{15} = 33.0 (28.3–38.1), MxT_{16} = 11.1 (10.2–12.8) (Ognev 1947, ZISP, SMF). Ranges for body mass in Kazakhstan, males: 140–720 g, females 120–540 g (Sludskij et al. 1969). The darkest and the largest animals occupy Betpak-Dala

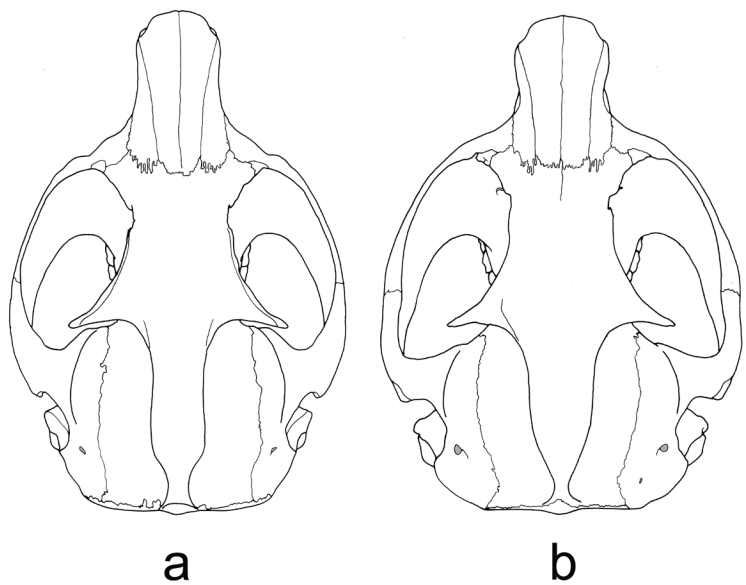


Fig. 42. Dorsal view of a skull in two subspecies of *Spermophilus erythrogenys*: *a – S. e. brevicauda* (adult female from the Tarbagatai Mts., Kazakhstan; SMF 70105); b – *S. e. pallidicauda* (adult female from the vicinity of Bayandalay, Mongolia; SMG M6779).
Obr. 42. Dorsální pohled na lebku dvou subspecií *Spermophilus erythrogenys*: *a – S. e. brevicauda* (adultní samice z pohoří Tarbagataj, Kazachstan; SMF 70105); b – *S. e. pallidicauda* (adultní samice z okolí lokality Bajandalaj, Mongolsko; SMG M6779).

Desert (mean head and body length for males/females = 227 mm/216 mm), the palest and the smallest are from the left bank of the river Ili (193 mm/184 mm for males/females; Ismagilov 1961). Karyotype: 2n = 36 (Voroncov & Lâpunova 1969, Frisman & Korablev 2007).

Geographic range (Fig. 39B) is between the rivers Irtyš and Išim, in the Kazakh highland, in Betpak-Dala and around Lake Balkaš and the river Ili (Gromov et al. 1965, Sludskij et al. 1969, Spiridonova et al. 2006); also occupy north-eastern Xinjiang in China (Zhang et al. 1997). Highest densities are between 45°20' – 47°20' northern latitude and 69°45' – 73°30' of eastern longitude (Ismagilov 1961). Populates semideserts, deserts and high elevation steppe up to 2100 m a.s.l. (Džungarian Alatau; Ismagilov 1961). Hibernates from late June–July till March, i.e. 256 days on average (Sludskij et al. 1969).

Spermophilus erytrogenys pallidicauda Satunin, 1903

Description. A relativelly small form of *S. erythrogenys* with moderately long tail (17–28% of HbL, mean = 22% HbL). Pelage is pale and lacks speckles. Dorsal region is light sand coloured, shaded pinkish buff or cinnamon-buff; dark base in individual hairs is short. Underside is white, faintly shaded with buffy. The head is of same colour as back; the top of the snout is rusty; eye circle is white; a rusty spot is below each eye and an ill-defined white stripe passes from the snout to the ear (Fig. 41b). Tail is rusty in the center above and below, fringed with long whitish or pale buff hair tips; black hair and the subterminal black border are missing entirely. Skull with expanded zygomatic arches, wide interorbital region, and short rostrum (Fig. 42b). Dimensions (in mm, W in grams; sexes pooled): HbL_{14} = 223.1 (195–242), TL_{14} = 47.9 (40–60), HfL_{14} = 39.9 (36–45), E_{10} = 7.6 (4–10), W_7 = 383.0 (228–505), CbL_{11} = 43.7 (39.1–47.6), ZgB_{13} = 31.2 (27.8–33.2), MxT_{15} = 11.0 (10.4–11.8) (Allen 1940, Ognev 1947, Stubbe & Chotolchu 1968, specimens in USNM). Descriptive statistics for Mongolian material (in mm): HbL = 210 (196–260), TL = 44 (31–59), HfL = 39 (33–49), CbL = 42.5 (34.3–51.2), ZgB = 31.2 (27.8–38.6), MxT = 11.0 (Bannikov 1954). Karyotype: 2n = 34 (Tsvirka et al. 2006b).

Geographic range (Fig. 39D) is most probably not contiguous with the remaining of *S. erythrogenys*, since there is a gap in north-western Mongol Altai (between lakes Ulungur Nor and Khara Usu Nur). *S. e. pallidicauda* occupy Mongolia and north-eastern China. In Mongolia, the range is mainly squeezed between the mountain ranges of Khangay in the north and Mongol Altai and Gobi Altai in the south and south-west; north-western records reach Lake Ubsa Nur at about 92° E longitude. Only central Nei Mongol (north-west of Hohhot) is inhabited in China (Zhang et al. 1997); Hoffmann & Smith (2008) mapped range of *pallidicauda* for the entire Nei Mongol and northern Gansu, which contradicts all authorities dealing with the *S. erythrogenys* group (Allen 1940, Bannikov 1954, Sokolov & Orlov 1980 ; Zhang et al. 1997). Main habitat is semi-desert and its transition to a *Stipa* steppe up to 2100 m of altitude (Ognev 1947). Hibernates from mid-September till early April (Bannikov 1954).

Spermophilus relictus (Kashkarov, 1923) – Relict souslik

1923 *Citellus musicus relictus* Kashkarov (in Kashkarov et al. 1923) (spelled Kaškarov in Ognev 1947, and Kaschkarow in Vinogardov & Gromov 1952). Type locality "Uŝel'e Kara-Bura i uŝel'e Kumyš-Tag v Talasskom Ala-Tau" (Ognev 1947) (= Ravine of Kara-Bura and ravine of Kumyš-Tag in the Talas Ala-Tau), Čatkal'sk Region, Talas District, Kyrgyzstan.

1925 *Citellus relictus* Kashkarov. Designated as a new species, but actualy change of rank.

1948 *Citellus relictus ralli* Kuznecov (spelled as Kuznezov in Vinogardov & Gromov 1952). Type locality: "Isykkul'skaâ kotlovina" (= valley of the Lake Issyk-Kul, Kyrgyzstan). Preoccupied by *Citellus pygmaeus ralli* Geptner, 1948 (Pavlinov & Rossolimo 1987).

1989 *Spermophilus relictus nilkaensis* Hou et Wang. Type locality: "5 km east of a village Zhaikou, altitude 1500 m", Nileke District, Xinjiang, China. This name is overlooked in Thorington & Hoffmann (2005).

Description. Medium sized and moderately long-tailed souslik (TL ≈ 31% HbL), with nude soles. Back is cinnamon-brown, tinted grey and indistinctly speckled, flankes are lighter. Head is grey-buff and speckled brown, snout and front are pinkish-buff with grey hues; eye ring is whitish, cheeks are greyish-white to yellowish, chin and throat are cream, belly is greyish-buff; paws are rusty buff. Tail is cinnamon-buff, mottled by dark hair tips; blackish-brown subterminal ring is visible also on the ventral side; tail is margined by yellowish-white hair tips (Figs 43, 44). Winter pelage is lighter and greyer. Females have 10 (exceptionally 11; Stroganova & Chu Tsing 1961) or 12 nipples (Afanas'ev et al. 1953). Skull has widely spanned zygomatic arches (ZgB = 64.8–705% CbL) and not much constricted interorbital region (width of constriction > 10 mm); MxT exceeds diastema; braincase is short; nasals are long. The zygoma forms smooth curve at its junction with rostrum. Cheeck-teeth rows converge posteriorly; hard palate is with distinct denticle; bullae are of globular shape. Supratemporal ridges do not merge into a crest. The profile of the skull is evenly convex, however the interorbital region protrudes (Fig. 45). Cheek-teeth rather hypsodont; P^3 is relatively large. Dimensions (in mm; W in grams), males: HbL = 190–280, TL = 41–90, HfL = 35.0–43.5, EL = 8–12, W = 245–475, CbL = 42.7–49.6, ZgB = 28.1–33.7, MxT = 10.5–13.4. Karyotype: 2n = 36 (Liapunova & Vorontsov 1970, Voroncov & L'apunova 1974).

Geographic range covers western and central Tian Shan and marginally Pamiro-Altai in E Uzbekistan, NW Tajikistan, Kyrgyzstan, Kazakhstan and western Xinjang. Specifically, the range includes a series of mountain ridges east of Tashkent and east of Lake Issyk-Kul (Čatkalskij, Kuraminskij, Ferganskij, Moldo-Tau, Kavak-Tau, Terskej Alatau, Kungej Alatau, Ketmen'); there is also an isolate in Gissarskij ridge to the south of Samarkand (Stroganova & Chu Tsing 1961, Davydov 1974). Typical habitat is a mountain steppe and semidesert with low vegetation at 1700–2600 m a.s.l. (750–3300 m; Davydov 1974). Hibernates for 6–7 months (Ajzin 1979),

Fig. 43. Relict souslik *Spermophilus relictus* from western Tian Shan Mts., Uzbekistan (photo by Boris Petrov).
Obr. 43. Sysel hnědavý *Spermophilus relictus* ze západu pohoří Tian Shan, Uzbekistan (foto Boris Petrov).

Fig. 44. Skin of *Spermophilus relictus* from Kurgan-Tash, western Tian Shan Mts., Uzbekistan (PMBg 134/56; photo by Milan Paunović).
Obr. 44. Balk *Spermophilus relictus* z lokality Kurgan-Taš, západ pohoří Ťan-Šan, Uzbekistan (PMBg 134/56; foto Milan Paunović).

between first half of July – mid-September (depends on the water content in food) and late February – March (Sludskij et al. 1969).

Subspecies. Two subspecies (the nominotypical and *ralli*) are recognized by majority of authors and Vasil'eva (1964) suggested that they represent distinct species. This was followed by Thorington & Hoffmann (2005) but opposed by Nadler et al. (1982) on grounds of biochemical comparisons. Thorington et al. (2012) mapped a broad sympatry of *relictus* and *ralli* around the Lake Issyk-Kul which contradicts a detailed study by Vasil'eva (1964). Nikolskii (1979) reported acoustic differences between the two taxa.

The name *ralli* Kuznecov is preoccupied by *Citellus pygmaeus ralli* Geptner, 1948 (Pavlinov & Rossolimo 1987). Another name (*nilkaensis;* Hou & Wang 1989) is available for relict sousliks from Lake Issyk-Kul and Xinjang but overlooked in the West. We use *nilkaensis* to replace *ralli*, assuming on geographic grounds that the two are most probably identical.

Spermophilus relictus relictus (Kashkarov, 1923)

Description. Smaller on average with shorter row of cheek-teeth and relatively shorter tail (TL ≈ 25% HbL). Back with bright rusty tints, head dark brown. A population isolated on Gissarskij ridge is more grey and speckled than the remaing animals (Stroganova & Chu Tsing 1961). Nasals expand anteriorly; in lateral view their anterior part protruds markedly above the smooth skull profile. Dimensions (in mm, W in grams; sexes pooled): HbL_{113} = 229 (190–250), TL_{113} = 53.7 (41–71), HfL_{35} = 36.0 (33–38), CbL_{113} = 45.3 (42.7–48.6), ZgB_{113} = 30.7 (29.0–32.8), MxT_{113} = 11.7 (11.0–12.5) (Stroganova & Chu-Tsing 1961, Vasil'eva 1964). Males are larger than females (sample from Tajikistan; Davydov 1974); males (n = 65): HbL = 244.1 (220–256), TL = 68.6 (44–73), HfL = 41.5 (39–44), CbL = 46.6 (43.8–48.8), ZgB = 31.6 (28.0–33.6); females (n = 49): HbL = 232.7 (220–256), TL = 58.5 (44–69), HfL = 39.8 (38–43), CbL = 45.9 (42.9–47.8), ZgB = 30.2 (28.6–31,5); body mass in spring in males = 304 (243–396), in females = 311 (235–388), body mass before hibernation in males = 457 (309–680), in females = 404 (345–575). Sousliks tend to be larger in lower altitudes in the Kuraminskij ridge of Tajikistan (Davydov 1974).

Geographic range (Fig. 46A). The range encompasses western part of the distribution area, east to Kavk-Tau and Moldo-Tau Mts.

Spermophilus relictus nilkaensis Hou et Wang, 1989

Synonym. *ralli*.

Description. Larger on average with a longer row of cheek-teeth and relatively longer tail (TL ≈ 33% HbL). Rusty tints restricted to posterior back; head shaded grey. Nasals are paralel; their anterior part does not markedly protrude above the smooth convex skull profile. Dimensions

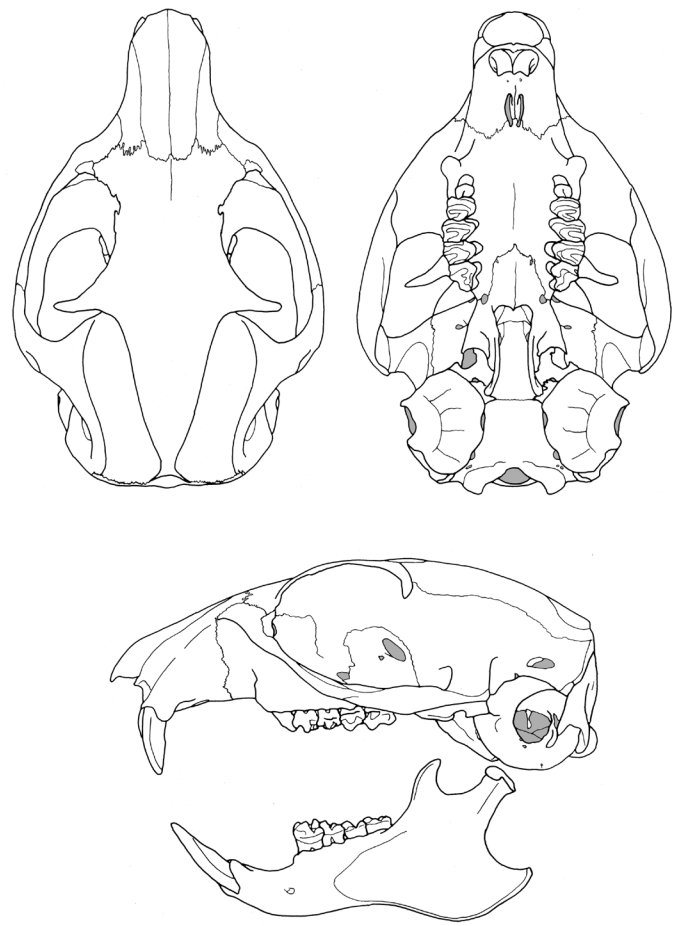


Fig. 45. Skull and mandible of *Spermophilus relictus* (south of lake Issyk Kul', Kirghizstan; SMF 47908).
Obr. 45. Lebka a mandibula *Spermophilus relictus* (jižně od jezera Issyk Kul', Kirgizstan; SMF 47908).

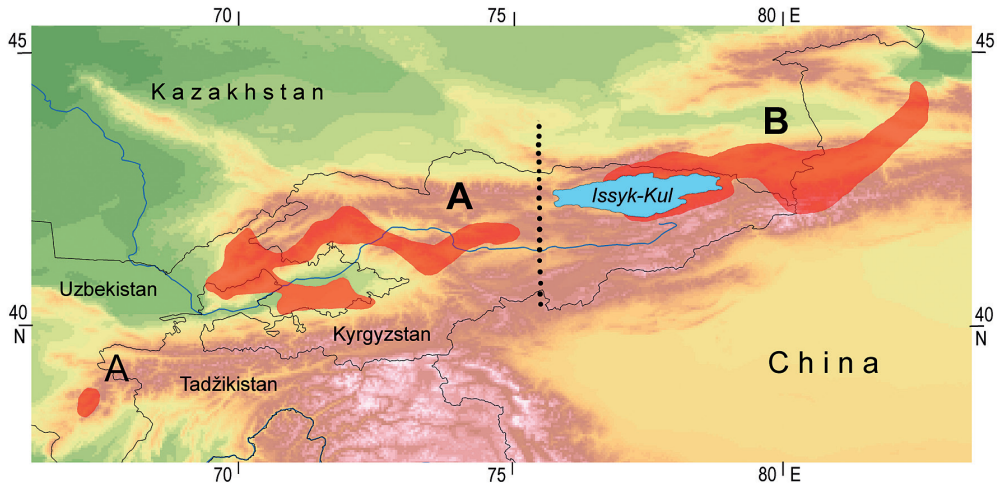


Fig. 46. Distribution of *Spermophilus relictus*. Compiled from the following sources: former Soviet Union – Stroganova & Chu Tsing (1961), Davydov (1964), Sludskij et al. (1969), Vasil'eva (1964); China – Zhang et al. (1997). Subspecies are delimited by a dotted line: A – *S. r. relictus*; B – *S. r. nilkaensis*.
Obr. 46. Rozšíření *Spermophilus relictus*. Zkompilováno z následujících pramenů: bývalý SSSR – Stroganova & Chu Tsing (1961), Davydov (1964), Sludskij et al. (1969), Vasil'eva (1964); Čína – Zhang et al. (1997). Areály poddruhů jsou ohraničeny tečkovanou čarou: A – *S. r. relictus*; B – *S. r. nilkaensis*.

(in mm; sexes pooled): HbL_{105} = 233 (195–280), TL_{105} = 75.3 (65–90), HfL_{88} = 46.0 (40–49), CbL_{105} = 46.8 (43.1–49.6), ZgB_{105} = 31.6 (29.0–33.7), MxT_{105} = 12.3 (11.4–13.1) (Stroganova & Chu-Tsing 1961, Vasil'eva 1964).

Geographic range (Fig. 46B) covers the eastern part of the distribution area, as west as Lake Issyk Kul (Vasil'eva 1964).

TAXONOMIC ANNEX

Sciurotamiini new tribe

History. The genus *Sciurotamias*, which is the only member of the new tribe, was established by Miller (1901) with *Sciurus davidianus* Milne-Edwards, 1867, as the type species. Position of *Sciurotamias* in the system of Sciuridae was highly controversial and the genus was suggested in to be a close relative to squirrels which are now in four different subfamilies of the family Sciuridae (sensu Thorington & Hoffmann 2005): to Callosciurinae (Black 1963), as part of *Rhinosciurus* (Trouessart 1897) or a close relative to *Dremomys* (Allen 1940); to Sciurinae (close to *Tamiasciurus*; Moore 1959); to Ratufinae (Callahan & Davis 1982); and to Xerinae (Ellerman 1940; Gromov 1965; Thorington & Hoffmann 2005). Within Xerinae, *Sciurotamias* was mainly associated with *Tamias* s. lat. (currently in the tribe Marmotini), largely on the basis of its well-developed os clitoris and a simple baculum (Callahan & Davis 1982); Moore (1959) noted similarities also with Xerini. Molecular reconstructions did not produce consistent

results, either placing *Sciurotamias* into Marmotini (a putative sister group to Tamiina; Steppan et al. 2004), or as a sister group to the lineage of Marmotini and Protoxerini combined (Mercer & Roth 2010); the latter is consistent with its small litter which is an ancestral character in Xerinae (Hayssen 2008).

Description. Part of Xerinae as evident from a multigenic phylogenetic reconstructions based on nuclear and mitochondrial genes (sequences of approximately 5000 bp in Steppan et al. 2004; 2659 bp in Mercer & Roth 2010), and possibly a sister group to the lineage of Marmotini and Protoxerini combined (Mercer & Roth 2010). Sciurotamiini new tribe differs from the remaining Xerinae in annulated glans penis and in a baculum which is heavily bent dorsally (Callahan & Davis 1982). In Sciurotamiini the cheek pouches are present (absent in Xerini and Protoxerini), and the auditory bulla has 3 transbullar septa (1–2 septa in Protoxerini, 2 septa in Marmotini; Moore 1959).

Type genus. *Sciurotamias* Miller, 1901.

Content. The new tribe contains the genus *Sciurotamias* Miller, 1901, with two species: *S. davidianus* (Milne-Edwards, 1867) and *S. forresti* (Thomas, 1922). Both species are endemic to China (Zhang et al. 2004).

SOUHRN

Základní taxonomickou revisi palearktických savců publikovali v polovině minulého století Ellerman & Morrison Scott (1951), kteří zkompilovali dosavadní taxony a utřídili je do polytypických druhů. Na jejich dílo navázal Corbet (1978), který doplnil nově popsané taxony a připojil určovací klíče a schematické mapky rozšíření. Protože v posledních desetiletích došlo, především díky molekulárně-genetickým metodám, k enormnímu nárůstu informací o příbuzenských vztazích jednotlivých druhů savců a o jejich vnitrodruhové variabilitě, nastala nutnost integrovat tyto poznatky do taxonomického systému v souladu s Mezinárodními pravidly zoologické nomenklatury (ICZN). Poslední taxonomické kompilace jsou v tomto směru buď málo podrobné, protože shrnují poznatky o celosvětové fauně savců (Wilson & Reeder 2005), nebo jsou věnovány pouze části Palearktu, např. Rusku (Pavlinov & Lissovskij 2012). Předložená práce je proto pokusem o podrobnou revisi jedné skupiny palearktických hlodavců, konkrétně burunduka *Eutamias sibiricus* a syslů rodu *Spermophilus*. Pro úplnost zahrnujeme i ze Severní Ameriky introdukovaného čipmanka východního (*Tamias striatus*). Jednotlivé druhy se snažíme definovat na základě jejich morfologie, genetických znaků, rozšíření a biotopových nároků.

Na základě excerpce stovek literárních pramenů a studia více než 2500 sbírkových exemplářů rozlišujeme 12 autochtonních druhů: burunduka *Eutamias sibiricus* (se třemi poddruhy – *sibiricus*, *senescens* a *barberi*), sysla obecného *Spermophilus citellus* (sspp. *citellus*, *gradojevici* a *karamani*), sysla taurského *S. taurensis,* sysla maloasijského *S. xanthoprymnus* (sspp. *xanthoprymnus* a *gelengius*), sysla perličkového *S. suslicus* (sspp. *suslicus* a *odessanus*), sysla alašanského *S. alaschanicus,* sysla daurského *S. dauricus,* sysla malého *S. pygmaeus* (sspp. *pygmaeus*, *musicus* a *planicola*), sysla žlutého *S. fulvus,* sysla velkého *S. major,* sysla rudolícího *S. erythrogenys* (sspp. *erythrogenys, heptneri, brevicauda* a *pallidicauda*), a sysla hnědavého *S. relictus* (sspp. *relictus* a *nilkaensis*).

Pro uvedené druhy byla shrnuta všechna nám známá jména ze skupiny druhu (celkem 119) 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.

U syslů rodu *Spermophilus* často dochází k introgresivní hybridizaci což někdy stírá jejich druhové hranice. Kladogramy vytvořené na podkladě molekulárních znaků potom často vedou k vytváření parafyletických nebo polyfyletických taxonů. Mezidruhová hybridizace, která je pravděpodobně způsobena

značnou promiskuitou a výskytem mnohačetné paternity byla zatím dokumentována u sedmi druhů syslů v těchto kombinacích: *S. major* × *S. fulvus*, *S. major* × *S. pygmaeus*, *S. major* × *S. suslicus*, *S. major* × *S. erythrogenys brevicauda*, *S. erythrogenys pallidicauda* × *S. alaschanicus*, *S. pygmaeus* × *S. suslicus*, and *S. citellus* × *S. suslicus*. Jednotlivé subspecie syslů jsou často odděleny velkými řekami. Naše revise tribového členění podčeledi Xerinae vyústila v popis nového tribu Sciurotamiini, který zahrnuje rod veverek *Sciurotamias* obývajích Čínu.

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