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Chromosomal forms and risk assessment of *Nannospalax* (superspecies *leucodon*) (Mammalia: Rodentia) in the Carpathian Basin

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A b s t r a c t . Available data on the distribution and karyology of *Nannospalax* (superspecies *leucodon*) from the Carpathian Basin are summarized. We argue that four chromosomal forms of the species complex are endemic to the Carpathian Basin and their former and recent distribution based on museum specimens, literature overview and our own observations is mapped. Based on current distribution data, a preliminary extinction risk-assessment is presented for each of these forms. In spite of the current IUCN category applied for the whole superspecies (i.e. "Least Concern"), one of the chromosomal forms is regarded hereby as Vulnerable, one as Endangered, and two as Data Deficient.

Key words: mole rat, cytogenetics, karyology, biogeographical regions, IUCN categories

Introduction

According to the different systematic views, the subfamily Spalacinae consists of either a single genus, *Spalax*, or two genera, the nominal one and *Nannospalax* (for historical overview see M u s s e r & C a r l e t o n 2005. T o p a c h e v s k i (1969) listed a range of cranial, dental and skeletal differences among mole rats that comply with the widely accepted morphological generic-level differences in rodents (e.g. B r a u n & M a r e s 1995, M u s s e r et al. 2005, 2006). Moreover, these morphological traits clearly correspond with the two basically distinct chromosomal arrangements (high diploid and fundamental numbers and no acrocentric autosomes in *Spalax* versus low diploid and fundamental numbers in *Nannospalax*) observed in the extant species (L y a p u n o v a et al. 1971) of the subfamily. Therefore, the two-genera concept of T o p a c h e v s k i is accepted here and the name *Nannospalax* (= *Microspalax* of T o p a c h e v s k i 1969 and with the same taxonomic content as the subgenera *Microspalax* + *Mesospalax* of M é h e l y 1909) denoting a full genus is used throughout this paper.

The lesser blind mole rat *Nannospalax leucodon* (N o r d m a n n, 1840) is an exclusively subterranean and highly specialised rodent. This animal is known as a typical inhabitant of the steppic grasslands, mountainous steppes and sand steppes, avoiding marshy areas and quicksand (T o p a c h e v s k i 1967, S a v i ć & S o l d a t o v i ć 1977, C s o r b a 1994, H o r v á t h et al. 2007).

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In the case of the closely related *Nannospalax ehrenbergi,* it has been shown that Israeli populations characterized by different chromosomal sets represent "good biological species" (Nevo 1991, Nevo et al. 1994) and were subsequently described as *Spalax (=Nannospalax) galili, Spalax (=Nannospalax) golani, Spalax (=Nannospalax) carmeli* and *Spalax (=Nannospalax) judaei* (Nevo et al. 2001). All these species are reproductively isolated from each other (Savić & Nevo 1990), with narrow hybrid zones in the area of parapatry (Nevo et al. 1993). The diversity of karyotypes (as expressed by diploid numbers and fundamental numbers of chromosomal arms) is much higher in *Nannospalax leucodon* than in "*Spalax (=Nannospalax) ehrenbergi* superspecies" (Savić & Soldatović 1974, Savić & Soldatović 1977, Savić & Nevo 1990, Sözen et al. 2006). Thus, the complex of chromosomal forms of lesser blind mole rat is also regarded as a "superspecies" (Savić & Nevo 1990, Musser & Carleton 2005). Until very recently, within the Carpathian Basin the variation in chromosomal structures had been investigated only in Serbia (Savić & Soldatović 1977, Soldatović & Savić 1983) and Romania (Raicu et al. 1968) and no data on the chromosomal structure of mole rats were available from Hungary.

As permitted by the Article 6.2 of International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999) "interpolated names of aggregates of species may be added in parentheses after the genus-group name to denote an aggregate of species within a genus-group taxon". Accordingly, the taxonomic meaning attributed to the *Nannospalax leucodon* aggregate can be expressed in the notation *Nannospalax* (superspecies *leucodon*). As for the species-level taxonomy of the superspecies *leucodon*, to date, only a few studies managed to correspond the chromosomal constitution to the described taxa (Savić & Soldatović 1974, 1977, Soldatović & Savić 1983). As there were no genetic investigations on the species- or subspecies-level distinction apart from gathering chromosomal data, herewith we refrain from any formal taxonomic action but use the names applied by previous authors, without explicitly assigning taxonomic ranks to the given chromosomal forms. At the same time, the ever-widening acceptance and application of the *Genetic Species Concept* (Baker & Bradley 2006) in mammal taxonomical research presents us with more and more incidences of taxa that are morphologically identical, but genetically distinguishable. These should be discussed separately e.g. when establishing conservation biological priorities.

To overcome the taxonomic uncertainties within the superspecies the *Evolutionary Significant Units* (ESU) concept (as defined by Moritz 1994) can be applied when conservation biological questions are addressed. In the case of mole-rats the reproductive isolation, parallel with the adaptation of different chromosomal forms to different ecological conditions (e.g. aridity, precipitation, temperature, see Nevo et al. 1995, 2000, Sözen et al. 1999) mean that there is a complete separation in gene flow between such populations, the different chromosomal forms are phylogenetically distinct and therefore represent different ESUs. Recognizing this is directly relevant to defining conservation priorities and long-term management issues.

The latest Red List of European mammals (Temple & Terry 2007, 2009) puts *Nannospalax* (superspecies *leucodon*) (under the name *Spalax leucodon*) in the Least Concern category but taking into consideration the taxonomic uncertainties, Kryštufek (1999) already warned that if "the taxon [*Nannospalax* (superspecies *leucodon*)] is split into several different species, some of these may warrant listings of threatened". The presence of different chromosomal forms between which gene flow is completely stalled, the limited

number of available records, the observed and projected decline in population size, along with the continuing habitat degradation and destruction within the Carpathian Basin render it an urgent task to (1) overview recent distributional status (2) to assess the karyological status of Hungarian populations and (3) present separate risk assessments for the different forms.

Material and Methods

Study area

The Carpathian Basin is a topographically well-defined unit of the European landscape. Its territory belongs to three Biogeographical Regions (BR) of the European Union: the Pannonian BR, which is almost completely contained within the Carpathian Basin, and relatively small parts of the Continental and Alpine BRs (Fig. 1). Different types of temperate grasslands (loess and sand steppes) are present within the Pannonian and Continental Regions. These ecosystems are important from a conservation viewpoint because they harbour high natural biodiversity and are rich in endangered and rare species (E E A 2002).

Map representation

On the map (Fig. 1) those localities are depicted which had either been published or supported by voucher specimens or checked in the field by the authors. Since earlier observations

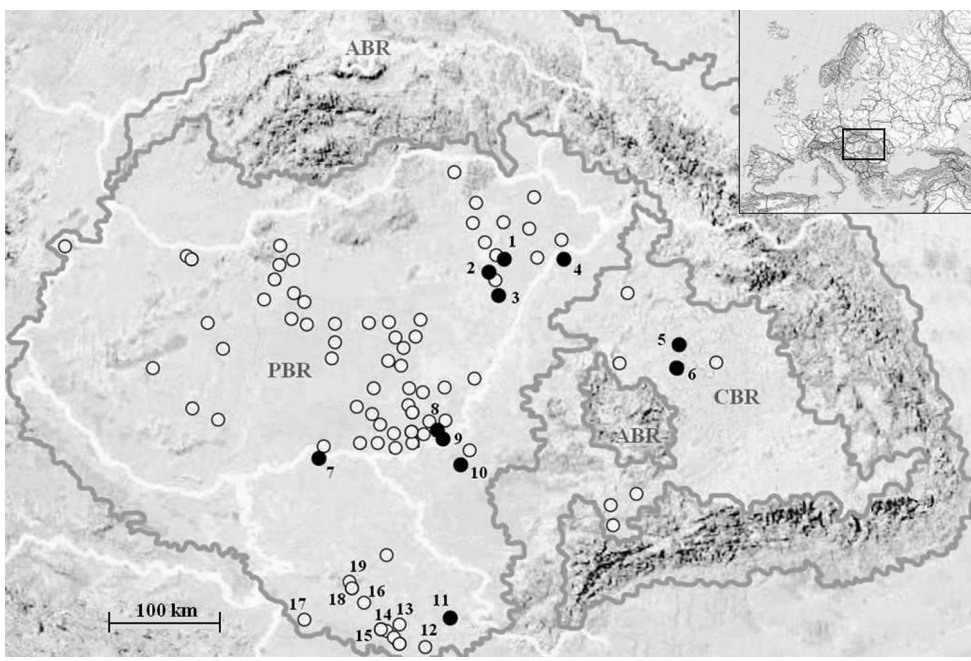

Fig. 1. Borders of biogeographical regions and the distribution of blind mole rats in the Carpathian Basin (ABR – Alpine Biogeographical Region, PBR – Pannonian Biogeographical Region, CBR – Continental Biogeographical Region). Empty circles – data collected before 1997; solid circles – data collected between 1997–2007. Localities mentioned in the text are numbered. 1 – Hajdúhadház, 2 – Debrecen-Józsa, 3 – Hajdúbagos, 4 – Urziceni, 5 – Dâbâca, 6 – Cluj-Napoca, 7 – Subotićka peščara, 8 – Kistompapuszta, 9 – Battonya, 10 – Hunedoara Timişanã, 11 – Deliblato, 12 – Udovice, 13 – Višnjica, 14 – Košutnjak, 15 – Banovo brdo, 16 – Stara Pazova, 17 – Bogatić, 18 – Stražilovo, 19 – Čortanovci.

(which are not supported by museum specimens) of mole rats from the dry grasslands of central Transylvania (called Mezőség) compiled by O r o s z (1904, 1906) did not distinguish *Nannospalax* (superspecies *leucodon*) and *Spalax graecus* at that time, these records are not depicted on the map. The presence of the latter species in the Mezőség was evidenced by S z u n y o g h y (1937). The names of all the localities and source of the data can be found in the Appendix.

S a m p l i n g o f H u n g a r i a n p o p u l a t i o n s

The karyology of Hungarian mole-rats was investigated in different populations from Northeast Hungary (Debrecen-Józsa, Hajdúbagos and Hajdúhadház, see Fig. 1). Due to the strictly protected status of the species in Hungary, the permits (14/1708-3/2005 and 14/05173-3/2006) issued by the Ministry of Environment and Water allowed us to catch (N é m e t h et al. 2007) only a limited number of specimens. We examined a single individual from each locality and employed the least-invasive sampling technique, instead of the more general direct metaphase preparation from colchicin-arrested bone-marrow. Blood was taken from the *vena saphena lateralis* or finger matrix after disinfection with 70% ethanol and local anaesthesia (for details see N é m e t h et al. 2006).

I U C N c l a s s i f i c a t i o n s a n d c a t e g o r i e s

Only locations that were confirmed to have extant populations during the last decade were included in the risk assessment analysis and listed below as "recent records". The ID number of a population corresponds to the location presented on the map. The Red List categories were assessed according to the 2001 criteria (I U C N 2001). Habitats and threats were classified (and terms used) according to the IUCN Habitats Classification Scheme 3.0 and Threats Classification Scheme 2.1, respectively (www.iucnredlist.org). The extent of the mole rats occurrence was taken or calculated from official websites of nature protection authorities (www.hnp.hu, www.kmnp.hu, www.ludas.rs) maps of different sources and using Google Earth 4.2 version. Population size estimations were based on the number of clusters of mounds counted in a smaller area (M i k e s et al. 1982) – the extent of which depends on the circumstances and varies between 1–10 ha – and then extrapolated to the whole area of the potential habitat patches. Although Z u r i & T e r k e l (1996) demonstrated the inaccuracy of mapping mole-rat territories according to the mound locations, at present there is no more reliable practical method. We regarded one population those stocks that inhabited more-or-less continuous, homogeneous habitats. Gene flow between the populations is quite improbable due to the geographic isolating barriers (distance and separating unsuitable habitats) amongst them.

Results

"transsylvanicus" form
"*Spalax leucodon* karyotype form *transsylvanicus*" R a i c u et al. (1968)
"*Spalax* population Jucu" S o l d a t o v i ć (1977)
"karyotypic form *transsylvanicus*" S a v i ć & S o l d a t o v i ć (1977)
Nannospalax leucodon transsylvanicus S o l d a t o v i ć & S a v i ć (1983)
Spalax leucodon transsylvanicus S a v i ć & N e v o (1990)

K a r y o l o g y

Chromosome number 2n=50, NF= 84 which consists of 4 pairs of metacentric autosomes, 7 pairs of submetacentric autosomes, 5 pairs of subtelocentric autosomes and 8 pairs of acrocentric autosomes. The X chromosome is large and metacentric, whereas the Y chromosome is large and submetacentric (R a i c u et al. 1968).

R e c e n t r e c o r d s

Hajdúhadház population (1)
Determination: based on karyological data (present paper). Population size: ca. 600 individuals. Habitat and extent of occurrence: 1 675 ha of temperate grassland (sand steppe). Major threats: presumably it does not face any major threats at present. Conservation measures: the area currently functions as a military shooting range but, it is proposed for Natura 2000 site.
Debrecen-Józsa population (2)
Determination: based on karyological data (N é m e t h et al. 2007). Population size: ca. 50 individuals. Habitat and extent of occurrence: in two fragments (areas of 60 and 7 ha, respectively) of pastureland (degraded loess steppe). Major threats: small-holder farming, human settlement as well as restricted range. Conservation measures: the area is protected by the local government.
Hajdúbagos population (3)
Determination: based on karyological data (present paper). Population size: ca. 200 individuals. Habitat and extent of occurrence: known from two populations spread over 260 and 10 ha, of temperate grassland (sand steppe) and pastureland, respectively. Major threats: industry, human settlement.. Conservation measures: the larger population fragment is protected as *Mole rat Reserve*, but the smaller fragment is a communal pasture subjected to small-scale industrial and housing development.
Urziceni population (4)
Localities include: Urziceni and Foieni. Determination: no karyological data or museum specimens are available; identification is based on geographic grounds as the Hajdúhadház population is located within 50 km and these localities are all part of the edaphologically well-defined Nyírség Sand Area. Population size: unknown. Habitat and extent of occurrence: in two fragments (470 and 250 ha, respectively) inhabiting temperate grassland (sand steppe) and pastureland. Major threats: restricted range. Conservation measures: both localities are included in the *Câmpia Careiului Site of Community Interest*.
Dăbâca population (5)
Localities include: Dăbâca, Fundătura, Iclod, Tioltiur, Bârlea and Lujerdiu. Determination: based on the identification of two specimens from Gherla and another one from Dăbâca by M é h e l y (1909); the karyologically investigated Cluj-Napoca population is very close geographically and the two areas had formed a continuous habitat in the past (M é h e l y 1909). Population size: 300–450 individuals. Habitat and extent of occurrence: cca. 1.800 ha of temperate grassland (hay meadow), arable land and pastureland. Major threats: human settlement, change of land management regime, small-holder farming and agro-industry farming. Conservation measures: the area is not protected.
Cluj-Napoca population (6)
Localities include: Cluj-Napoca; Apahida, Sânnicoară, Câmpeneşti, Jucu de Mijloc, Juc-Herghelie, Feiurdeni and Pădureni. Determination: based on karyological data (R a i c u

et al. 1968). Population size: 1 000–1 500 individuals. Habitat and extent of occurrence: 7 000 ha of temperate grassland (hay meadow), arable land and pastureland. Major threats: human settlement, change of land management regime, small-holder farming, agro-industrial farming. Conservation measures: less than 10% of the area is protected as *Fânaţele Clujului Nature Reserves* and the *Apahida Spalax Reserve*.

R i s k a s s e s s m e n t

The "*transsylvanicus*" form is proposed to be ranked as Vulnerable B1ab(iii); B2ab(iii). Rationale: extent of occurence and area of occupancy are estimated to be no more than 120 square kilometres, known to exists at no more than 10 locations and estimates indicate a continuing decline in area, extent and quality of habitat. Accession of Romania to the EU is expected to result in agricultural intensification in near future.

"hungaricus" form
"*Spalax leucodon* karyotype form *martinoi*" S a v i ć & S o l d a t o v i ć (1974)
Spalax martinoi S o l d a t o v i ć (1977)
"karyotypic form *martinoi* (=*hungaricus*)" S a v i ć & S o l d a t o v i ć (1977)
Nannospalax leucodon hungaricus S o l d a t o v i ć & S a v i ć (1983)
Spalax leucodon hungaricus S a v i ć & N e v o (1990)

K a r y o l o g y

2n= 48, NF= 84 which consists of 4 pairs of metacentric autosomes, 8 pairs of submetacentric autosomes, 5 pairs of subtelocentric autosomes and 6 pairs of acrocentric autosomes. The X chromosome is large and metacentric, whereas the Y chromosome is middle sized and subtelocentric (S o l d a t o v i ć 1977).

R e c e n t r e c o r d s

Subotićka peščara population (7)
Determination: based on karyological data from Hajdukovo (S a v i ć & S o l d a t o v i ć 1974). Population size: estimated to be between 50 and 100 individuals. Habitat and extent of occurrence: 400 ha of temperate grassland (sand steppe). Major threats: small-scale wood plantations, change of land management regime, small population size (D e l i ć 2007). Conservation measures: the whole area is protected as part of the *Subotićka peščara Protected Area*.
Tompapuszta population (8)
Determination: no karyological data or museum specimens are available; the identification is based on geographic grounds as Mezőhegyes (type locality of *Spalax typhlus hungaricus* Nehring, 1897) is only 15 km apart. Population size: 20–30 individuals (H o r v á t h & V a d n a i 2006). Habitat and extent of occurrrence: 21 ha of temperate grassland (loess steppe). Major threats: small population size, restricted range. Conservation measures: the whole area is protected as *Tompapusztai Löszgyep Protected Area*.
Battonya population (9)
Determination: no karyological data or museum specimen is available; the identification is based on geographic grounds as Mezőhegyes (type locality of *Spalax typhlus hungaricus*

Nehring, 1897) is only 15 km apart. Population size: probably less than 100 individuals. Habitat and extent of occurrence: 37 ha of temperate grassland (loess steppe) and pastureland; plus some hectars of rural gardens. Major threats: small-holder farming, human settlement, restricted range. Conservation measures: part of the area is protected by the local government.

Hunedoara Timişană population (10)

Determination: no karyological data or museum specimen is available; the identification is based on geographic grounds as Mezőhegyes (type locality of *Spalax typhlus hungaricus* Nehring, 1897) is only 45 km apart. Using skull characteristics specimens from a nearby former locality (Arad) were investigated and determined as such by Méhely (1909). Population size: estimated to be less than 50 individuals. Habitat and extent of occurrence: 50 ha of pastureland. Major threats: restricted range, land transport development. Conservation measures: part of the territory is included in the *Hunedoara Timişană Special Protected Area*.

Deliblato population (11)

Localities include: Deliblato, Šušara, Dolovo. Determination: based on karyological data (Savić & Soldatović 1974). Population size: >10.000 (Mikes et al. 1982). Habitat: 29.350 ha predominantly of temperate grassland (loess and sand steppe). Major threats: wood plantations, small-holder farming. Conservation measures: The whole area is protected as *Deliblatska peščara Special Nature Reserve*.

Risk assessment

The "*hungaricus*" form is proposed to be ranked as Endangered B1ab(iii); B2ab(iii)

Rationale: the extent of occurrence and area of occupancy are estimated to be approximately 300 square kilometres; estimates indicate severely fragmented populations in no more than five locations; continuing decline observed in area, extent and quality of habitats. More than 95% of the population is contained in one subpopulation.

" syrmiensis" form

"*Spalax leucodon* karyotype form *syrmiensis*" Savić & Soldatović (1974)
Spalax syrmiensis Soldatović (1977)
"karyotypic form *syrmiensis*" Savić & Soldatović (1977)
Nannospalax leucodon syrmiensis Soldatović & Savić (1983)
Spalax leucodon syrmiensis Savić & Nevo (1990)

Karyology

2n= 54, NF= 90 which consists of 3 pairs of metacentric autosomes, 9 pairs of submetacentric autosomes, 5 pairs of subtelocentric autosomes and 9 pairs of acrocentric autosomes. The X chromosome is large and submetacentric, the Y chromosome is large and acrocentric (Soldatović 1977).

Recent records

No definite record from the last ten years. Savić & Soldatović (1977) characterized its habitat as "steppe habitat in territories of the Pannonian Lowland and Ancient-Pannonian

coast". The latest information on the occurrence of this form (determinations were based on karyological data) was published by the same authors (S o l d a t o v i ć & S a v i ć 1983). These former localities included Udovice (12), Višnjica (13), Košutnjak (14), Banovo brdo (15), Stara pazova (16) and Bogatić (17). Since 1983, no data pertaining to the distribution and abundance of *syrmiensis* have been published. It is also possible that this form is extinct (B. K r y š t u f e k, pers. comm.).

R i s k a s s e s s m e n t

Data Deficient

"montanosyrmiensis" form
"*Spalax leucodon* karyotype form *montanosyrmiensis*" S a v i ć & S o l d a t o v i ć (1974)
Spalax montanosyrmiensis S o l d a t o v i ć (1977)
"karyotypic form *montanosyrmiensis*" S a v i ć & S o l d a t o v i ć (1977)
Nannospalax leucodon montanosyrmiensis S o l d a t o v i ć & S a v i ć (1983)
Spalax leucodon montanosyrmiensis S a v i ć & N e v o (1990)

K a r y o l o g y

2n= 54, NF= 86 which consists of 2 pairs of metacentric autosomes, 8 pairs of submetacentric autosomes, 5 pairs of subtelocentric autosomes and 11 pairs of acrocentric autosomes. The X chromosome is large and metacentric, the Y chromosome is medium sized and acrocentric (S o l d a t o v i ć 1977).

R e c e n t r e c o r d s

No definite record from the last ten years. This form is known from only two localities, Stražilovo (18) and Čortanovci (19), described by S a v i ć & S o l d a t o v i ć (1977) as "steppe habitat of Sub-Pannonian hilly and piedmont areas". The latest information on the occurrence of this form was published by the same authors (S o l d a t o v i ć & S a v i ć 1983). In the last 25 years no information on the status and distribution of this form has been published; therefore, the Data Deficient category applies best.

R i s k a s s e s s m e n t

Data Deficient.

Discussion

The occurrence of mole rats within the Carpathian Basin is restricted to the Pannonian and Continental Regions, where four different karyological forms occur parapatrically and all of them are present within the boundaries of the Pannonian BR. Since none of these karyotypes can be found outside of the region investigated, they are regarded as Carpathian Basin endemics.

Even though the majority of known locations is under some kind of protection, some populations are threatened by land use changes (e.g. intensification of agricultural practices, wood plantations, industrial developments), connected to changes in the agri-environment

scheme, resulting in the disappearance of extensive grasslands (F e k e t e et al. 2005, B í r ó et al. 2008). This threat is probably similarly imminent on the largest and most important Romanian and Serbian habitats. At the time of writing it is unknown whether the current population fragments reach the minimum viable size, that is, whether they can subsist on a long term basis. Before any action plan for the lesser blind mole rat species-complex will be put into practice, a study to investigate and compare the ecological needs of the different chromosomal types must be carried out. Depending on the results of such a study, different management plans for the sustenance of the different chromosomal forms may be required. So far there have only been suggestions concerning translocations (H o r v á t h & V a d n a i 2006, D e l i ć 2007), but in any case, it is prudent to avoid translocating individuals between different ESUs.

Although it is probable that further field studies will reveal more locations where *Nannospalax* (superspecies *leucodon*) exists, the continuing decline of its population and shrinking of its area of occupancy is evident from the available information. It is also clear that the present state of our general knowledge on many aspects of the biology of mole rats (including population size, habitat preference, life cycle, activity patterns, long-term effects of inbreeding in isolated populations) is limited. Further research involving the whole of the superspecies is needed, especially as most of the available information is older than a couple of decades. Keeping in mind the current land use trends, significant decline in the extent and quality of habitats can be predicted not only within the Carpathian Basin, but also outside of it.

A c k n o w l e d g e m e n t s

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Appendix. List of all known records of *Nannospalax* (superspecies *leucodon*) from the Carpathian Basin. Former Hungarian names of settlements are given in parenthesis.

Locality	Country	Reference	Last known data
Apahida	Romania	HNHM Mammal Collection	1928
Arad	Romania	Méhely 1909	1902
Avala	Serbia	Savić & Soldatović 1984	1984
Banovo brdo	Serbia	Savić & Soldatović 1984	1984
Bârlea	Romania	pers. obs.	2007
Békéscsaba	Hungary	HNHM Mammal Collection	1934
Békésszentandrás	Hungary	Sterbetz 1966	1960
Bogatić	Serbia	Savić & Soldatović 1984	1984
Boglárlelle	Hungary	HNHM Mammal Collection	1905
Budapest	Hungary	HNHM Mammal Collection	1900
Budesti (Budatelke)	Romania	Orosz 1904	1902
Cegléd	Hungary	HNHM Mammal Collection	1905
Cluj-Napoca (Kolozsvár)	Romania	Orosz 1904	1902
Čortanovci	Serbia	Savić & Soldatović 1984	1984
Csanádpalota	Hungary	Bodnár 1928	1928
Csorvás	Hungary	Festetics 1956	1955
Dăbâca (Doboka)	Romania	Orosz 1904	1903
Dabas	Hungary	HNHM Mammal Collection	1905
Debrecen-Józsa	Hungary	HNHM Mammal Collection	2007
Deliblato (Deliblát)	Serbia	HNHM Mammal Collection	1990
Dolovo (Dolova)	Serbia	Savić & Soldatović 1984	1984
Dunakeszi	Hungary	Orosz 1904	1903
Feiurdeni (Fejérd)	Romania	Orosz 1904	1901
Földeák	Hungary	HNHM Mammal Collection	1928
Fundătura	Romania	pers. obs.	2007
Gherla (Szamosújvár)	Romania	HNHM Mammal Collection	1903
Hajdúbagos	Hungary	HNHM Mammal Collection	2007
Hajdúdorog	Hungary	Csapody 1996	1803
Hajdúhadház	Hungary	HNHM Mammal Collection	2007
Hajdukovo (Hajdújárás)	Serbia	Savić & Soldatović 1984	1984
Halásztelek	Hungary	Sterbetz 1960	1943
Hateg (Hátszeg)	Romania	Lendl 1900	1900
Hódmezõvásárhely	Hungary	Sterbetz 1960	1958
Huedin (Bánffy-Hunyad)	Romania	Orosz 1904	1903
Hunedoara (Vajdahunyad)	Romania	HNHM Mammal Collection	1915
Iclod	Romania	pers. obs.	2007
Igmánd	Hungary	Orosz 1904	1903
Iuriu de Cămpie (Mezõõr)	Romania	HNHM Mammal Collection	1900
Jajinci	Serbia	Savić & Soldatović 1984	1984
Juc-Herghelie	Romania	pers. obs.	2007
Jucu de Mijloc (Zsuk)	Romania	Raicu et al. 1968	1968
Kálozd	Hungary	Csapody 1996	1803
Kardoskút	Hungary	Sterbetz 1966	1952
Kecskemét	Hungary	Orosz 1909	1909
Kelebia	Hungary	HNHM Mammal Collection	2008
Kétpó	Hungary	Vásárhelyi 1929	1929

Kistompapuszta	Hungary	pers. obs.	2007
Kisújszálás	Hungary	Vásárhelyi 1960	1924
Košutnjak	Serbia	Savić & Soldatović 1984	1984
Köröstarcsa	Hungary	HNHM Mammal Collection	1960
Kunágota	Hungary	HNHM Mammal Collection	1932
Lujerdiu (Lozsárd)	Romania	Orosz 1904	1903
Makó	Hungary	HNHM Mammal Collection	1949
Mártély	Hungary	Sterbetz 1960	1953
Méra	Hungary	HNHM Mammal Collection	1930
Mezõhegyes	Hungary	HNHM Mammal Collection	1936
Mezõkovácsháza	Hungary	HNHM Mammal Collection	1932
Mezõtúr	Hungary	Vásárhelyi 1960	1924
Nagyszénás	Hungary	Sterbetz 1960	1942
Nyírbéltek	Hungary	Sterbetz 1966	1966
Nyíregyháza	Hungary	Méhely 1909	1909
Ófehértó	Hungary	HNHM Mammal Collection	1926
Orastie (Szászváros)	Romania	Orosz 1904	1903
Orosháza	Hungary	Sterbetz 1966	1952
Ördögmalom	Hungary	Orosz 1904	1903
Pădureni	Romania	pers. obs.	2007
Pitvaros	Hungary	Orosz 1904	1903
Pusztaszentmihály	Hungary	Orosz 1904	1903
Pusztaszer	Hungary	Csizmazia 1973	1971
Pusztavacs	Hungary	Méhely 1909	1903
Rákos	Hungary	Horváth 1918	1817
Sânnicoarã (Pusztaszentmiklós)	Romania	pers. comm.	2007
Sarkad	Hungary	HNHM Mammal Collection	1931
Sárszentmihály	Hungary	HNHM Mammal Collection	1924
Sopron	Hungary	Orosz 1904	1903
Stara Pazova (Ó-Pazua)	Serbia	Savić & Soldatović 1984	1984
Stražilovo	Serbia	Savić & Soldatović 1984	1984
Subotićka Peščara	Serbia	Delic 2007	2007
Šušara (Fejértelep)	Serbia	Savić & Soldatović 1984	1984
Szarvas	Hungary	Vásárhelyi 1932	1936
Szeged	Hungary	Sterbetz 1960	1948
Szolnok	Hungary	HNHM Mammal Collection	1927
Téglás	Hungary	HNHM Mammal Collection	1902
Tioltiur (Tötör)	Romania	Orosz 1904	1903
Tiszavasvári	Hungary	HNHM Mammal Collection	1929
Tokaj	Hungary	Csapody 1996	1803
Törökszentmiklós	Hungary	HNHM Mammal Collection	1903
Túrkeve	Hungary	Vásárhelyi 1960	1924
Udovice	Serbia	Savić & Soldatović 1984	1984
Vácz	Hungary	Méhely 1909	1900
Veresegyház	Hungary	Orosz 1904	1903
Višnjica	Serbia	Savić & Soldatović 1984	1984
Zrenjanin (Nagybecskerek)	Serbia	Lendl 1900	1900