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Mus spicilegus.

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Mus spicilegus Petenyi, 1882

Mound-building Mouse

M. spicilegus Petenyi, 1882:114. Type locality not specified exactly, Felsóbesnyó near Budapest, Hungary, as restricted by Csorba and Demeter, 1991 (*acervator* Petenyi, *acervifex* Petenyi, *canicularis* Petenyi, *caniculator* Petenyi were proposed as alternative names).
Mus mehelyi Bolkay, 1925:12. Type locality Bosnia, Yugoslavia.
Mus sergii Val'kh, 1927:49. Type locality southern Ukraine.

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Murinae, Genus *Mus* (Musser and Carleton, 1993). *M. spicilegus* is monotypic.

DIAGNOSIS. *M. spicilegus* has homogeneous gray fur (occasionally light-bellied) with no reddish colors (Fig. 1). The tail of *M. spicilegus* is thinner than tails of other species of the *Mus musculus* superspecies complex. Throughout almost its entire range, *M. spicilegus* is sympatric with *M. m. musculus* and in some regions of western Europe is sympatric with *M. m. domesticus*. *M. m. domesticus* is dark, sometimes black in color, and length of tail is equal to or longer than length of body (Marshall, 1986). Length of tail of *M. spicilegus* is always shorter than length of body (Mezhzherin, 1994). *M. spicilegus* is distinguished from *M. m. musculus* by width of anterior molar process relative to width of upper zygomatic arch (greater in *M. spicilegus*; 0.50–0.80 vs. 0.38–0.49 for *M. m. musculus*), by distance from occipital condyle to cross-section of interparietal and parietofrontal sutures (greater in *M. spicilegus*; 7.3–14.1, vs. 5.58–6.28 for *M. m. musculus*), and by width of upper zygomatic arch (narrower in *M. spicilegus*; <0.8 mm, vs. >0.8 mm for *M. m. musculus*—Lyalyukhina et al., 1991; Migulin, 1937; Orsini et al., 1983; Sharleman, 1937; Sokolov et al., 1990).

Typical of *M. spicilegus* are shape (acute angle) of proximal end of incisive foramen (Willenig, 1987), shape of first M1-diastema (root of M1 does not project—Mezhzherin and Zagorodnyak, 1989), and usual lack of an aperture on masseteric plate (Orsini et al., 1983). Skulls (Fig. 2) of *M. spicilegus* are tall dorsoventrally, but short longitudinally. As a result, the rostrum is relatively the deepest and shortest in the genus *Mus* and the narrow zygomatic plate is also the tallest and narrowest (Marshall, 1986; Marshall and Sage, 1981). Dorsally the rostrum is narrow, and zygomatic plates seem pinched together.

Gerasimov et al. (1990) used discriminant analysis of skull measurements to identify five species of *Mus*. Highly significant values were mostly from jaws, particularly measurements of molars and mandibular tooth row, as well as distance between alveoli insisivi lateralis.

The forms of glans penis and os penis of *M. spicilegus* and *M. m. musculus* differ. *M. spicilegus* has a glans penis with slightly rounded papilla centralis (lateral view), whereas papilla centralis of *M. m. musculus* is sharpened. Heads of spermatozoa in *M. m. musculus* and *M. spicilegus* also differ (Lavrenchenko, 1990). Heads of spermatozoa in *M. spicilegus* are smallest (mean 7.57 by 3.07 μm) of the *M. musculus* superspecies complex. Depth of posterior flap in *M. spicilegus* is deep, and posterior part of head is long, thin, and evenly rounded. Depth of posterior flap in *M. m. musculus* is not deep and posterior part of head is not evenly rounded.

During the reproductive season, testes of mound-building mice are two to three times as heavy as those of *M. m. musculus* (Sokolov et al., 1988*a*, 1990). The most important behavioral character specific to *M. spicilegus* is its ability to construct mounds, which are supplied with grain and seeds in autumn.

GENERAL CHARACTERS. *M. spicilegus* is a small mouse with a gray homogeneous or contrasting two-colored coat. Mice from

FIG. 1. Adult male *M. spicilegus* from Kishinev city, Moldova.

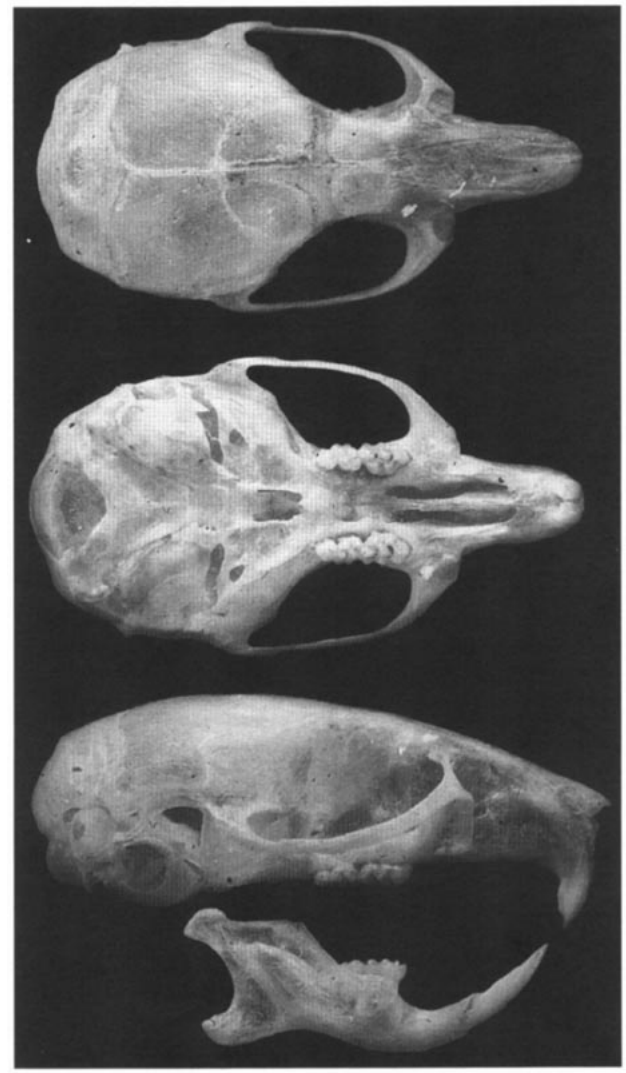

FIG. 2. Dorsal, ventral, and lateral view of the skull and lateral view of the mandible of *M. spicilegus* from Kirovograd town, Ukraine (adult male, collection of E. Kotenkova). Greatest length of skull is 19.5 mm.

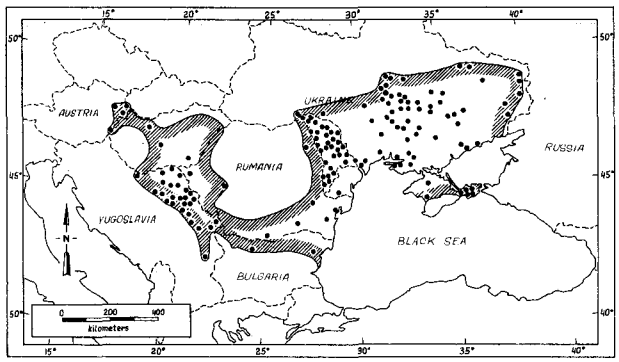

FIG. 3. Distribution of *M. spicilegus* (Baues et al., 1988; Hamar, 1960; Kotenkova et al., 1994; Lyalukhina et al., 1989; Sokolov et al., 1990). Dots represent documented *M. spicilegus* captures or mounds.

Romania have light backs and white bellies (Hamar, 1960). *M. spicilegus* from Hungary, the former Yugoslavia, and Austria is similar in coloration to *M. m. musculus* in the same area (Marshall, 1986). *M. spicilegus* from central Ukraine has a homogeneously gray-colored coat, but the belly is lighter than the back (Mezhzherin and Zagorodnyuk, 1989). The dorsum of mound-building mice in Moldova is darker than that of *M. m. musculus* (Sokolov et al., 1990). Mound-building mice from southern parts of Ukraine have bicolored coats with lighter gray backs and light bellies (Mezhzherin and Zagorodnyuk, 1989).

Average external measurements (in mm) of *M. spicilegus* from Kirovograd region, Ukraine (n = 130—Sokolov et al., 1990), Dnepropetrovsk region, Ukraine (n = 23—Pisareva, 1948), Charkov region, Ukraine (n = 17—Ladygina, 1964), Dobrudzha, Romania (n = 32—Hamar, 1960), and Moldova, Romania (n = 18—Simionescu, 1965), respectively, are as follows: length of body, 78.6, 69.7, 80.5, 73.5, 75.1; length of tail, 64.3, 55.2, 62.3, 64.0, 61.4; length of hind foot, 15.9, 15.3, 16.5, 15.8, 15.7; length of ear, 10.4, 10.3, 12.5, –, 12.1.

Dental formula of *M. spicilegus* is i 1/1, c 0/0, p 0/0, m 3/3, total 16 (Bobrinskii et al., 1965). Mean values of skull measurements (in mm) of *M. spicilegus* from central Ukraine (n = 132), from southeastern Ukraine (n = 20), and Moldova, the former USSR (n = 22), respectively, are as follows: greatest length of cranium, 20.3, 20.2, 20.7; condylobasal length, 18.5, 18.8, 19.7, length of diastema, 5.3, 5.1, 5.6; length of maxillary toothrow, 3.5, 3.4, 3.6; length of mandibular toothrow, 3.1, 3.1, 3.0 (Lyalyukhina et al., 1991).

DISTRIBUTION. *M. spicilegus* occurs in Ukraine, Moldova, some regions of Romania, the former Czechoslovakia, Hungary, the former Yugoslavia, Bulgaria, and Austria (Fig. 3). *M. spicilegus* extends from the Moldova steppes into the woody steppe zones of Ukraine, including some parts of the Crimea and the Kerch Peninsula (Ausländer and Hellwing, 1957; Bauer et al., 1988; Eibl-Eibesfeldt, 1950; Engels, 1980; Festetics, 1961; Hamar, 1958, 1960; Kotenkova et al., 1994; Lyalyukhina et al., 1989; Marshall, 1986; Martino, 1930; Mikesh, 1961; Naumov, 1940; Papadopol and Chizelea, 1965; Paspalaev et al., 1950; Petrov, 1954; Petrov and Rŭzic, 1985; Sokolov et al., 1990). No fossils of this species are known.

FORM AND FUNCTION. The level of metabolism in *M. spicilegus* declines from spring to autumn and subsequently increases to reach its maximum value in winter (Ladygina, 1954). Oxygen consumption (ml kg^{-1} h^{-1}) is 9,958 in summer, 9,633 in autumn, and 10,371 in winter (when temperatures are 25°, 15°C, and 5°C, respectively). Oxidative processes in mound-building mice are higher than those in *M. m. musculus*. As temperature drops from 25° to 5°C, oxygen consumption by *M. spicilegus* increases from 145 to 192% or 7.2–9.6% per one degree ambient temperature (Ladygina, 1954, 1964). Thermal insulation in *M. spicilegus* is less effective than in *M. m. musculus*. Thermal conductivity of winter fur in *M. spicilegus* is high compared with *M. m. musculus*. Presumably in mound- building mice in autumn, heat irradiation declines due to accumulation of fat reserves rather than because the fur is becoming thicker. When given a gradient of temperature in captivity, *M. spicilegus* prefers 33°C in summer, 29°C in autumn, and 28°C in winter. The main type of thermoregulation in *M. spicilegus* is chemical (Ladygina, 1954, 1964; Medvedeva, 1950).

ONTOGENY AND REPRODUCTION. Newborn mound-building mice are naked, without teeth, and toes are not separated. Formation of fur begins on day 1 or 2, and young are covered with fur by the end of the second week. Pinnae become erect on day 3 or 4; lower incisors erupt at 13–14 days; upper incisors erupt at 14–15 days; and eyes open at 17–18 days. Development of *M. spicilegus* is 2–3 days slower than *M. m. musculus* (Zagoruiko and Kotenkova, 1992).

Mound-building mice breed seasonally. In the Dnepropetrovsk region, pregnant females have been trapped from February to October (Pisareva, 1948). In southeastern and central Ukraine, mound-building mice breed from late March to mid-October, with 44.4–73.1% of females pregnant during these months (Naumov, 1940; Sokolov et al., 1990). In spring, females that have spent winter in mounds and are 6–8 months of age will breed. In summer, those born in spring and early-summer will breed. Females can breed in the third month of life; incidence of parturition in younger females is rare (Naumov, 1940; Sokolov et al., 1990). During the breeding season, a female has 4–5 litters. Litter size ranges from 4 to 11. Average litter size for field-caught mound-building mice from central Ukraine is 6.7; in captivity average litter size is 5.4 (Sokolov et al., 1990).

ECOLOGY. Mound-building mice inhabit a variety of agroecosystems and, as a rule, are numerous throughout their range (Festetics, 1961; Hamar, 1960; Lozan, 1970; Mikesh, 1959; Naumov, 1940; Pisareva, 1948, 1953, 1955). Most mound-building mice dwell on cultivated land and migrate with crop distribution (Naumov, 1940; Sutova, 1971). Distribution of mounds, and hence of mice, is limited mainly by two factors: maturation of crops and abundance of forage (Naumov, 1940). The greatest population densities in autumn (7.0–10.5/ha) are in areas with forage crops, root crops, and winter and spring cereal crops. In the Dnepropetrovsk region, mound-building mice populate not only cropfields and vegetable gardens, but also pine forests, coniferous plantations, and sandy soils of Dniper islands (Pisareva, 1948).

A distinctive character of *M. spicilegus* is its grain-hoarding activity. In autumn, groups of 4–14 mice construct special mounds (*kurgans*) in which to store food and live for the winter (Brauner, 1899; Naumov, 1940; Pisareva, 1948; Sokolov et al., 1990). Construction of mounds occurs from mid-August to mid-November with peak construction occurring mid to late September after seed maturation of forage plants and cessation of breeding (Naumov, 1940; Pisareva, 1948; Sokolov et al., 1990). Juveniles aged 3–4 weeks and presumably members of the same family (Kotenkova et al., 1989*b*; Sokolov et al., 1990) begin constructing mounds. Less frequently, some adult individuals, presumably the parents, cohabit the mounds (Brauner, 1899). Earliest dates for single mound construction occurred in the region of Kherson in the late 19th century, where construction began in June (Silantiev, 1898). Construction of a mound takes from 7 to 25 days but is normally completed after 14–21 days (Naumov, 1940; Pisareva, 1948). Diameter of mounds ranges from 50 to 400 cm, with most 100–200 cm (Festetics, 1961; Hamar, 1960; Lozan, 1970; Rusev, 1989). Maximum diameters (ca. 400 cm) are found on sandy soils in the region of Dnepropetrovsk (Pisareva, 1948). Mound size and mass of stored forage is positively correlated with number of animals involved in construction (Naumov, 1940; Sokolov et al., 1990).

Within mounds of *M. spicilegus*, seeds of 84 species of plants belonging to 29 families have been found; 28 species of these are main forage plants (Ausländer and Hellwing, 1957; Festetics, 1961; Lozan, 1970; Mikesh, 1961; Naumov, 1940; Pisareva, 1948; Rusev, 1989; Sokolov et al., 1990). Members of the Graminacae and Asteracae are most commonly hoarded. The area from which mound-building mice collect forage varies with abundance of desirable seeds and ranges from 45 to 140 m^2 (Sokolov et al., 1990).

In March and April many mound-building mice leave their mounds to live in summer burrows of simpler design for the entire spring-summer season. If mounds are not destroyed by agrotechnical measures, mice may return to those used previously. During summer both young and old mice are found in mounds (Lyalyukhina, 1984; Naumov, 1940; Sokolov et al., 1990). Home range

sizes of males and females inhabiting burrows are 150–260 m². Intra- and interspecific overlap in home ranges is common (Hamar and Sutova-Hamar, 1969).

In contrast to house mice (*M. m. musculus* and *M. m. domesticus*), which display pronounced ecological plasticity by living both in human structures and in the wild, *M. spicilegus* is narrowly specialized to life in agroecosystems (Sokolov et al., 1990). One factor limiting distribution of mound-building mice is how deeply the ground freezes during winter (Naumov, 1940).

BEHAVIOR. Exploratory behavior has been investigated in the laboratory in small chambers (0.4 m²) and large enclosures (16 and 30 m²—Kotenkova et al., 1995; Meshkova et al., 1986). In small chambers, the only difference in exploratory behavior of commensal *M. m. musculus* and *M. spicilegus* was that the number of observations of upright posture (mouse sitting or standing on hind legs and looking around) by *M. m. musculus* was twice that of *M. spicilegus*. In large enclosures, however, *M. spicilegus* explored only the floor of its new territory, whereas *M. m. musculus* investigated elevated sites as well. In large enclosures locomotory activity was twice as high for *M. m. musculus* as for *M. spicilegus*, and frequency of escape attempts was 13 times higher in *M. m. musculus*. Escape behavior of *M. m. musculus* was more variable and complicated than that of *M. spicilegus*. Differences in exploratory behavior are not species-specific but are correlated with ecological conditions (Sokolov et al., 1990). Exploratory strategy of *M. m. musculus* trapped in populations inhabiting agroecosystems was the same as that of *M. spicilegus*, but different from *M. m. musculus* trapped in commensal populations (Kotenkova et al., 1995).

Social behavior of *M. spicilegus* was investigated using small cages (1 m²; two males, two females) and large enclosures (16 m² and 30 m²; three males, three females—Sokolov et al., 1988*b*, 1990). In groups formed with mound-building mice from different mounds, females and males formed a hierarchial structure. In groups consisting of conspecifics, female *M. spicilegus* were more aggressive than female *M. m. musculus*. In *M. spicilegus* groups maintained in cages of 1 m², subordinate males and females usually died 10–15 days after the start of group formation. Subsequently, the dominant pair started to breed. In cages and large enclosures containing mixed groups (four-six individuals) of male and female *M. spicilegus* and *M. m. musculus*, neither species dominated. Hierarchial status of males was determined by individual characters. In nature mound-building mice and house mice sometimes live in the same habitats (Migulin, 1937; Sokolov et al., 1990), and competitive exclusion of one species by the other has not been demonstrated.

Behavior of caged mound-building mice from the same mound differs strongly from that of individuals from different mounds. Agonistic behavior never occurred within groups from the same mound, but all members of such groups were aggressive to intruders, whether males or females (Sokolov et al., 1988*b*, 1990).

In captivity, the highest level of aggressive behavior in dyadic encounters occurs in autumn when mice are immature, and this trend is the same for both males and females of field-caught *M. spicilegus* (Kotenkova et al., 1989*b*). In spring, level of agonistic behavior declines. During spring mound building, mice leave mounds in search of mates and thus exhibit low levels of aggression. Low levels of aggression continue throughout summer (Kotenkova et al., 1989*b*). Presumably, level of aggressive behavior is a function of breeding activity and living conditions of mice in different seasons.

M. spicilegus and *M. m. musculus* hybridize in the laboratory with little reduction of fertility, but they are genetically isolated in the wild. Thus precopulatory isolating mechanisms may exist between *M. m. musculus* and *M. spicilegus* in sympatry. Reproductive behavioral patterns of *M. spicilegus*, *M. m. musculus*, and *M. m. domesticus* are very similar (Kotenkova et al., 1989*b*; Sokolov et al., 1990; Thuessen, 1977). Although no qualitative patterns of behavior that could serve as mechanisms of isolation were recorded during paired encounters of males and estrous females, quantitative differences may be important (Potanskyi and Kotenkova, 1992).

M. spicilegus can distinguish the odor of conspecifics from that of other species. Time spent investigating urine of conspecifics is significantly longer than for urine of other species (Sokolov et al., 1983, 1984). Mound-building mice spend equal time investigating urine of sympatric and allopatric *M. m. musculus*. Both *M. spicilegus* and *M. m. musculus* spend more time investigating odors of conspecifics, which suggests that their odors differ, although similar substances are excreted in estrus (Lyalyukhina, 1984; Sokolov et al., 1990). Humans can also distinguish odors of these species because *M. spicilegus* does not have the mouse odor usually associated with *M. m. musculus* (Sokolov et al., 1990). *M. spicilegus* can distinguish the odor of estrous females from conspecific males and from closely related species (Sokolov et al., 1985). Exposure to conspecific (but not heterospecific) females in estrus significantly increases testosterone levels in the blood plasma of males (Kotenkova et al., 1989*a*; Sokolov et al., 1988*a*). Physiological isolating mechanisms between *M. spicilegus* and *M. m. musculus* may include species-specific hormonal responses of males exposed to estrous females (Kotenkova, 1994).

GENETICS. *M. spicilegus* has a diploid chromosome number of 40. C- and G-banding of *M. spicilegus* from different regions (Kishinev: Moldova, Kirovograd; Crimea: Ukraine) reveal general characteristics of the karyotype (Bulatova, 1990; Bulatova and Kotenkova, 1990; Sokolov et al., 1990): a uniform heterochromatic and dimly-stained Y chromosome of reduced size (i.e., ca. 50% of the smallest autosome); profoundly pericentromeric staining of every autosome without any heterochromatic locations; X chromosome with tiny centromeric staining and slightly dim chromosome arms; a picture of G-banded chromosome corresponding to the standard karyotype of the house mouse (Committee, 1972).

Loci of *M. spicilegus* that are diagnostic for distinguishing *Mus musculus* and *M. spicilegus* are Idg-1, Mpi-1, Sod-1, Es-1, Es-2, and for distinguishing *M. spicilegus* and *M. macedonicus* are Alb, Pgm-2, Sod-2, Es-3 (Bonhomme et al., 1984; Mezhzherin, 1987; Mezhzherin and Kotenkova, 1992; Milishnikov et al., 1989). Alleles $Alb^{101,100}$, $Sod\text{-}2^{B}$, and Hbb-d are fixed in *M. spicilegus* (Frisman et al., 1990; Mezhzherin, 1994; Mezhzherin and Kotenkova, 1992). The T-complex has not been found in *M. spicilegus* (Sokolov et al., 1990).

Hybrids between *M. spicilegus* and other sympatrically distributed mice have not been found in nature. Bonhomme et al. (1983) obtained viable hybrids between male *M. spicilegus* and female strain C57Bl6, but hybrid males were sterile. Two hybrid male offspring from a cross between a male *M. spicilegus* and a female white laboratory mouse had karyotypes with 21 meiotic patterns (19 bivalents and 2 univalents) in diakinesis (Bulatova et al., 1986). When natural hybrids between *M. m. musculus* and *M. m. domesticus* from Batumy (Caucasus) were crossed with *M. spicilegus*, the resulting offspring failed to breed. The offspring resembled *M. m. domesticus* in being mostly black and having long tails. In their home cages (1 m² in floor area), offspring constructed mounds from sawdust and stored forage in them (Sokolov et al., 1990).

Male and female *M. spicilegus* crossed with *M. m. musculus* had F1 and F2 hybrids that were viable and fertile (Bulatova et al., 1986). No meiotic disturbances were recorded. According to Bonhomme et al. (1983), *M. macedonicus* and *M. spicilegus* were too aggressive to cross under experimental conditions. *M. spicilegus* and *M. macedonicus* from other populations crossed with each other, but all hybrids were weak and died at age 2–4 months (Lavrenchenko, 1990; Lavrenchenko et al., 1989).

REMARKS. The mound-building mouse was supposedly first described by Nordmann (1840) from the Botanical Garden of Odessa, Ukraine, as the species *Mus hortulanus*. He did not mention mounds, which are typical of *M. spicilegus*, and indicated that the color of *M. hortulanus* was brown. In the Zoological Museum of the Russian Academy of Science, Saint Petersburg, we located one skull of a mouse from Odessa (N4460) identified by Nordmann as *M. hortulanus*. The skull is badly damaged, but the breadth of the process of the maxillary (>0.8 mm) suggests that the skull is actually of *M. m. musculus*. Gerasimov et al. (1990) used discriminant function analysis to show that this specimen is in fact *M. m. musculus*. The color of fur of the second mouse collected by Nordmann is mixed with red. The skull is absent. These observations suggest that what Nordmann described was the wild form of *M. m. musculus*. This form is widely spread throughout the steppes of southern Ukraine and Moldova (Mezhzherin and Zagorodnyak, 1989; Sokolov et al., 1990).

In 1882 Petenyi described the mound-building mouse as the species *Mus spicilegus*. The type series is still preserved in good condition in the Hungarian Natural History Museum, Budapest (Csorba and Demeter, 1991), and skulls and skins of two individ-

uals are preserved in the British Museum (Natural History) in London (J. T. Marshall, in litt.). The type series of *M. spicilegus* was investigated by Demeter et al. (1993), and the authors confirmed that these specimens are mound-building mice. The type series of the Hungarian Natural History Museum includes 15 mice, 12 mounted and 3 in alcohol. According to specimen labels, Petenyi collected these mice in 1852 and 1853 in two localities of Hungary: Felsóbesnyó and Rákoskeresztúr (Csorba and Demeter, 1991). According to Csorba and Demeter (1991), the lectotype is an adult male, mounted, N 161.7 from Felsóbesnyó, collected 15 April 1852. Specimen N 94.7.261 (male, Hungary) from the British Museum (Natural History), which was previously considered the holotype, should now be considered the syntype.

The Russian zoologist Val'kh (1927) later described this mouse as a species under the name *Mus sergii.* He named the small mouse "sergii," after his son, who caught the mouse alive for his father. Other common names of the mound-building mouse are kurgan mouse, hillock mouse, and grain-storing mouse.

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The unfortunate death of the senior author, Academician Vladimir Sokolov, occurred shortly before this account was published. He was a member of the Russian Academy of Science and one of the best-known zoologists in Russia. E. Kotenkova and A. Mikhailenko dedicate this account to him.

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