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Review of chromosome races in blind mole rats (*Spalax* and *Nannospalax*)

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Abstract. The blind mole rats (Spalacinae) reveal fascinating chromosomal variation, resulting from complex karyotype re-arrangements. This variation occurs between species, between populations of single species (polytypy) and within populations (polymorphism). This article reviews the current knowledge on blind mole rats' karyotypes and their variation. A special attention is paid to differentiation of the karyotype within a species and the patterns of chromosomal variation, which result in evolution of distinct chromosomal races (cytotypes). The chromosome races are defined as a group of geographically contiguous or recently separated populations which share a similar chromosome complement by descent. The present review indicated the existence of 73 distinct chromosome races recorded in blind mole rats classified within the genus *Nannospalax*, along with the seven species recognized within the genus *Spalax*. In total, 12 distinct diploid numbers of chromosomes were reported (2n = 36-62); and variation in chromosome morphologies was observed between populations with the same number of chromosomes (NF = 62-124). The blind mole rats classified in the genus *Spalax* revealed rather uniform karyotype both between and within the recognized species. Considering the traditional species classified in the *Nannospalax* genus, 25 races can be distinguished within *N. leucodon*, 28 races within *N. xanthodon* and 20 races within *N. ehrenbergi*. Hybrids between the races are found only exceptionally and they seem to be almost absent in extensive areas (Europe, Turkey). This fact indicates that chromosomal evolution in blind mole rats may be related to speciation processes. The definitive phylogenetic and taxonomic conclusions can be derived only after application of reliable molecular markers and setting of estimates of genetic distances and gene flow between populations.

Key words: karyotype, evolution, cytotypes, speciation

Introduction

The blind mole rats are effectively blind subterranean rodents with various specific features that emphasize their adaptation to underground life (Topachevskii 1969, Nevo 1979, Savić 1982, Savić & Nevo 1990). The blind mole rats are solitary animals living in isolated assemblages and the fragmented distribution pattern is believed to support the speciation events. The blind mole rats occur in eastern and south-eastern Europe, the eastern Mediterranean area and the Middle East, and north-eastern Africa (Musser & Carleton 2005). The blind mole rats inhabit cultivated areas, sparse woodland, steppes and mountain slopes, but do not occur in dense forests (Savić 1982, Savić & Nevo 1990, Nevo 1993, Sözen 2005, Yiğit et al. 2006, Kryštufek &Vohralík 2009). They are confined to grounds suitable for burrowing and in some parts of their range they are considered pests, causing damage to crops. The disturbance resulting from burrowing influences the composition of the grassland significantly but it does not cause a difference in the plant species richness, diversity and total cover, which suggests that grassland has adapted to these natural processes (Zimmermann et al. 2014). On the other hand, it is apparent that many populations and species of blind mole rats are under serious threat, mainly because of loss and fragmentation of their natural habitats. This results in the occurrence of localized endemic and small-sized populations (Németh et al. 2013b, Csorba et al. 2015). That is why they

are generally included among seriously threatened taxa, particularly in the European part of the range (Kryštufek et al. 2009); and individual species, apart from Least Concern, and Data Deficient, are assessed in the categories Endangered, Vulnerable and Near Threatened in the IUCN Red Data List (IUCN 2014). The unresolved taxonomic problems constitute serious drawback on the correct conservation assessment.

The blind mole rats have become an important biological model in research of various general topics, such as tolerance to environmental stress, including hypoxia (Avivi et al. 2010, Nevo 2013, Fang et al. 2014), circadian system (Avivi et al. 2004), sensory research (Nevo 1999, Burda 2006), phylogenomics and subterranean adaptation (Du et al. 2015) or resistance to cancer (Gorbunova et al. 2012, Manov et al. 2013). A particular feature, characteristic for the blind mole rats, is a fascinating pattern of extensive karyotypic variation within and between populations and presumptive species. This unusual extent of chromosomal variation seems to be related to the specific fossorial way of life of blind mole rats, which results in frequent fragmentation of the range and promotes isolation of individual populations (Savić 1982, Savić & Nevo 1990, Gülkaç & Yüksel 1999).

The blind mole rats, Spalacinae are currently classified within the rodent family Spalacidae, which includes also zokors (Myospalacinae), bamboo rats (Rhizomyinae) and African mole rats (Tachyoryctinae) (Musser & Carleton 2005). The phylogenetic relationships among the spalacid subfamilies remain unresolved, due to the convergence in morphological traits and the incongruence of molecular evidence. However Lin et al. (2014) indicated a sister group relationships between zokors and bamboo rats, suggesting that the subfamily Myospalacinae is rather more closely related to Rhizomyinae, than to Spalacinae.

The systematic and phylogenetic relationships of mole rats within the subfamily Spalacinae have not yet been definitively resolved. The mole rats are traditionally difficult to be systematically studied because of distinct convergent tendencies, leading to a uniform phenotype adapted to their fossorial way of life. Morphological approaches have been frequently used to elucidate taxonomy and phylogeny of the blind mole rats (Topachevskii 1969, Kıvanç 1988, Nevo et al. 1988b, Coşkun 1998, Kankılıç et al. 2006, 2014, Puzachenko 2006, Korobchenko & Zagorodniuk 2009, Németh et al. 2013a). However, these contribute information of limited value only, due to the uniform external appearance and gross cranial morphology of the blind mole rats, resulting from their strictly subterranean way of life.

Savić & Nevo (1990), Musser & Carleton (2005) and Kryštufek & Vohralík (2009) treated the family as monogeneric, including only the single genus *Spalax*, whereas other authors preferred to distinguish two genera, currently named *Spalax* Güldenstaedt, 1770 and *Nannospalax* Palmer, 1903 (Topachevskii 1969, Savić 1982, Savić & Soldatović 1984, Németh et al. 2009, 2013a). The genus *Spalax* includes larger species, possessing karyotypes with higher diploid chromosome numbers (2n = 60 or 62) and usually no acrocentric autosomes. The species of the genus *Nannospalax* are smaller, their karyotypes are extremely variable (2n = 36-62) and include acrocentric autosomes (Topachevskii 1969, Lyapunova et al. 1974, Savić & Soldatović 1984). The separation of the large-bodied and small-bodied blind mole rats at the genus level (*Spalax* and *Nannospalax*, respectively), suggested earlier on morphological grounds, has been supported by recent molecular evidence (Hadid et al. 2012, Chişamera et al. 2014). The species of *Spalax* have so far been distinguished from each other by external, cranial and dental traits, especially in respect of the outline of sutures of the cranium, and the shape and relative size of the nasal and parietal bones. Musser & Carleton (2005) recognized six *Spalax* species, i.e. *S. graecus* Nehring, 1898, *S. zemni* (Erxleben, 1777), *S. arenarius* Reshetnik, 1938, *S. microphthalmus* Güldenstaedt, 1770, *S. giganteus* Nehring, 1898 and *S. uralensis* Tiflov et Usov, 1939. Németh et al. (2013a) suggested separation of additional species from *S. graecus* in Romania, namely *S. antiquus* Méhely, 1909 and *S. istricus* Méhely, 1909, based on mitochondrial DNA sequences and detailed anatomical comparisons.

Most authors recognize three species within *Nannospalax*, *N. ehrenbergi* (Nehring, 1898), *N. leucodon* (Nordmann, 1840) and *N. xanthodon* (Nordmann, 1845) (Musser & Carleton 2005, Kryštufek & Vohralík 2009). *N. ehrenbergi* is distributed in the Near East (south-eastern Anatolia in Turkey, Iraq, Syria, Lebanon, Israel, Jordan and Egypt), *N. xanthodon* (formerly *N. nehringi*, see Kryštufek & Vohralík 2009) in Transcaucasia, most of Turkish Anatolia and certain East Aegean islands and *N. leucodon* in parts of central and south-eastern Europe. Various authors have lumped *N. xanthodon* and *N. leucodon* into a single *N. leucodon* superspecies (e.g. Nevo et al. 1995, Sözen et al. 2006a).

Separation of several additional species has been proposed within *Nannospalax*. Savić & Soldatović (1984) analysed chromosomal differentiation and

divergence in other characters in blind mole rats from the Balkan Peninsula and individual populations with distinct karytypes were taxonomically evaluated at the species or subspecies rank. They concluded that the genus *Nannospalax* in Europe and western parts of Asia Minor consists of the following species and subspecies:
Nannospalax montanoserbicus (Savić et Soldatović, 1974);
N. syrmiensis (Méhely, 1909);
N. hercegovinensis (Méhely, 1909);
N. turcicus (Méhely, 1909);
N. bulgaricus (Savić et Soldatović, 1984);
  N. bulgaricus bulgaricus (Savić et Soldatović, 1984);
  N. bulgaricus srebarnensis (Savić et Soldatović, 1984);
N. nehringi (Satunin, 1898);
  N. nehringi anatolicus (Méhely, 1909);
N. hellenicus (Méhely, 1909);
  N. hellenicus hellenicus (Méhely, 1909);
  N. hellenicus thracius (Savić, 1982);
  N. hellenicus strumiciensis (Savić et Soldatović, 1974);
  N. hellenicus epiroticus (Savić, 1982);
  N. hellenicus thermaicus (Hinton, 1920);
  N. hellenicus thessalicus (Ondrias, 1966);
  N. hellenicus peloponnesiacus (Ondrias, 1966);
N. makedonicus (Savić et Soldatović, 1974);
N. hungaricus (Nehring, 1898);
  N. hungaricus hungaricus (Nehring, 1898);
  N. hungaricus transsylvanicus (Méhely, 1909);
N. leucodon (Nordmann, 1840);
N. montanosyrmiensis (Savić et Soldatović, 1974);
N. monticola (Nehring, 1898);
N. serbicus (Méhely, 1909);
  N. serbicus serbicus (Méhely, 1909);
  N. serbicus ovchepolensis (Savić et Soldatović, 1974);
  N. serbicus tranensis (Savić et Soldatović, 1984);
  N. serbicus sofiensis (Savić et Soldatović, 1984);
N. rhodopiensis (Savić et Soldatović, 1984).

This approach was followed in some subsequent papers (e.g. Csorba et al. 2015), but it was also criticized (Kryštufek 1997). The introduced new names scarcely meet the most basic requirements of the International Code of Zoological Nomenclature. Savić & Soldatović (1974, 1984) classified chromosomal forms either as species or subspecies, with an evident lack of any clear criteria. For new names they proposed, diagnoses were based only on the karyotype and the type was never designated (Kryštufek 1997).

There are several available names (now under *Nannospalax*) for populations from Anatolia and neighbouring regions introduced in older papers (see Ellermann & Morrison-Scott 1951, Kryštufek & Vohralík 2009): *Spalax typhlus xanthodon* Nordmann, 1840 (type locality İzmir in western Anatolia); *Spalax intermedius* Nehring, 1898 (İskenderun, south-eastern Anatolia); *Spalax kirgisorum* Nehring, 1898 (type locality unknown, possibly northern Syria); *Spalax aegyptiacus* Nehring, 1898 (Ramleh near Alexandria, Egypt); *Spalax nehringi* Satunin, 1898 (Göle, Kars Province, eastern Anatolia); *Spalax berytensis* Miller, 1903 (Beyrout, Lebanon); *Spalax monticola cilicicus* Méhely, 1909 (Madenköy, Niğde Province, central Anatolia); *Spalax monticola anatolicus* Méhely, 1909 (near İzmir, western Anatolia); *Spalax monticola armeniacus* Mehely, 1909 (Göle, eastern Turkey); *Spalax labaumei* Matschie, 1919 (Eskişehir, western parts of central Anatolia); *Spalax monticola corybantium* Hinton, 1920 (Murat Dağı, Uşak Province, western Anatolia); *Spalax monticola captorum* Hinton, 1920 (Çankırı, northern Anatolia); *Spalax monticola vasvarii* Szunyoghy, 1941 (Malatya, eastern Anatolia); *Spalax ehrenbergi* var. *ceyhanus* Szunyoghy, 1941 (Ceyhan, Adana Province, south-eastern Anatolia).

Kıvanç (1988) recognized five subspecies of blind mole rats in Turkey on morphological grounds, i.e. *S. leucodon nehringi*, *S. l. armeniacus*, *S. l. cilicicus*, *S. l. turcicus* and *S. l. anatolicus*. These names were subsequently applied for various *Nannospalax* chromosomal forms discovered in Anatolia. Coşkun et al. (2010a) proposed that *N. ceyhanus* may be a valid name for populations from the environs of Adana in south-eastern Anatolia classified previously within *N. ehrenbergi*. Hadid et al. (2012) differentiated populations from central interior Anatolia, possessing a high number of chromosomes (2n = 60-62) as the *vasvarii* lineage. The populations from the same area with 2n = 52, 54, 56, 58 and 60 were recognized as *N. labaumei* by Kankılıç & Gürpınar (2014) and Kankılıç et al. (2014). Kankılıç et al. (2015) studied allozyme variation and concluded that four species can be differentiated among Anatolian populations of blind mole rats, i.e. *N. xanthodon*, *N. ehrenbergi*, *N. cilicicus* and *N. nehringi*. Furthermore, Coşkun described three additional taxa: *Spalax nehringi tuncelicus* from a site near Tunceli in eastern Anatolia (Coşkun 1996a), *Spalax nehringi nevoi* from the vicinity of Gaziantep (Coşkun 1996b) and *Nannospalax munzuri* from Ovacık in the Tunceli Province in eastern Anatolia (Coşkun 2004a). Nevo

et al. (2001) proposed the species status for four chromosome races found in Israel, i.e. *Spalax golani*, *S. galili*, *S. carmeli* and *S. judaei*. Hadid et al. (2012) recognized the northern African population examined in Egypt as *S. aegyptiacus*, originally described near Alexandria. It is obvious that the taxonomy within blind mole rats in the Asiatic part of their range has not yet been definitively resolved and the species delimitation is often not clear.

The first data on chromosomes of the mole rats were obtained by Matthey (1959), who found 48 chromosomes in the diploid complement of animals originating from the Caucasus. Walknowska (1963) examined chromosomes of a female from Bulgaria and she reported the diploid number of 54 chromosomes. In Israel, four allopatric or parapatric chromosomal races, with 2n = 52, 54, 58 and 60 chromosomes, were discovered (Wahrman et al. 1969a, b) and subsequently intensively studied. A comprehensive review on chromosomes of almost all extant species was published by Lyapunova et al. (1974). Extensive research was later done in south-eastern Europe (summarized in Savić & Soldatović 1984) and in Anatolia; the later appeared to be one of the core areas of chromosomal differentiation in the blind mole rats (e.g. Nevo et al. 1995, Sözen 2004, Arslan & Zima 2014). Nevo et al. (1994b) estimated the number of described chromosome races at about 50 and considered individual cytotypes as presumptively good biological species. The exceptional karyotype diversification is particularly confined to the genus *Nannospalax*. In this paper, we accept the traditional division of this genus into three nearly parapatric species or species groups, *N. leucodon*, *N. xanthodon* and *N. ehrenbergi* (Musser & Carleton 2005, Kryštufek & Vohralík 2009). At the same time, we are aware that this treatment is only provisional and revision at the species level will be necessary in the future.

A symptomatic feature of chromosome variation in mole rats and, particularly, in *Nannospalax* species, is the occurrence of populations, possessing a specific karyotype and distributed in a parapatric or allopatric pattern. Populations or groups of populations sharing identical chromosomal sets are usually called cytotypes. We assume that the term corresponds to the definition of chromosome races as defined by Hausser et al. (1994), who noted that the recognition, naming and systematics of populations with different karyotypes pose a serious problem. They therefore proposed, on the example of the common shrew, *Sorex araneus*, rules and conventions to name, group and describe the races. A chromosome race is defined as a group of geographically contiguous or recently separated populations, which share the same chromosome complement by descent. Geographically separated populations sharing the same karyotype should be attributed to the same race, only if there are convincing indications that their separation is recent and that they share all their chromosomes by common descent. We believe that this definition can be adopted equally well also to the blind mole rats and we follow it in discrimination of individual races. Populations with similar karyotypes differing particularly in the number of chromosomal arms or even in the chromosome diploid number, may be exceptionally included in the same race. This solution is usually related to the fact that variations within the chromosome race may result from population polymorphism but can equally well be an artefact of comparisons of findings published in different papers. In this review, the names of races are usually derived either from the name of an available species group taxon and/or from a geographic name confined to the locality of the first reliable original description and surrounding area (specified as the Description locality). We should stress that the names of races introduced in this paper have no implications in respect of the International Code of Zoological Nomenclature. We use also the term "cytotype" for a particular karyotype characterized by the diploid number (2n) and the number of chromosomal (NF) or autosomal arms (NFa). The chromosome races recorded subsequently in the three recognized *Nannospalax* species are listed, according to their increasing diploid chromosome numbers and chromosome arm numbers. Deviations from this principles were few (e.g. in the polymorphic Jordan races).

In the figures showing examples of the karyotypes, we follow the arrangement of chromosomes applied in some previous papers (Ivanitskaya et al. 1997, 2008). Two large acrocentric autosomal pairs, which can be reliably recognized are arranged as the first and second pairs in the complement. The other biarmed and acrocentric autosomes are arranged according to their size, respectively.

The extensive karyotype variation in *Nannospalax* is the result of various chromosomal rearrangements, the nature of which is still not sufficiently known, because the cytogenetic studies that use banding techniques or molecular approaches are hitherto rather rare (Ivanitskaya et al. 1997, 2008, Arslan et al. 2011a, 2014a, Matur et al. 2013, Arslan & Zima 2015a, b). Ivanitskaya et al. (1997) ascertained that chromosomes of all studied Turkish cytotypes of

N. xanthodon (2n = 60) and *N. ehrenbergi* possess a similar pattern of G-band sequences. They also indicated centromeric fusions and additions/deletions of C-heterochromatin, as well as occasional pericentric inversions, euchromatin deletions, missing chromosomes and centromeric shifts, as major mechanisms of chromosomal change.

Savić & Soldatović (1979b) assumed that the evolution of karyotypes of the Balkan Spalacinae was driven by Robertsonian re-arrangements and most probably took the form of a decrease in the number of acrocentric autosomes and consequently of the diploid number of chromosomes. Similarly, Ivanitskaya et al. (2005) and Matur et al. (2011, 2013) considered chromosomal fusion as the major force of karyotype evolution in blind mole rats. On the contrary, Nevo et al. (1994b, 2000) suggested an opposite trend of the increasing diploid chromosome numbers in both Turkey and Israel. The number of acrocentrics was supposed to increase through Robertsonian fissions of metacentrics, whereas changes in the fundamental numbers were supposed to be derived from centromeric shifts. Yüksel & Gülkaç (1990) reviewed data on blind mole rat karyotypes from Balkan Peninsula, Asia Minor and the Caucasus, and proposed a phylogenetic dendrogram. A phylogenetic tree of chromosome races from Anatolia was proposed also by Matur et al. (2013).

Nevo et al. (1994b) assumed that chromosomal speciation and adaptive radiation of mole rats in Asia Minor and the Middle East are correlated to increased ecological stress, and that this correlation can be generalized in all members of the extant blind mole rat taxa. Species and races with the highest diploid numbers in Israel, North Africa, Balkans, Ukraine, and Russia, as well as in Turkey occupy the most xeric regions, whereas the races with the lowest diploid numbers occur in mesic environments in the centre of the spalacine range. The trends of chromosome evolution in blind mole rats thus involve increase in the diplod number along gradients of increased aridity (Nevo et al. 1994b, 1995). This hypothesis was criticized by Matur et al. (2011).

Genetic and molecular markers have been applied in blind mole rat studies for a long time (Nevo & Shaw 1972, Nevo & Sarich 1974, Vorontsov et al. 1977, Nižetić et al. 1988) but a comprehensive phylogenetic study is still missing. Nevo et al. (1994a, b) estimated evolutionary divergence times, based on allozymes. Nevo & Beiles (1992), Nevo et al. (1993, 1999) and Reyes et al. (2003) studied mtDNA polymorphisms in Israeli populations. Nuclear sequences in these populations were investigated by Catzeflis et al. (1989), Suzuki et al. (1996) and Polyakov et al. (2007). Malik et al. (2011) investigated genetic relationships within closely related families, and Popa et al. (2014) developed nuclear microsatellite markers for *N. leucodon*. Molecular phylogenetic studies of the extant blind mole rats were provided by Hadid et al. (2012), Németh et al. (2013a) and Chişamera et al. (2014) and monophyletic nature of both recognized genera was supported. Kryštufek et al. (2012) established a cytochrome *b* phylogeny for 15 cytotypes, belonging to all three species recognized on morphological grounds, i.e. *N. leucodon*, *N. xanthodon* and *N. ehrenbergi*. Phylogenetic reconstructions yielded two highly divergent groups, which were in agreement with the current division into two subgenera (*Nannospalax*, including *ehrenbergi* and *Mesospalax*, including *leucodon* and *xanthodon*). The former subgenus comprised samples from south-eastern Turkey, Israel and Egypt (the morphospecies *N. ehrenbergi*). Hadid et al. (2012) also supported separation of the lineage *Spalax* from *Nannospalax*, the clade *leucodon* from *xanthodon* and, as mentioned earlier, differentiated a new "*vasvarii*" clade. Other molecular phylogenies of certain populations, using allozymes, nuclear and mitochondrial sequences were proposed by Kankılıç et al. (2005, 2013, 2014, 2015), Polyakov et al. (2007), Arslan et al. (2010), Kandemir et al. (2012) and Kankılıç & Gürpınar (2014). These studies indicated deep divergences between individual lineages but the overall phylogenetic pattern in all extant blind mole rats is far from resolved.

List of races

Nannospalax leucodon (Fig. 1)

In this review, we follow the opinion of Kryštufek & Vohralík (2009) that *N. leucodon* is endemic to Europe. Its occurrence on certain Aegean islands (e.g. the Limnos Island) still remains questionable. A recent view of the geographic range of the species was published by Kryštufek & Amori (2008).

1. Bulgaricus

2n = 46, NFa = 72, NF = 76

The complement includes seven pairs of large and medium-sized metacentric, five pairs of submetacentric (the first two are the largest elements of the set), two pairs of subtelocentric (the first pair is among the largest in the set, the others are of medium size) and eight pairs of small acrocentric autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome a small subtelocentric (Peshev 1981).

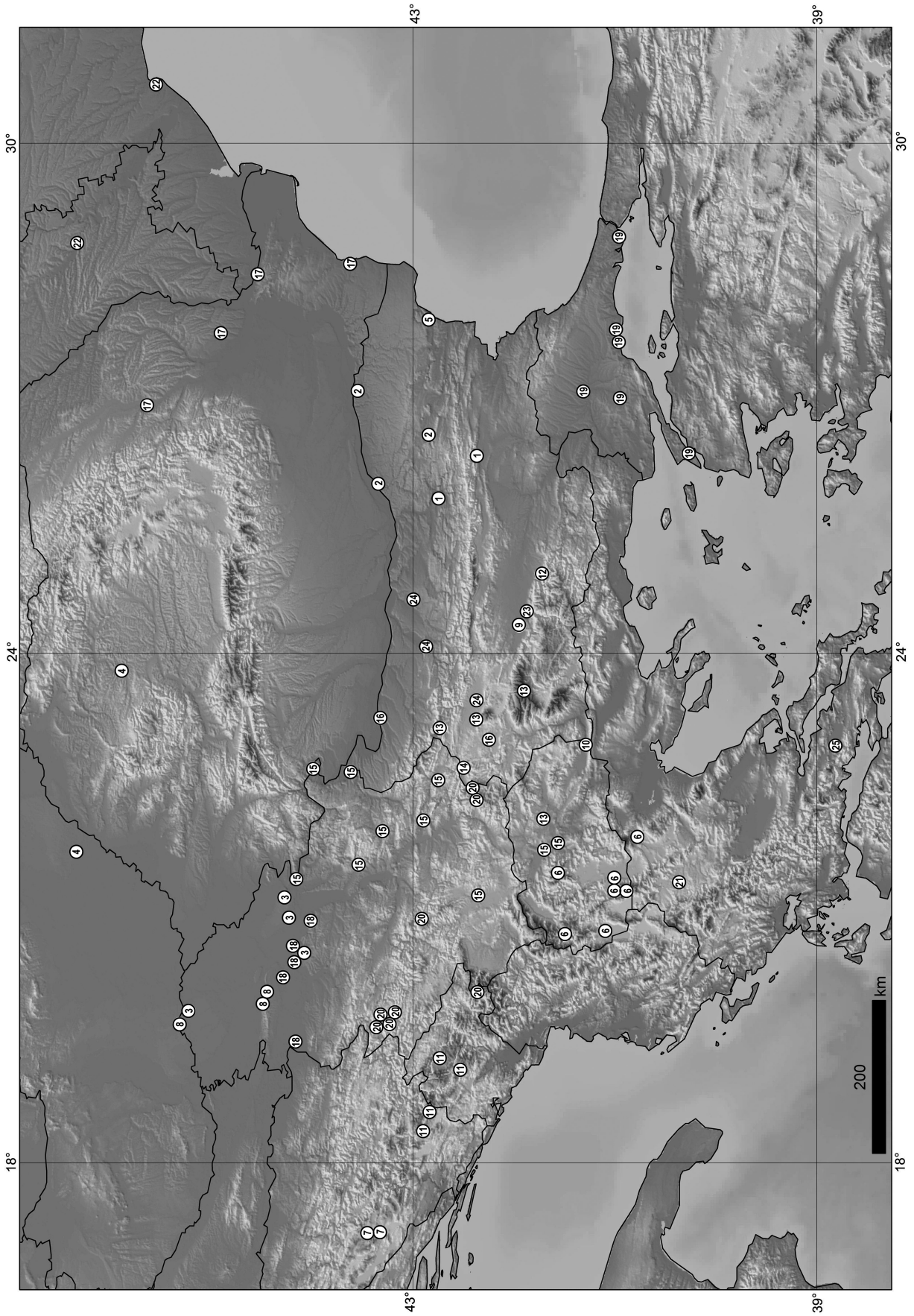

Fig. 1. Distribution map of the chromosomal races recorded within *Nannospalax leucodon*. See text for numbering of the races.

Description locality
Kozarevets near Veliko Tarnovo, Sliven region, 370 m a.s.l., Bulgaria (Peshev 1981).
Distribution
Known from the slopes of the Balkan (Stara Planina) Mts. in the eastern parts of central Bulgaria, east of the range of the Sofiensis race.
Additional information
This race was described as *Nannospalax bulgaricus bulgaricus* by Savić & Soldatovic (1984).

2. Srebarnensis
2n = 48, NFa = 74, NF = 78
The complement includes five pairs of metacentric (the last one is the smallest element in the set), seven pairs of submetacentric (the first two are the largest elements in the set), a large and a medium-sized subtelocentric pairs and nine pairs of small acrocentric autosomes. The X chromosome is medium-sized submetacentric, the Y chromosome was not distinguished (Peshev 1981).
Description locality
Srebarna, right bank of the River Danube, 80 m a.s.l., Bulgaria (Peshev 1981).
Distribution
Russe, Targoviste and Silistra regions in north-eastern Bulgaria (Peshev 1981).
Additional information
The race was described as *Nannospalax bulgaricus srebarnensis* by Savić & Soldatović (1984).

3. Hungaricus
2n = 48, NFa = 80, NF = 84
The complement includes four larger pairs of metacentric, eight pairs of submetacentric, five pairs of subtelocentric (some of them represent the largest elements) and six acrocentric autosomal pairs which are the smallest elements. The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric with distinct short arms (Soldatović et al. 1966a).
Description locality
Dolovo, southern Banat, Serbia (Soldatović et al. 1966a).
Distribution
The Pannonian lowland of Bačka and Banat in northern Serbia. The southern border of the range is on the slopes of Mt. Avala towards the Danube, where this race meets the Syrmiensis race (Soldatović et al. 1966a, 1967, Savić & Soldatović 1974, 1984, Soldatović & Savić 1974).
Additional information
The race was recognized as *S. leucodon martinoi* Petrov, 1971 by Soldatović (1971, 1977) and Savić & Soldatović (1974), later as *Nannospalax hungaricus hungaricus* by Savić & Soldatović (1984).

4. Transsylvanicus
2n = 50, NFa = 80, NF = 84
The karyotype includes four pairs of metacentric, seven pairs of submetacentric, five pairs of subtelocentric (two of them are distinctly large) and eight pairs of acrocentric autosomes. The X chromosome is large and submeta- or metacentric, whereas the Y chromosome is submetacentric or acrocentric (Raicu et al. 1968).
Description locality
Jucu, Cluj-Napoca region, Transylvania, Romania (Raicu et al. 1968).
Distribution
North-western Romania (Raicu et al. 1968) and eastern Hungary (Németh et al. 2006, 2009).
Additional information
The race was recognized as *Nannospalax hungaricus transsylvanicus* by Savić & Soldatović (1984).

5. Varna
2n = 52, NFa = 76, NF = 80
The complement includes three pairs of medium-sized or small metacentric, eight pairs of submetacentric, a large and a small pair of subtelocentric and 12 small acrocentric pairs of autosomes. The X chromosome is a large metacentric, the Y chromosome is a small acrocentric. The largest autosomal pair is always heteromorphic (submetacentric/subtelocentric) and both homologous autosomes differ distinctly in their size. A possible reason for this variation can be amplification of a short arm in an originally large subtelocentric autosome. Heteromorphism occurs also in the X chromosomes of the female complement, which may differ both in centromeric position and size (Peshev 1983).
Description locality
Varna at the Black Sea coast, eastern Bulgaria (Peshev 1983).
Distribution
The race is known only from the description locality.

6. Makedonicus (Fig. 2)
2n = 52, NFa = 82, NF = 86
The complement includes two metacentric, seven submetacentric, seven subtelocentric (two of them are the largest elements in the set) and nine small

acrocentric pairs of autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome is an acrocentric with visible short arms (Savić & Soldatović 1974). Zima et al. (1997) and Zima (2004) described the G-banding chromosome pattern.

Description locality

Mt. Jakupica (mountain pastures under the Solunska Glava peak), Macedonia /FYROM/ (Savić & Soldatović 1974).

Distribution

This race was originally recorded at high altitudes (about 2200 m a.s.l.) in Macedonia, and later it was also found at lower elevations in Pelagonia (from Prilep to Bitola) and in the Lake Ohrid basin (Soldatović & Savić 1974, Savić & Soldatović 1984, Zima et al. 1997), as well as in valleys of northern Greece (Giagia et al. 1982).

Additional information

The race was recognized as *Nannospalax macedoniensis* by Soldatović (1971, 1977) and later as *N. makedonicus* by Savić & Soldatović (1984).

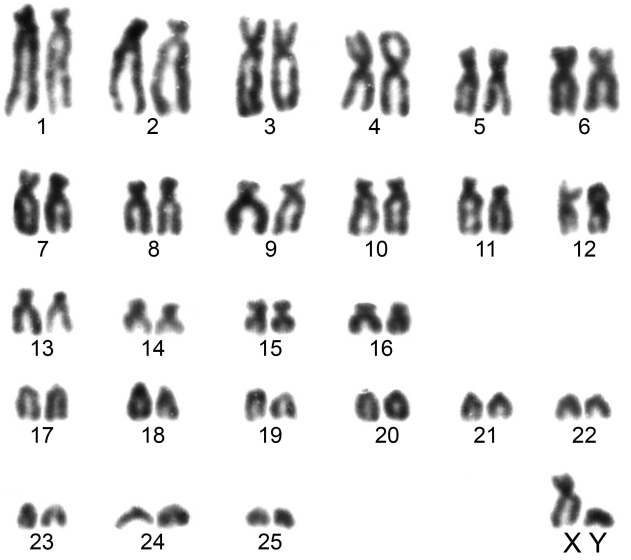

Fig. 2. Karyotype of the Makedonicus race (2n = 52, NF = 86) from Bistra Planina in Makedonia.

7. Monticola

2n = 54, NFa = 80, NF = 84

The complement includes two pairs of metacentric, seven pairs of submetacentric, five pairs of subtelocentric and 12 pairs of small acrocentric autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome a small acrocentric with apparent short arms (Savić & Soldatović 1974).

Description locality

Gornji Malovan, the edge of the Kupreško polje field, Bosnia and Herzegovina (Savić & Soldatović 1974).

Distribution

The Dinaric Mts. in western Bosnia (around Kupres) and the southern slopes of Mt. Ljubuša in Herzegovina. The description locality is at the western border of the range of blind mole rats.

Additional information

This race was recognized as *Nannospalax monticola* by Soldatović (1971, 1977) and Savić & Soldatović (1984).

8. Montanosyrmiensis

2n = 54, NFa = 82, NF = 86

The complement includes two pairs of metacentrics of medium size, eight pairs of submetacentric, five pairs of subtelocentric (the largest elements in the complement) and 11 pairs of small acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome is a small acrocentric or metacentric (Savić & Soldatović 1974). The karyotypes of two populations studied from Serbia appear similar but they differ in the centromere position on the Y chromosome. In the Stražilovo population, this chromosome is polymorphic, whereas all males examined from Čortanovci possess a metacentric Y chromosome (Savić & Soldatović 1974, Soldatović & Savić 1974).

Description locality

Stražilovo, Serbia (Savić & Soldatović 1974).

Distribution

This race occurs at the foothills of Mt. Fruška Gora, in the southern edge of the Pannonian plain in Serbia (Savić & Soldatović 1974, 1984, Soldatović & Savić 1974) and in neighbouring regions (Kelebia) in Hungary (Németh et al. 2013b). The ranges of the Hungaricus, Syrmiensis and Montanosyrmiensis races are geographically close but probably allopatric (Soldatović et al. 1966a, 1967, Savić & Soldatović 1974, 1984, Soldatović & Savić 1974).

Additional information

This race was recognized as *Nannospalax montanosyrmiensis* by Savić & Soldatović (1984).

9. Pazardzhik

2n = 54, NFa = 82, NF = 86

The complement includes three pairs of medium-sized metacentric, nine pairs of submetacentric, three pairs of subtelocentric (two of them are the largest elements in the set), and 11 pairs of small acrocentric autosomes. The X chromosome is a medium-

sized submetacentric, the Y chromosome is a small acrocentric (Peshev 1983).
Description locality
Pazardzhik, central Bulgaria (Peshev 1983).
Distribution
Known only from the description locality where two males were examined.

10. Strumiciensis
2n = 54, NFa = 84, NF = 88
The complement includes four pairs of medium-sized metacentric, six pairs of submetacentric (two pairs are distinctly smaller than the other), six pairs of subtelocentric (two of them are the largest elements of the set) and ten pairs of small acrocentric chromosomes. The X chromosome is a large submetacentric, the Y chromosome a smaller acrocentric (Savić & Soldatović 1974).
Description locality
Strumičko pole, south-eastern Macedonia /FYROM/ near the borders with Bulgaria and Greece (Savić & Soldatović 1974).
Distribution
Only one population is known from the Strumica valley and three specimens were examined. The race apparently occurs in the border region between the Macedonian hilly and piedmont area and the Rila-Rhodope mountain system (Savić & Soldatović 1974, 1984).
Additional information
The race was recognized as *Nannospalax hellenicus strumiciensis* by Savić & Soldatović (1984).

11. Hercegovinensis
2n = 54, NFa = 86, NF = 90
The complement includes three pairs of metacentric (the last one is the smallest of the set), six pairs of large or medium-sized submetacentric, eight pairs of subtelocentric and nine pairs of small acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome is a small acrocentric with distinct short arms (Soldatović et al. 1967).
Description locality
Čemerno, Bosnia and Herzegovina (Soldatović et al. 1967).
Distribution
The race occupies habitats in altitudes beyond 1000 m a.s.l. in the Dinaric mountain range in Bosnia and Herzegovina and Montenegro (Soldatović et al. 1967, Savić & Soldatović 1974, 1984, Soldatović & Savić 1974).
Additional information
It was recognized as *Nannospalax herzegovinensis* by Soldatović (1971, 1977) and Savić & Soldatović (1984).

12. Rhodopiensis
2n = 54, NFa = 88, NF = 92
The complement includes a pair of large metacentric, seven pairs of medium-sized and small submetacentric, ten pairs of subtelocentric (the first two are the largest elements of the set) and eight pairs of small acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome was not distinguished (Peshev 1981).
Description locality
Dobrostan near Asenovgrad, 1200 m a.s.l., Bulgaria (Peshev 1981).
Distribution
Northern slopes of the Rhodopi Mts. in the southern parts of central Bulgaria (Peshev 1981).
Additional information
This race was described as *Nannospalax rhodopiensis* by Savić & Soldatović (1984). The animals examined by Walknowska (1963) probably belonged to this race (Savić & Soldatović 1979b, Peshev 1981).

13. Ovchepolensis
2n = 54, NFa = 90, NF = 94
The complement includes four pairs of medium-sized metacentric, eight pairs of submetacentric, seven pairs of subtelocentric (some of them are the largest elements in the set) and seven pairs of small acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome is a small acrocentric (Soldatović & Savić 1973).
Description locality
Ovče pole, north-eastern Macedonia /FYROM/ (Soldatović & Savić 1973).
Distribution
The range of this form covers parts of north-eastern Macedonia and the environs of Sofia in Bulgaria (Soldatović & Savić 1973, 1974, Peshev 1981, 1983). The populations from the region situated west of Sofia in Bulgaria were originally described as a separate form named Sofia West (Peshev 1981), but Savić & Soldatović (1984) lumped it with Ovchepolensis.
Additional information
The race was recognized as *Nannospalax serbicus ovchepolensis* by Savić & Soldatović (1984).

14. Tranensis

2n = 54, NFa = 92, NF = 96

The complement includes four pairs of medium-sized and small metacentric, nine pairs of medium-sized and small submetacentric, seven pairs of subtelocentric (the first two are the largest elements of the set) and six pairs of small acrocentric autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome was not determined (Peshev 1981).

Description locality

Tran, the upper course of the River Nišava in westernmost Bulgaria, 700 m a.s.l. (Peshev 1981). Single female examined only.

Additional information

The karyotype appears intermediate between the Ovchepolensis and Serbicus/Lom races. This race was described as *Nannospalax serbicus tranensis* by Savić & Soldatović (1984).

15. Serbicus

2n = 54, NFa = 94, NF = 98

The complement includes four metacentric, ten submetacentric, seven subtelocentric and five small acrocentric autosomal pairs. The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric with apparent short arms (Savić & Soldatović 1974).

Description locality

Pirot, eastern Serbia (Savić & Soldatović 1974).

Distribution

The race occurs in lowlands of Serbia on the right bank of the River Danube and in valleys of central Macedonia and presumably Kosova. The range spreads from the Danube southwards down the Great Morava valley till Veles on the River Vardar in Macedonia (Savić & Soldatović 1974, 1984, Soldatović & Savić 1974).

Additional information

The race was recognized as *Nannospalax serbicus serbicus* by Soldatović (1971, 1977) and Savić & Soldatović (1984).

16. Lom

2n = 54, NFa = 94, NF = 98

The complement includes one pair of large and four pairs of medium-sized or small metacentric, 11 pairs of medium-sized and small submetacentric, five pairs of subtelocentric (the first two are the largest elements in the set) and five small pairs of acrocentric autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome was not distinguished (Peshev 1983).

Description locality

Lom, right bank of the River Danube, north-western Bulgaria (Peshev 1983).

Distribution

Two isolated areas of distribution were recorded in western Bulgaria, in north-western and south-western parts of the country, respectively (Peshev 1983).

Additional information

The karyotype is similar to that of the Serbicus race, occurring in eastern Serbia not far from the Bulgarian border. The argument against lumping these two races into one is that a detailed arrangement of chromosomes into morphological groups yielded slight differences (Peshev 1983, Savić & Soldatović 1984).

17. Dobrudzha

2n = 54-56, NFa = 74-80, NF = 78-84

In the complement with 56 chromosomes, Raicu et al. (1968) reported 13 bi-armed and 14 acrocentric pairs of autosomes (NFa = 80), but Raicu et al. (1973) distinguished 12 bi-armed and 15 acrocentric pairs of autosomes (NFa = 78). Additionally, the sample examined from Isaccea in Dobrudzha appeared polymorphic (Raicu et al. 1973). A standard karyotype with 56 chromosomes and NFa = 78 was found in five animals studied, but a single female showed only 54 chromosomes in the complement. This karyotype (NFa = 74) differs from the standard set by the absence of one bi-armed chromosomal pair. The X chromosome is a large subtelocentric or submetacentric, the Y chromosome is a small subtelocentric. The sex chromosomes were not distinguished in the female with 54 chromosomes.

Description locality

Constanta, Dobrudzha (Dobrogea in Romanian), Romania (Raicu et al. 1968).

Distribution

Dobrudzha, Black Sea coast, Moldavia (Perinei, Bacau) in Romania (Raicu et al. 1968, 1973, Raicu & Duma 1969).

Additional information

The karyotype with 56 chromosomes seems similar to that of the Leucodon race. The Dobrudzha race was included in *Nannospalax leucodon* by Savić & Soldatovic (1984). *Spalax dolbrogeae* Miller, 1903 was described from Malcoci in Dobrudzha (Ellermann & Morrison-Scott 1951).

18. Syrmiensis

2n = 54-56, NFa = 86-90, NF = 90-94

The race includes two different cytotypes. The complement with 2n = 54 contains three pairs of

metacentric (the last element is the smallest in the set), nine submetacentric, five subtelocentric (the largest elements in the set) and nine acrocentric pairs of autosomes. The complement with 56 chromosomes includes one additional subtelocentric pair of autosomes. The X chromosome is a large submetacentric, the Y chromosome is a small acrocentric or subtelocentric (Soldatović et al. 1967, Savić & Soldatović 1974). Soldatović et al. (1967) and Savić & Soldatović (1979b, 1984) found 2n = 56 in a population studied in Banovo brdo near Beograd, whereas 2n = 54 was recorded in six other populations sampled in the same area.

Description locality

Stara Pazova (Srem), Serbia (Savić & Soldatović 1974).

Distribution

The race occured in Pannonian plain in Srem (where from it has mostly vanished since 1950) and the area of the city of Beograd. It inhabits the right bank of the River Sava and spreads along the right bank of the River Danube up to Smederevo. To the south of the River Sava blind mole rats of this race do not build their typical molehills (Savić & Soldatović 1974, 1979b, 1984).

Additional information

The race was recognized as *Nannospalax syrmiensis* by Soldatović (1971, 1977), Soldatović & Savić (1974) and Savić & Soldatović (1984).

19. Turcicus (Fig. 3)

2n = 56, NFa = 72-74, NF = 76-78

The complement with NFa = 74 includes two pairs of medium-sized metacentric, five pairs of submetacentric, three pairs of subtelocentric (two of them are the largest elements in the set), and 17 pairs of acrocentric autosomes (Savić & Soldatović 1977, Soldatović & Savić 1978). The karyotype with NFa = 72 contains nine pairs of bi-armed and 18 pairs of acrocentric autosomes and it is reported from Eceabat (Sözen 2004) and Babaeski (Arslan at al. 2014a). The X chromosome is submetacentric or metacentric, the Y chromosome is a small acrocentric. Arslan et al. (2014a) recorded an exceptionally small X chromosome, which belonged to the smallest elements of the complement.

Dark C-bands appear in the pericentromeric areas of all bi-armed and of most acrocentric autosomes. Slight telomeric C-positive bands are located in the short arms of the three largest bi-armed autosomes. The X chromosome has a centromeric C-positive area and the Y chromosome possesses a distinct dark pericentromeric C-band, extending over the proximal third of the chromosome (Matur et al. 2013, Arslan et al. 2014a). The NORs are detected in the telomeric regions of the short arms of five bi-armed autosomal pairs (Arslan et al. 2014a).

Description locality

Çorlu, Lower Thrace, Turkey (Soldatović & Savić 1978).

Distribution

Lower Thrace in the European part of Turkey, up to the coast of the Marmara Sea and Gallipoli (Gelibolu) Peninsula (Savić & Soldatović 1977, Soldatović & Savić 1978, Sözen 2004, Sözen et al. 2006a, Matur et al. 2013, Arslan et al. 2014a).

Additional information

The race was recognized as *Nannospalax turcicus* by Savić & Soldatović (1984). Matur et al. (2013) designated this race as 56Tr.

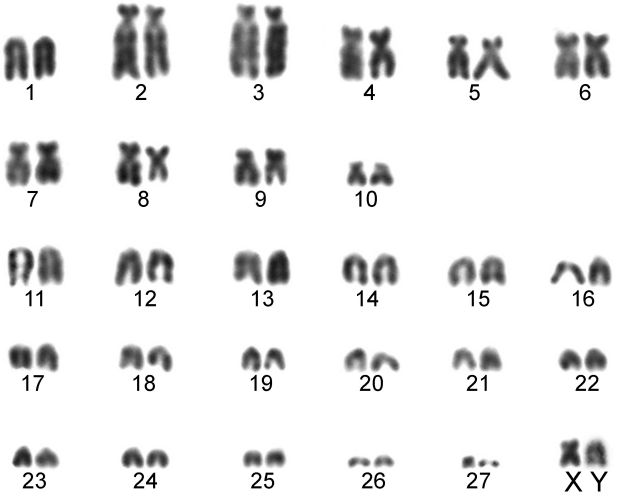

Fig. 3. Karyotype of the Turcicus race (2n = 56, NF = 76) from Babaeski, Kırklareli, in European Turkey.

20. Montanoserbicus

2n = 56, NFa = 76-78, NF = 80-82

The complement includes two metacentric, six submetacentric, four subtelocentric which are among the largest elements in the set and 15 small acrocentric pairs of autosomes (NFa = 78). Another complement is reported from a single site (Lake Vlasina – Klisura) in south-eastern Serbia. This karyotype has the same number of chromosomes, but it includes five submetacentric and 16 acrocentric autosomal pairs (NFa = 76). The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric with prominent short arms (Soldatović et al. 1966b, Savić & Soldatović 1984).

Description locality
Čajetina, western Serbia (Soldatović et al. 1966b).
Distribution
The range covers the mountains of Tara, Zlatibor and Čigota in western Serbia, Kopaonik in south-western Serbia and southern Dinaric Mts. in Montenegro (Čakor) at altitudes above 700 m a.s.l. Presumably also in Kosova and various mountain ranges in southern Serbia as east as Mt. Vlasina. Local populations are seemingly isolated (Soldatović et al. 1967, Savić & Soldatović 1974, 1984, Soldatović & Savić 1974).
Additional information
The race was recognized as *Nannospalax montanoserbicus* by Soldatović (1971, 1977) and Savić & Soldatović (1984).

21. Epiroticus
2n = 56, NFa = 80, NF = 84
The complement includes one pair of medium-sized metacentric, six pairs of submetacentric, six pairs of subtelocentric autosomes (two of them are the largest in the set) and 14 pairs of small acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome is a small acrocentric or subtelocentric (Savić & Soldatović 1977, 1978).
Description locality
Lefkothea near Ioannina in Epirus, Greece (Savić & Soldatović 1977, 1978).
Distribution
Epirus in north-western Greece, where two specimens from a single population were studied (Savić & Soldatović 1977, 1978, 1984).
Additional information
This race was recognized as *Nannospalax hellenicus epiroticus* by Savić & Soldatović (1984).

22. Leucodon
2n = 56, NFa = 80, NF = 84
The complement includes two pairs of metacentrics of different size, three pairs of submetacentrics, eight pairs of mostly large subtelocentrics (two subtelocentric pairs are the largest in the set) and 14 pairs of small acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome is a small acrocentric with distinct short arms (Lyapunova et al. 1974).
Description locality
Odessa, south-western Ukraine (Lyapunova et al. 1974).
Distribution
Odessa region in south-western Ukraine and Orgeev region in Moldova (Lyapunova et al. 1974, Martynova et al. 1975).
Additional information
Lyapunova et al. (1974) distinguished the specimens studied as *Mesospalax leucodon*. The race was later recognized as *Nannospalax leucodon* (the type locality near Odessa) by Savić & Soldatovic (1984). The karyotype is quite similar to some populations of the Dobrudzha race and the chromosomal similarity of these races is considered as evidence for recent dispersal of *N. leucodon* into Moldova and southern Ukraine from the south-west (Lyapunova et al. 1974).

23. Thracius
2n = 56, NFa = 84, NF = 88
The complement includes one pair of medium-sized metacentric, seven pairs of submetacentric, seven pairs of subtelocentric (two of them are distinctly large) and 12 pairs of small acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome is a smaller subtelocentric (Savić & Soldatović 1977, Soldatović & Savić 1978).
Description locality
Novo selo, 30 km SW of Plovdiv, Bulgaria (Soldatović & Savić 1978).
Distribution
Upper Thrace, central Bulgaria (Savić & Soldatović 1977, Soldatović & Savić 1978). Only two males were examined.
Additional information
The race was recognized as *Nannospalax hellenicus thracius* by Savić & Soldatović (1984).

24. Sofiensis
2n = 56, NFa = 86, NF = 90
The complement includes two pairs of smaller metacentric, nine pairs of medium-sized and small submetacentric, five pairs of subtelocentric (the first two are the largest elements in the set) and 11 pairs of small acrocentric autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric (Peshev 1981).
Description locality
Cherven Briag, Bulgaria (specified by Peshev 1983).
Distribution
The central parts of northern Bulgaria between the Balkan (Stara Planina) Mts. and the River Danube and the Pleven region. East of the range of the Lom and Ovchepolensis races (Peshev 1983).
Additional information
Peshev (1981, 1983) designated this race as Sofia East and Savić & Soldatović (1984) later described it as *Nannospalax serbicus sofiensis*. Another race described from Petrohan in the Rila Mts. west to Sofia

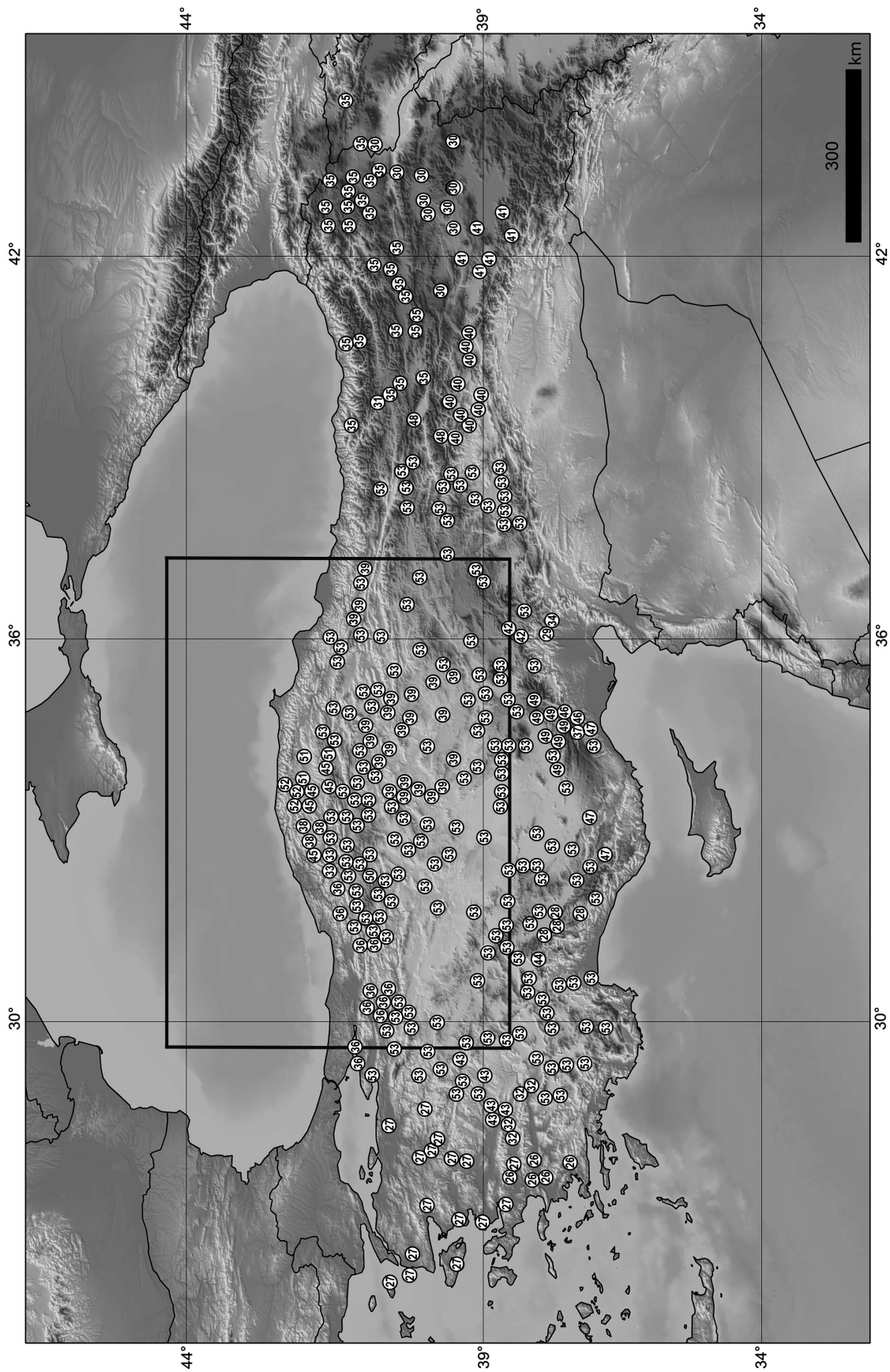

Fig. 4. Distribution map of the chromosomal races recorded within *Nannospalax xanthodon*. For more details inside the inset see Fig. 5. See text for numbering of the races.

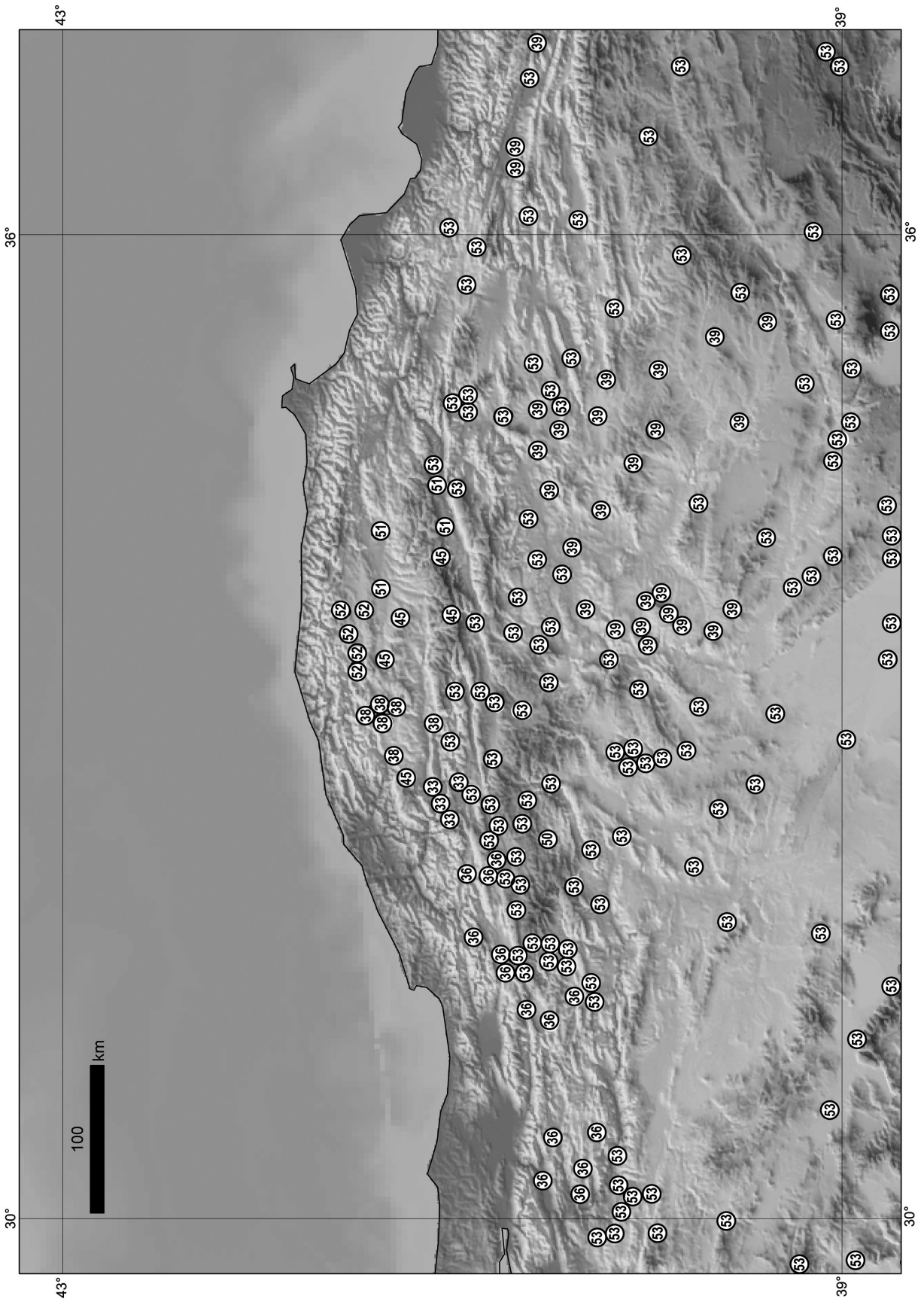

Fig. 5. An inset of the distribution map of the chromosomal races recorded within *Nannospalax xanthodon* in the northern parts of the range. See text for numbering of the races.

(Sofia West in Peshev 1981) had the same karyotype as the Ovchepolensis race (2n = 54, NFa = 90, NF = 94) and was included within that race (Savić & Soldatović 1984).

25. Hellenicus

2n = 58, NFa = 84, NF = 88

The complement includes one pair of medium-sized metacentric, seven pairs of submetacentric, six pairs of subtelocentric autosomes and 14 small acrocentric pairs of autosomes. The X chromosome is a medium-sized metacentric and the Y chromosome is a small acrocentric with apparent short arms (Savić & Soldatović 1977, 1978).

Description locality

Hagios Spyridon village near Levadia, Viotia, Greece Savić & Soldatović (1977, 1978).

Distribution

A single site known from Viotia in Greece. The population occurred on river banks at about 250 m a.s.l. (Savić & Soldatović 1977, 1978, 1984). Only two males were examined.

Additional information

This race was recognized as *Nannospalax hellenicus hellenicus* by Savić & Soldatović (1984).

Nannospalax xanthodon (Figs. 4, 5)

This species is nearly endemic to Turkish Anatolia (Kryštufek & Vohralík 2009). Its occurrence on some Aegean islands (Lesbos, Bozcaada, Gökçeada) is supported by chromosomal findings. Recent views of the geographic range were presented by Bukhnikashvili et al. (2008) and Kryštufek & Vohralík (2009).

26. Xanthodon (Fig. 6)

2n = 36, NFa = 66, NF = 70

The complement includes five pairs of metacentric, nine pairs of submetacentric (one of these pairs is the largest in the set), two pairs of large subtelocentric and one pair of small acrocentric autosomes. The X chromosome is submetacentric, the Y chromosome metacentric (Sözen et al. 1999, Arslan et al. 2013, Matur et al. 2013).

Distinct centromeric C-positive regions, including relatively large centromeric areas occur in seven pairs of bi-armed autosomes. Other autosomes have slight centromeric C-bands, except for the acrocentric pair. Two bi-armed autosomes have interstitial C-heterochromatic bands on the long and short arm, respectively. The presumed X chromosome has a slight centromeric C-positive band (Arslan et al. 2013, Matur et al. 2013). The Ag-NOR regions are located in the telomeric region of the short arm of three bi-armed autosomal pairs (Arslan et al. 2013).

Description locality

Bayındır, 50 km E of İzmir, İzmir Province, Anatolia, Turkey (Sözen et al. 1999).

Distribution

Central and southern parts of the Aegean region in western Anatolia, in the Provinces of İzmir, Aydın and Muğla (Sözen et al. 1999, 2013, Kankılıç et al. 2010, Arslan et al. 2013, Matur et al. 2013).

Additional information

The type locality of *N. xanthodon* is located at İzmir (formerly Smyrna). Kankılıç & Gürpınar (2014) included this race within a separate species, *N. xanthodon*, distributed in western Anatolia.

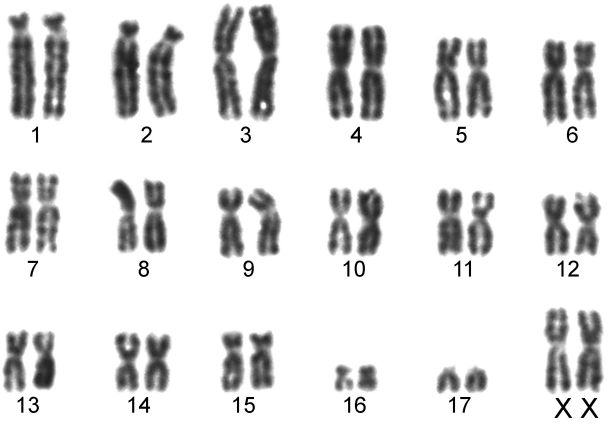

Fig. 6. Karyotype of the Xanthodon race (2n = 36, NF = 70) from Aydın in Anatolia, Turkey.

27. Anatolicus (Fig. 7)

2n = 38, NFa = 70, NF = 74

The complement includes six pairs of metacentric, eight pairs of submetacentric (the last two pairs are distinctly smaller than the others), three pairs of large subtelocentric and one pair of small acrocentric autosomes. The X chromosome is a large submetacentric or subtelocentric, the Y chromosome is a small acrocentric (Savić & Soldatović 1979a, Arslan et al. 2013).

C-heterochromatic short arms appear in three subtelocentric autosomal pairs in specimens from the Manisa Province (Arslan et al. 2013, Matur et al. 2013). Additionally, centromeric C-bands of varying intensity occur in most other meta- and submetacentric autosomes but C-positive staining is lacking in the acrocentric pair. The presumed X chromosome has a centromeric C-positive band. Ag-NOR regions are located in three bi-armed autosomal pairs in distal areas of the short arm (Arslan et al. 2013).

Description locality
Havran, Balıkesir Province, Aegean coast of Anatolia, Turkey (Savić & Soldatović 1979a).
Distribution
The range includes northern and central parts of the Aegean region up to the Marmara coast in western Anatolia in the Provinces of İzmir, Balıkesir, Bursa, Çanakkale and Manisa (Nevo et al. 1995, Tez et al. 2002, Sözen 2004, Kankılıç et al. 2009, Matur et al. 2013, Sözen et al. 2013). It occurs also on several Aegean islands – the Lesbos Island (Polychnitos) belonging to Greece (Giagia et al. 1982) and Bozcaada (Tenedos in Greek) and Gökçeada (Imbros in Greek) Islands belonging to Turkey (Sözen et al. 2013).
Additional information
The race was recognized as *Nannospalax nehringi anatolicus* by Savić & Soldatović (1984) and designated as the İzmir cytotype by Kryštufek & Vohralík (2009). Kankılıç et al. (2009) recognized the studied 38 chromosome populations as *N. leucodon anatolicus* and Kankılıç & Gürpınar (2014) included this race in a separate species, *N. xanthodon*.

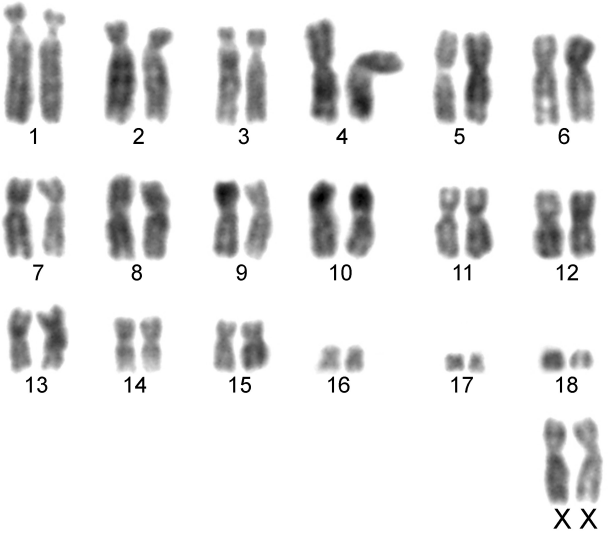

Fig. 7. Karyotype of the Anatolicus race (2n = 38, NF = 74) from Kırkağaç, Manisa, in Turkey.

28. Beyşehir (Fig. 8)
2n = 40, NFa = 68, NF = 72
The complement includes eight pairs of metacentric or submetacentric (one submetacentric pair is the largest in the set), seven pairs of submetacentric or subtelocentric and four pairs of small acrocentric autosomes. The X chromosome is a large subtelocentric or metacentric, the Y chromosome is a small submetacentric (Nevo et al. 1995, Arslan et al. 2011a).
The short arms are completely C-heterochromatic in four pairs of bi-armed autosomes, whereas both sex chromosomes are C-negative (Arslan et al. 2011a, Matur et al. 2013). Active Ag-NOR occur in telomeric areas of the short arm in one large and three medium-sized submetacentric pairs of autosomes (Arslan et al. 2011a). Matur et al. (2013) studied the G-banding chromosome pattern.
Description locality
Beyşehir 60 km S, Konya Province, Anatolia, Turkey (Nevo et al. 1995).
Distribution
Humid areas on the northern and western edge of Lake Beyşehir in the Isparta and Konya Provinces, in the southern parts of central Anatolia (Nevo et al. 1995, Kankılıç et al. 2010, Arslan et al. 2011a, Matur et al. 2013, Sözen et al. 2013).
Additional information
Kankılıç & Gürpınar (2014) included this race within a separate species, *N. xanthodon*, distributed in western Anatolia.

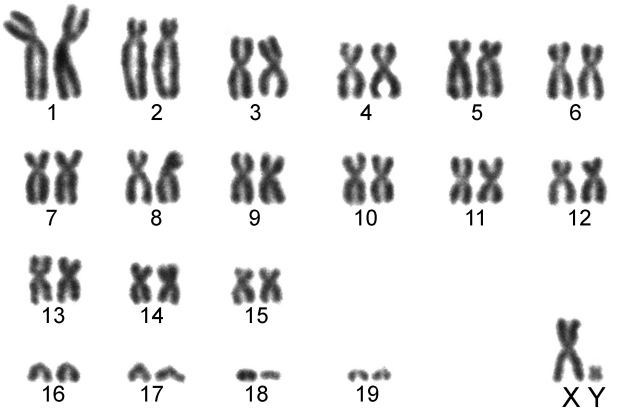

Fig. 8. Karyotype of the Beyşehir race (2n = 40, NF = 72) from Beyşehir, Konya, in Turkey.

29. Yirce (Fig. 9)
2n = 46, NFa = 66, NF = 70
The karyotype consists of 46 chromosomes, including a large acrocentric, a large subtelocentric and a large submetacentric, five metacentric or submetacentric, four subtelocentric and ten smaller acrocentric autosomal pairs of gradually diminishing size. The X chromosome is a medium-sized submetacentric and the Y a small subtelocentric (Arslan et al. 2014b).
Distinct dark C-bands occur in centromeric or pericentromeric areas of all the bi-armed autosomes. A C-heterochromatic short arm appears in an autosomal pair. Only three acrocentric autosomal pairs have slightly positive centromeric bands. The sex chromosomes have centromeric positive bands.

NORs occur in the telomeric region of the short arms of two autosomes (Arslan et al. 2014b).

Description locality

Yirce Yaylası, north of Osmaniye, southern Anatolia, Turkey (Arslan et al. 2014b).

Distribution

Known only from the description locality, where two males were examined.

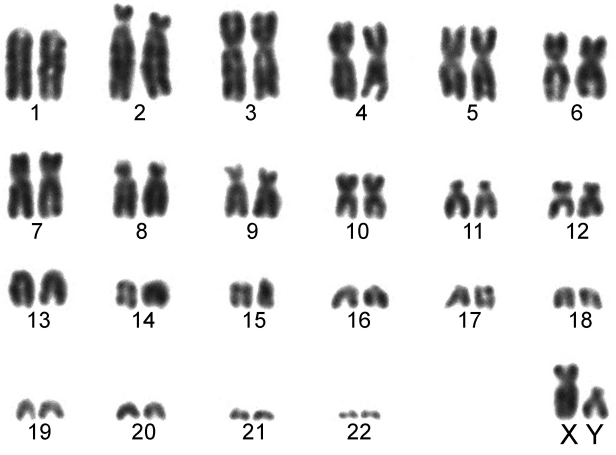

Fig. 9. Karyotype of the Yirce race (2n = 46, NF = 70) from Yirce Yaylası, Osmaniye, in Turkey.

30. Van

2n = 48, NFa = 64-68, NF = 68-72

The complement includes nine pairs of bi-armed (metacentric and submetacentric) and 14 pairs of acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome a small acrocentric (Coşkun 2003). Coşkun et al. (2009) distinguished a different proportion of the bi-armed and acrocentric autosomes (NFa = 68, NF = 72) in the karyotype of specimens examined in the vicinity of the city of Van. Distinct dark C-bands occur in the centromeric or pericentromeric areas of all the bi-armed autosomes and C-heterochromatic short arms appear in two autosomal pairs. In some autosomal pairs, interstitial dark C-bands are apparent on the long arm. The X chromosome has a centromeric C-positive area, the Y chromosome is entirely C-positive. NORs are located in the telomeric areas of the short heterochromatic arms of two autosomal pairs (Arslan & Zima, in press).

Description locality

Lake Van in eastern Turkey (Coşkun 2003).

Distribution

The Ağrı, Van, Muş, Iğdır and Erzurum Provinces in eastern Turkey, possibly parts of Armenia (Matthey 1959, Coşkun 2003, Coşkun et al. 2009, 2012b, Coşkun & Kaya 2013, Arslan & Zima, in press). The blind mole rat examined by Matthey (1959) from the Caucasus (2n = 48) might be close to this race. According to Lyapunova et al. (1974), the specimen studied by R. Matthey probably originated from the Talin region of Armenia.

Additional information

Spalax monticola armeniacus was probably described near Göle in the Kars Province in eastern Turkey (Kryštufek & Vohralík 2009). In the same area, however, *Spalax nehringi* was also described and populations with 50 chromosomes have solely been reported from this region.

31. Gümüşhane

2n = 48, NFa = 66-67, NF = 70-71

The complement includes 10 bi-armed, 12 acrocentric pairs of autosomes and, occasionally, one heteromorphic (subtelocentric/acrocentric) large autosomal pair. The X chromosome is medium-sized submetacentric, the Y chromosome small acrocentric (Sözen et al. 2006b, Arslan & Zima, in press).

Dark centromeric C-bands were observed in ten bi-armed and two acrocentric autosomal pairs. In a metacentric autosomal pair, dark C-staining includes a large proximal part of the long arm. C-heterochromatic short arms are not present in any autosomal pair. The X chromosome possesses centromeric C-positive band and the Y chromosome is entirely C-positive. NORs are located in the telomeric regions of the short arms of the four autosomal pairs (Arslan & Zima, in press).

Description locality

Şamanlı plateau, 35 km E of Gümüşhane, NE Anatolia, Turkey (Sözen et al. 2006b).

Distribution

It is known only from the area of original description, which is distant from the range of the Van race.

Additional information

An aberrant karyotype with 2n = 49, NFa = 72 was described by Coşkun et al. (2010b) from Pülümür-Kangallı in the Tunceli Province, eastern Anatolia. The odd number of chromosomes was found in three individuals and the autosomal complement includes 12 bi-armed and 11 acrocentric pairs and a single metacentric element. The X chromosome is a large submetacentric, the Y chromosome a small acrocentric. The collection site is situated north-east from the range of the Tuncelicus race with 54 chromosomes (about 50 km from the closest site recorded). The ranges of the Nehringi and Gümüşhane races are relatively distant from this site.

32. Pamukören (Fig. 10)
2n = 50, NFa = 68-70, NF = 72-74
The complement includes 10-11 bi-armed and 14-13 acrocentric pairs of autosomes, resulting in a varying number of autosomal arms (NFa = 68: Arslan & Zima 2015b, NFa = 70: Nevo et al. 1995, Matur et al. 2011, Sözen et al. 2013). Arslan & Zima (2015b) discriminated in the complement a large submetacentric and a large subtelocentric, eight submetacentric or subtelocentric and 14 smaller acrocentric autosomal pairs of gradually diminishing size. The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric.
Matur et al. (2011, 2013) recognized several bi-armed chromosomes, possessing C-positive band on short arms. The X-chromosome is C-negative, while the Y-chromosome reveales pericentromeric C-heterochromatin. In the karyotype of specimens from Kiraz in the İzmir Province (Arslan & Zima 2015b), no positive C-bands occur in three pairs of bi-armed and most acrocentric autosomes. C-heterochromatic short arms are present in four bi-armed autosomal pairs. The X chromosome has a pericentromeric C-positive band and the Y chromosome is entirely C-negative. NORs appear in the telomeric regions of the short arms of three medium-sized biarmed autosomes. The G-banding chromosome pattern was studied by Matur et al. (2013).
Description locality
Pamukören 35 km E, Aydın Province, western Anatolia, Turkey (Nevo et al. 1995).
Distribution
The Aydın, Manisa and İzmir Provinces in western Anatolia (Nevo et al. 1995, Matur et al. 2011, 2013, Sözen et al. 2013, Arslan & Zima 2015b).

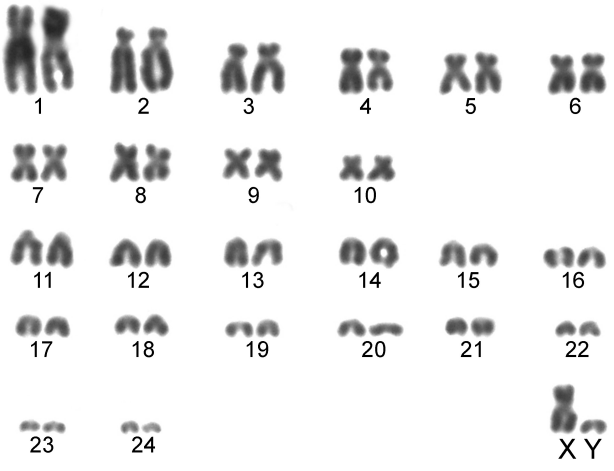

Fig. 10. Karyotype of the Pamukören race (2n = 50, NF = 72) from Kiraz, İzmir, in Turkey.

Additional information
This race was designated as 50W (Nevo et al. 1995, Matur et al. 2011, 2013).

33. Keltepe
2n = 50, NFa = 66, NF = 70
The complement includes nine bi-armed (a large subtelocentric and eight metacentric, submetacentric or subtelocentric pairs of varying size) and 15 acrocentric pairs of autosomes. The X chromosome is a large or medium-sized submetacentric, the Y chromosome is an acrocentric (Sözen 2004).
Distinct dark C-bands occur in the centromeric or pericentromeric areas of all bi-armed autosomes and C-heterochromatic short arms appear in two bi-armed pairs. Dark centromeric bands are also apparent in most acrocentric autosomes. The X chromosome has a centromeric C-positive area. NORs are located in the telomeric regions of the short heterochromatic arms of two autosomes (Arslan & Zima 2015b). Matur et al. (2011) described the G- and C-banding patterns.
Description locality
The Keltepe Mountain, Karabük Province, northern Anatolia, Turkey (Sözen 2004).
Distribution
A small area around the description locality in the Karabük Province in northern Anatolia (Sözen 2004, Sözen et al. 2006a, 2013). The race is surrounded by 2n = 60 (Vasvarii race) populations from the south and east, 2n = 56 (Safranbolu race) from the north and 2n = 52 (Abant race) from the west (Sözen et al. 2013).
Additional information
This race was designated as 50N (Sözen 2004, Matur et al. 2011).

34. Andırın (Fig. 11)
2n = 50, NFa = 66-67, NF = 70-71
The complement includes nine bi-armed (a large subtelocentric, a large submetacentric and seven medium-sized submetacentric or subtelocentric) and 15 acrocentric pairs of autosomes (one distinctly large pair and 14 acrocentric pairs of gradually diminishing size). The X chromosome is a medium-sized submetacentric, the Y chromosome is small and probably bi-armed (Matur et al. 2011). A heteromorphic autosomal pair was recorded in two specimens, consisting of a subtelocentric and an acrocentric chromosome (NFa = 67, Arslan & Zima 2015b).
Dark C-bands occur in the centromeric or pericentromeric areas of eight bi-armed and six acrocentric autosomes. C-heterochromatic short arms

appear in two autosomal pairs. The X chromosome has a distinct pericentromeric C-positive band and the Y chromosome has a slight centromeric C-positive band. NORs are localized in the telomeric areas of the C-heterochromatic short arms of two medium-sized bi-armed autosomal pairs (Arslan & Zima 2015b). Matur et al. (2011) described the G- and C-banding chromosome patterns.

Description locality

Andırın, Kahramanmaraş Province, south-eastern Anatolia, Turkey (Matur et al. 2011).

Distribution

Description locality.

Additional information

Matur et al. (2011) designated this race as 50S.

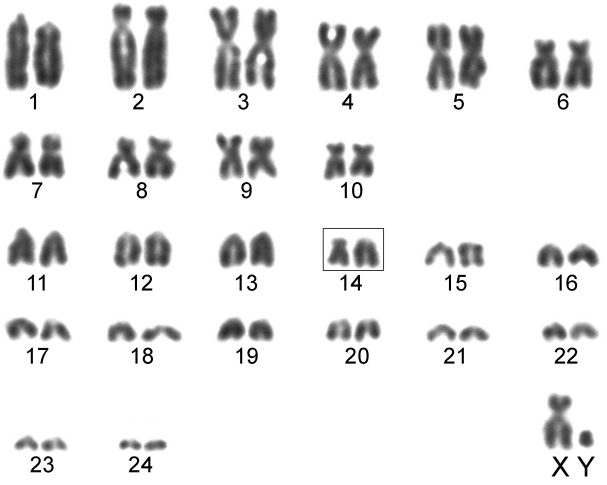

Fig. 11. Karyotype of the Andırın race (2n = 50, NF = 71) from Andırın, Kahramanmaraş, in Turkey. The chromosome pair in the frame is heteromorphic.

35. Nehringi (Fig. 12)

2n = 50, NFa = 66-68, NF = 70-72

The complement includes nine or ten bi-armed and 15 or 14 acrocentric autosomes (NFa = 66 reported by Nevo et al. 1995, Coşkun et al. 2012b and Arslan & Zima 2015b, whereas NFa = 68 was determined by the other authors). Several marker chromosomes can be recognized in the conventionally stained karyotype, i.e. a large acrocentric, a large metacentric and a large subtelocentric pair. The X chromosome is a medium-sized submetacentric, the Y chromosome is acrocentric and the smallest in the set (Lyapunova et al. 1974).

Dark C-bands occur in the centromeric or pericentromeric areas of all bi-armed and five acrocentric autosomes. C-heterochromatic short arms are located in the large subtelocentric autosomal pair. The X chromosome has a distinct pericentromeric C-positive band and the Y chromosome has a slight centromeric C-positive band. NORs occur in the telomeric regions of the short arms of four autosomes (Arslan & Zima 2015b). Matur et al. (2011) reported a different C-banding pattern, showing the presence of almost entirely C-positive short arms in eight bi-armed autosomal pairs. Both sex chromosomes are characterized as C-negative. Matur et al. (2011) compared the G-banding patterns in each of the 2n = 50 races.

Description locality

Pambak range, Armenia (Lyapunova et al. 1974).

Distribution

Armenia (Pambak, Maralik), the Erzurum, Kars, Erzican, Ardahan, Rize, Giresun, Trabzon, and Bayburt Provinces in eastern Turkey (Orlov 1969, Lyapunova et al. 1974, Sözen et al. 2000a, 2006a, Coşkun 2003, Kankılıç et al. 2007a, b, Ulutürk et al. 2009, Coşkun et al. 2012b, Arslan & Zima 2015b).

Additional information

This race was designated as 50E by Nevo et al. (1995) and Matur et al. (2011). Lyapunova et al. (1974) recognized the specimens studied in Armenia as *Mesospalax nehringi*. Kıvanç (1988) classified the specimens from Ardahan and Susuz as *Spalax leucodon intermedius* and those from Erzurum as *S. l. nehringi.* Kankılıç et al. (2007a) recognized the population examined in Göle as *N. leucodon armeniacus* and Kankılıç & Gürpınar (2014) and Kankılıç et al. (2014, 2015) included it within a separate species, *Nannospalax nehringi*, which was described near Göle in the Kars Province (cf. Kryštufek &Vohralík 2009).

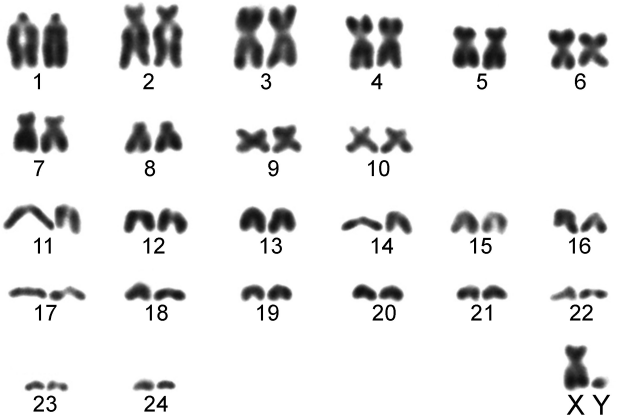

Fig. 12. Karyotype of the Nehringi race (2n = 50, NF = 70) from Maçka, Trabzon, in Turkey.

36. Abant (Fig. 13)

2n = 52, NFa = 66-68, NF = 70-72

The complement includes eight pairs of bi-armed and 17 pairs of acrocentric autosomes. The autosomes

consist of a large and two medium-sized subtelocentric, two metacentric, three submetacentric and 17 smaller acrocentric pairs of gradually diminishing size (NFa = 66: Sözen 2004, Arslan & Zima 2015a). Matur (2009) recognized nine pairs of bi-armed and 16 pairs of acrocentric autosomes in the complement of specimens from Yalova (NFa = 68). The X chromosome is reported as subtelocentric or metacentric, the Y chromosome as acrocentric or metacentric.

Dark centromeric C-bands occur in five bi-armed and in some of the acrocentric autosomes. In two acrocentric autosomal pairs, the position of the dark C-bands appears interstitial, not directly involving the centromeric region. C-heterochromatic short arms are not reported in any autosomal pair. The sex chromosomes have distinct pericentromeric C-positive bands. The NORs are localized in the telomeric regions of the short arms of three bi-armed autosomes (Arslan & Zima 2015a).

Description locality

Abant Lake, Bolu Province, northern Anatolia, Turkey (Sözen 2004).

Distribution

The Yalova, Kocaeli, Bilecik, Sakarya and Bolu Provinces in north-western Anatolia (Sözen 2004, Matur & Sözen 2005, Kankılıç et al. 2007b, Matur et al. 2013, Sözen et al. 2013, Arslan & Zima 2015a). Records from Karamürsel in the Kocaeli Province (Sözen 2004) and Yalova (Matur et al. 2013, Sözen et al. 2013) in the easternmost part of the southern coast of the Marmara Sea are apparently geographically isolated from findings at the eastern side of the River Sakarya. The ranges of the western (Kocaeli, Yalova) and eastern (Bilecik, Bolu) populations of this race are obviously separated, because populations with 2n = 60 (Vasvarii race) were recorded on the western side of the River Sakarya in the Bilecik Province (Matur & Sözen 2005). The population from Dörtdivan in the Bolu Province is in close contact with populations possessing 2n = 60 and occurring 3 km apart, with no geographical barriers recognized between them (Sözen et al. 2013).

Additional information

This race was designated as 52N by Sözen (2004) and Matur et al. (2013). Kankılıç & Gürpınar (2014) included this race within a separate species, *N. xanthodon*.

37. Sebil (Fig. 14)

2n = 52, NFa = 68, NF = 72

The complement includes nine pairs of bi-armed and 16 pairs of acrocentric autosomes. The bi-armed autosomes are composed of a large submetacentric and a large subtelocentric pair, two metacentric pairs, five submetacentric or subtelocentric pairs of medium size and 16 acrocentric pairs of gradually diminishing size. The X chromosome is a large submetacentric and the Y chromosome a small acrocentric (Sözen & Kıvanç 1998b, Arslan & Zima 2015a).

Distinct dark C-bands occur in the centromeric areas of most bi-armed autosomes and in a single acrocentric autosome. Tiny positive centromeric bands are apparent also in some other acrocentric pairs. The sex chromosomes have a centromeric C-positive area. The NORs are localized in telomeric areas of the short

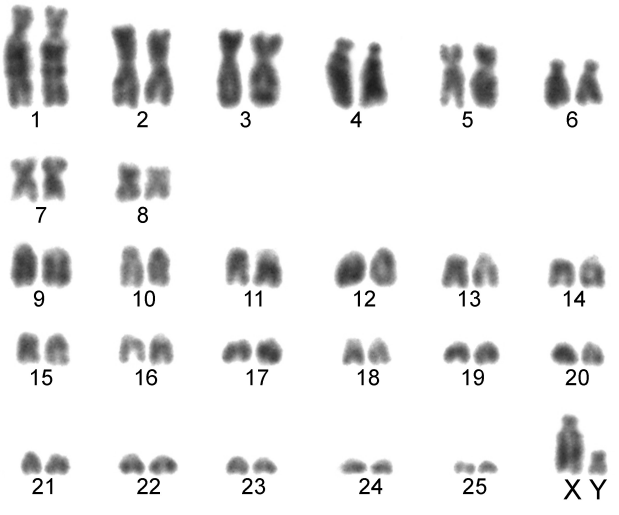

Fig. 13. Karyotype of the Abant race (2n = 52, NF = 70) from Gerede, Bolu, in Turkey.

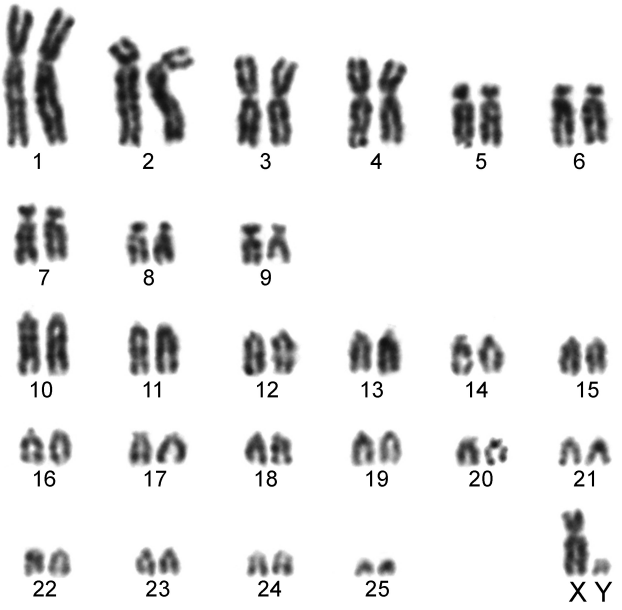

Fig. 14. Karyotype of the Sebil race (2n = 52, NF = 72) from Çamlıyayla, İçel (Mersin), in Turkey.

arms of three medium-sized and smaller bi-armed autosomes (Arslan & Zima 2015a).

Description locality

Sebil, Mersin Province, Anatolia, Turkey (Sözen & Kıvanç 1998b).

Distribution

The Mersin and Adana Provinces in southern Anatolia (Sözen & Kıvanç 1998b, Sözen et al. 2000b, Arslan & Zima 2015a).

Additional information

The race was included in the species *Nannospalax labaumei*, together with races possessing 54, 56, 58 and 60 chromosomes from interior Anatolia by Kankılıç & Gürpınar (2014) and Kankılıç et al. (2014). However, Kankılıç et al. (2015) recognized this race as *N. cilicicus*.

38. Eflani (Fig. 15)

2n = 54, NFa = 68-70, NF = 72-74

The complement includes eight to nine pairs of bi-armed and 19 or 18 pairs of acrocentric autosomes. Three submetacentric autosomal pairs are distinctly larger than the other bi-armed autosomes. The X chromosome is submetacentric, the Y chromosome is dot-like acrocentric. The karyotype with NFa = 68 was described by Sözen (2004) and this author also observed variation in chromosome morphologies between populations studied (NFa up to 70). Matur et al. (2013) recorded nine bi-armed autosomal pairs in the complement of the specimens studied (NFa = 70) and investigated the C- and G-banding chromosome patterns.

Description locality

Eflani 12 km W, Karabük Province, N Anatolia, Turkey (Sözen 2004).

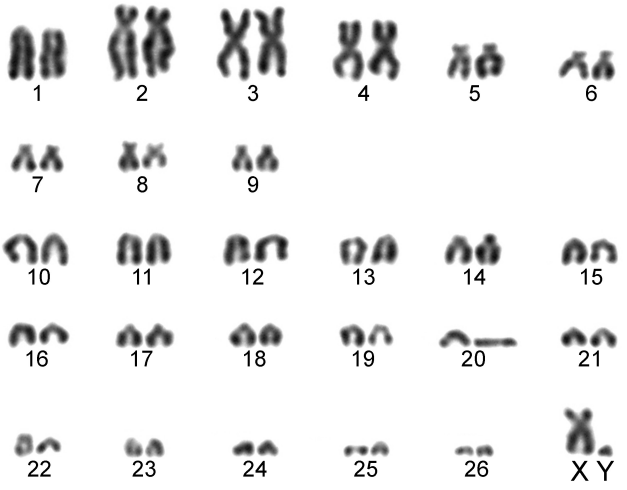

Fig. 15. Karyotype of the Eflani race (2n = 54, NF = 72) from Eflani, Karabük, in Turkey.

Distribution

The Bolu, Karabük and Kastamonu Provinces in northern Anatolia (Sözen 2004, Sözen et al. 2006b, Matur et al. 2013).

Additional information

Matur et al. (2013) designated this race as 54N. A similar karyotype was reported from Bolu by Nevo et al. (1995) and designated as 2n = 54W (NF = 74), but populations with this complement were never found in the same location again (Sözen et al. 2013, Matur unpublished data).

39. Yozgat (Fig. 16)

2n = 54, NFa = 70-71, NF = 74-75

The complement includes three metacentric, two submetacentric, four subtelocentric and 17 acrocentric pairs of autosomes. Two metacentric and two subtelocentric autosomal pairs are distinctly larger than the other chromosomes. The X chromosome is submetacentric, the Y chromosome is subtelocentric or acrocentric (Yüksel & Gülkaç 1995, Arslan et al. 2011b). Variation in morphology of certain autosomes is reported in the Başçiftlik sample, Tokat Province (Sözen 2004). Heteromorphism in one relatively large autosomal pair (subtelocentric/acrocentric) resulting in NFa = 71, was recorded in some specimens from Erbaa (Sözen et al. 2006a).

C-heterochromatin occurs in pericentromeric areas and short arms of some bi-armed autosomal pairs and tiny dark bands appear in pericentromeric areas of several acrocentric autosomes. The X chromosome has a centromeric dark C-band; the Y chromosome is C-negative. The NORs are located in distal areas of the C-heterochromatic short arms of two submetacentric and two subtelocentric autosomal pairs (Arslan et al. 2011b).

Description locality

Yozgat, Anatolia, Turkey (Yüksel & Gülkaç 1995).

Distribution

The Middle Kızılırmak river basin, the Çankırı, Kırıkkale, Çorum, Nevşehir, Kırşehir, Kayseri, Yozgat and Tokat Provinces in central and northern Anatolia (Yüksel & Gülkaç 1995, 2001, Sözen 2004, Sözen et al. 2006a, 2011, 2015, Kankılıç et al. 2007b, Aşan & Yağcı 2008, Arslan et al. 2011b). The Yozgat race is supposedly surrounded by populations possessing 2n = 60 (Vasvarii race) in central Anatolia (Sözen et al. 2015). This is the only race penetrating deeply inside the distribution area of populations with 60 chromosomes. The River Kızılırmak is assumed to form a barrier between populations with 54 and 60 chromosomes in the western parts of the range (Sözen et al. 2015).

Additional information
Yüksel & Gülkaç (1995) recognized populations from the Middle Kızılırmak basin as *N. cilicicus* and Kankılıç et al. (2015) proposed the same solution for populations from Kırıkkale and Kırşehir. Sözen et al. (2011, 2015) designated populations from the Çankırı, Çorum, Nevşehir and Kırşehir Provinces as 54C. The karyotype is similar to those of the Eflani and Tuncelicus races but these races apparently have disjunct distributions.

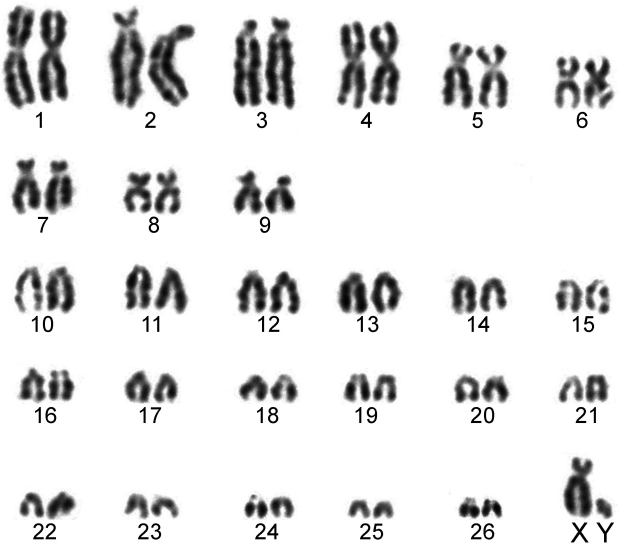

Fig. 16. Karyotype of the Yozgat race (2n = 54, NF = 74) from Kırıkkale in Turkey.

40. Tuncelicus
2n = 54, NFa = 70, NF = 74
The complement includes nine pairs of bi-armed and 17 pairs of acrocentric autosomes. Two submetacentric autosomal pairs are distinctly larger than the other chromosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome a small subtelocentric or acrocentric (Nevo et al. 1995).
Description locality
Bingől 10 km S, Anatolia, Turkey (Nevo et al. 1995).
Distribution
The Bingől, Elazığ and Tunceli Provinces in eastern Anatolia (Nevo et al. 1995, Coşkun 2004a, Coşkun et al. 2009, 2010b). It occurs on the right bank of the Rivers Euphrates and Murat, north of the Keban Dam Lake (Coşkun et al. 2010b).
Additional information
Nevo et al. (1995) designated this race as 2n = 54E. Populations possessing 54 chromosomes from interior Anatolia were included in *N. labaumei* by Kankılıç & Gürpınar (2014) and Kankılıç et al. (2014). The range of this race is probably allopatric in respect of the Yozgat, Eflani and Bitlis races. Coşkun (1996a) described a new subspecies, *Spalax nehringi tuncelicus*, from Gömemiş village, 16 km NE from Tunceli. The original description was based solely on morphological characters, with no chromosomal data provided. In a later paper, Coşkun (2004a) recognized this form as a separate species (*Nannospalax tuncelicus*) and reported the karyotype with 2n = 54 and NF = 74.

41. Bitlis
2n = 54, NFa = 70, NF = 74
The karyotype consists of nine pairs of meta- or submetacentric and 17 pairs of acrocentric autosomes. The largest autosome is submetacentric and distinctly larger than the other chromosomes. The X chromosome is large and submetacentric; the Y chromosome is dot-like and acrocentric (Coşkun et al. 2009).
Description locality
Tatvan-Kuskunkıran, Bitlis Province (Coşkun et al. 2009).
Distribution
The Bitlis and Muş Provinces on the western and southern side of Lake Van in eastern Anatolia (Coşkun et al. 2009).
Additional information
The populations found around Bitlis may be geographically separated from the others that possess 54 chromosomes. They are probably in geographical contact with the Nehringi race in the northern parts of the latter's range and separated from the Van race (2n = 48) by Mt. Süphan (Coşkun et al. 2009).

42. Adana
2n = 54, NFa = 70, NF = 74
The karyotype contains nine submetacentric or subtelocentric and 17 acrocentric pairs of autosomes. Only females were examined and the X chromosome was tentatively identified as a medium-sized submetacentric (Sözen et al. 2015).
The karyotypes of populations with 2n = 54 vary in the proportion of bi-armed and acrocentric autosomes or in the morphology of marker chromosomes. The complement recorded in populations of the Bitlis race includes a single large bi-armed marker autosome, whereas that of populations of the Yozgat and Tuncelicus race has two distinctly large bi-armed pairs (Yüksel & Gülkaç 1995, Coşkun 2004a). The populations from the Adana Province (Sözen et al. 2015) have no distinctly large bi-armed autosomes.
Description locality
Tufanbeyli, Adana Province, south-eastern Anatolia, Turkey (Sözen et al. 2015).

Distribution
It is known from two sites in the Adana Province.
Additional information
This race was designated as 54S (Sözen et al. 2015). Populations in the Adana Province seem to be geographically isolated from other populations possessing 54 chromosomes.

43. Kula (Fig. 17)
2n = 56, NFa = 68-70, NF = 72-74
The karyotype includes seven bi-armed and 20 acrocentric autosomal pairs of gradually diminishing size (NFa = 68). The first acrocentric pair is distinctly larger than the others. Specimens from Alaşehir in the Manisa Province possess two large acrocentric, two large metacentric, six medium-sized to small submetacentric or subtelocentric and 17 acrocentric autosomal pairs of gradually diminishing size (NFa = 70, Arslan et al. 2014a). The X chromosome is submetacentric and the Y acrocentric (Kankılıç et al. 2009, Arslan et al. 2014a).
Arslan et al. (2014a) found that the C-banding pattern and NOR distribution are similar in the two distinct NF cytotypes recorded in the Manisa Province. Dark C-bands occur in pericentromeric areas of five smaller bi-armed and four acrocentric autosomes. Both metacentric autosomal pairs were C-negative. The X and Y chromosomes have distinct centromeric C-positive bands. NORs are localized in the telomeric region of the short arms of three medium-sized bi-armed pairs of autosomes. The C- and G-banding chromosome patterns were studied also by Matur et al. (2013).

Description locality
Kula, Manisa Province, western Anatolia, Turkey (Kankılıç et al. 2009).
Distribution
The Manisa and Uşak Provinces in western Anatolia (Kankılıç et al. 2009, 2010, Matur et al. 2013, Sözen et al. 2013, Arslan et al. 2014a).
Additional information
This race from western Anatolia was also designated as 56W (Matur et al. 2013) and was included in *N. labaumei* by Kankılıç & Gürpınar (2014) and Kankılıç et al. (2014). However, Kankılıç et al. (2009, 2015) recognized populations with 56 chromosomes from Manisa and Uşak as *N.* (*leucodon*) *cilicicus*.

44. Isparta (Fig. 18)
2n = 56, NFa = 68, NF = 72
The complement originally described in Isparta (Kankılıç et al. 2007b) includes seven bi-armed and 20 acrocentric pairs of autosomes. The X chromosome is a medium-sized metacentric or submetacentric, the Y chromosome is a small acrocentric. Arslan et al. (2014a) differentiated in the autosomal set of specimens from Yılanlı a large acrocentric, a large submetacentric and a large metacentric, five submetacentric or subtelocentric and 19 acrocentric autosomal pairs of gradually diminishing size. The X and Y chromosomes are small submetacentrics. The presence of a large submetacentric and a large metacentric autosomal pair is the distinguishing feature of this race.
Dark C-bands occur in the pericentromeric areas of seven bi-armed and four acrocentric autosomes.

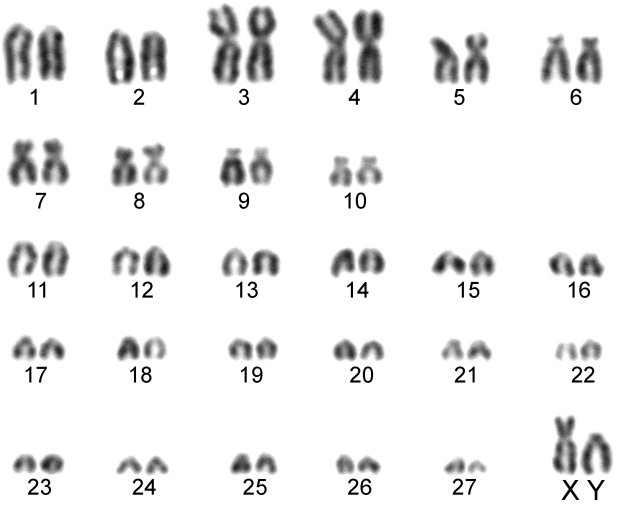

Fig. 17. Karyotype of the Kula race (2n = 56, NF = 74) from Alaşehir, Manisa, in Turkey.

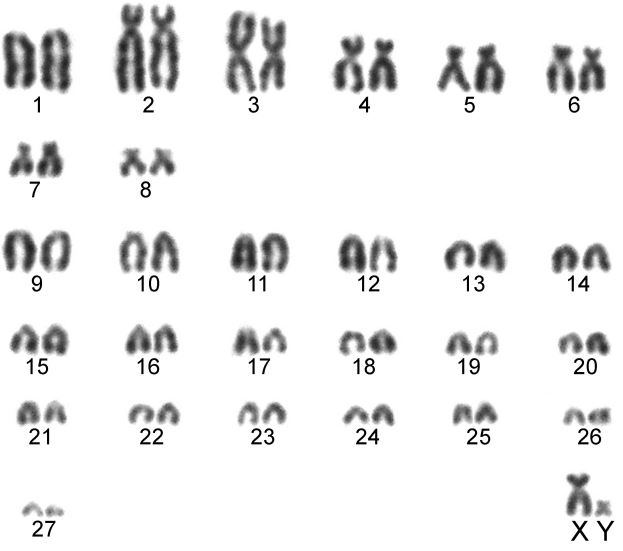

Fig. 18. Karyotype of the Isparta race (2n = 56, NF = 72) from Yılanlı, Isparta, in Turkey.

The X chromosome has a distinct pericentromeric C-positive band and the Y chromosome has a slight centromeric C-positive band. NORs are located in the telomeric regions of the short arms of three smaller bi-armed autosomes (Arslan et al. 2014a).

Description locality

Yılanlı, Isparta Province, Anatolia, Turkey (Kankılıç et al. 2007b).

Distribution

The Isparta Province in central Anatolia.

Additional information

Kankılıç et al. (2014) recognized populations with 56 chromosomes from Isparta as *N. labaumei*, whereas Kankılıç et al. (2015) as *N. cilicicus*.

45. Safranbolu (Fig. 19)

2n = 56, NFa = 68-70, NF = 72-74

The complement includes seven or eight pairs of bi-armed and 20 or 19 pairs of acrocentric autosomes. A large submetacentric, a large metacentric, and six smaller subtelocentric autosomal pairs can be differentiated. One acrocentric pair is distinctly larger than the others. The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric. Sözen (2004) and Sözen et al. (2006b) recorded NFa = 70 in several population samples from the Kastamonu and Karabük Provinces whereas Sözen et al. (2006b) reported NFa = 68 in Ilgaz Mts.

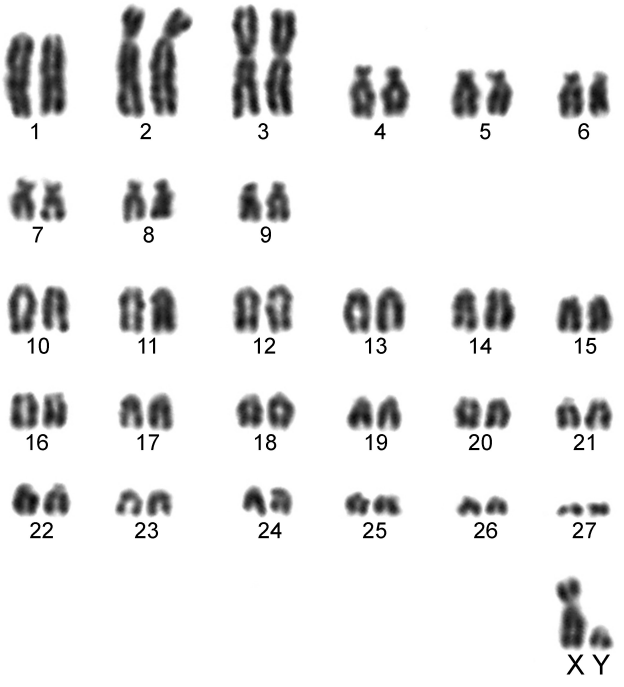

Fig. 19. Karyotype of the Safranbolu race (2n = 56, NF = 74) from Safranbolu, Karabük, in Turkey.

Description locality

Safranbolu 10 km N, Karabük Province, Anatolia, Turkey (Sözen 2004).

Distribution

The Karabük and Kastamonu Provinces, north-western Anatolia, Turkey (Sözen 2004, Sözen et al. 2006b, 2011). The area of occurrence of this race is surrounded by populations with 2n = 50, 54, 58 and 60 (Keltepe, Eflani, Taşköprü, Kastamonu and Vasvarii races, respectively; Sözen 2004, Sözen et al. 2006b).

Additional information

This race is obviously isolated from other races with 2n = 56 and it was designated as 56N by Sözen (2004).

46. Gülek

2n = 56, NFa = 66-68, NF = 70-72

The complement includes six or seven bi-armed and 21 or 20 acrocentric pairs of autosomes. The X chromosome is a medium-sized metacentric or submetacentric, the Y chromosome is a small acrocentric (Sözen & Kıvanç 1998a). Arslan et al. (2014a) differentiated in the autosomal complement two large acrocentric, a metacentric, six submetacentric or subtelocentric and 18 smaller acrocentric autosomal pairs of gradually diminishing size.

Dark C-bands occur in the pericentromeric areas of seven bi-armed and a single small acrocentric autosomal pair. The X chromosome has a pericentromeric C-positive band and the Y chromosome is entirely C-negative. NORs occur in the telomeric regions of the short arms of two subtelocentric autosomes (Arslan et al. 2014a).

Description locality

Gülek, Mersin Province, south-eastern Anatolia, Turkey (Sözen & Kıvanç 1998a).

Distribution

South-eastern parts of central Anatolia, north of the Mediterranean Sea coast, in the Karaman, Mersin, Adana and Kahramanmaraş Provinces (Sözen & Kıvanç 1998a, Sözen et al. 2000b, 2006a, 2015, Arslan et al. 2014a).

Additional information

Kankılıç & Gürpınar (2014) and Kankılıç et al. (2014) suggested that populations with 56 chromosomes from south-eastern Anatolia are closely related to *N. ehrenbergi*.

47. Karaman

2n = 56, NFa = 66, NF = 70

The complement includes a pair of large submetacentrics, five pairs of medium-sized bi-armed

and 21 acrocentric autosomal pairs. The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric (Sözen et al. 2015).

Populations from Anatolia with 56 chromosomes have varying structure of the karyotype and can be divided into several geographically separated races (Kula, Isparta, Safranbolu, Gülek, Karaman). The complements of populations from western Anatolia (Manisa and Uşak Provinces) include two large or medium-sized metacentric autosomal pairs (Kankılıç et al. 2009, Arslan et al. 2014a). A large metacentric and a large subtelocentric were found in the complement of the specimens from northern Anatolia (Kastamonu and Karabük Provinces, Sözen et al. 2006b) and central Anatolia (Isparta Province, Arslan et al. 2014a). A single large submetacentric autosomal pair is present in complements of populations from southern Anatolia (Karaman), whereas in populations from Gülek, such large bi-armed marker chromosomes are missing (Arslan et al. 2014a, Sözen et al. 2015). In addition, the populations within some races differ slightly in the detailed pattern of distribution of positive C-bands and NORs (Arslan et al. 2014a). Dark C-bands are apparent in the pericentromeric areas of most of the bi-armed and a few acrocentric autosomal pair. The X and Y chromosomes have pericentromeric C-positive bands but the Y chromosome can be entirely C-negative in some populations (Gülek). NORs are located in the telomeric areas of the short arms of two, three or four bi-armed autosomes.

Description locality

Karaman 20 km S, Karaman Province, S Anatolia.

Distribution

It is known from three sites in the Karaman and Mersin Provinces in southern Anatolia. The pattern of distribution of the races with 56 chromosomes is apparently disjunct.

Additional information

Sözen et al. (2015) designated populations from the Karaman and the eastern parts of the Mersin Provinces as 56K (Karaman) and proposed to distinguish them as a distinct race, in respect of presumed geographic isolation.

48. Munzurii (Fig. 20)

2n = 58, NFa = 62-64, NF = 66-68

The complement includes four (Coşkun 2004a) or three pairs of bi-armed (Arslan & Zima 2013) and 25 or 24 pairs of acrocentric autosomes and the number of autosomal arms varies accordingly. Distinct short arms are sometimes apparent in a large acrocentric pair. The X chromosome is submetacentric, the Y chromosome is acrocentric or submetacentric. The karyotype described by Coşkun et al. (2010b) is similar to the complement reported by Arslan & Zima (2013).

C-heterochromatin regions occur in the centromeric and pericentromeric areas or in the short arms of some bi-armed autosomal pairs and in the pericentromeric areas of a few acrocentric autosomes. Two bi-armed autosomes have C-heterochromatic short arms separated from the dark pericentromeric area by a narrow light band. The X chromosome has a centromeric C-positive band and the short arm of the Y chromosome appears to be C-positively stained. NORs are located in distal heterochromatin area of the short arms of two pairs of bi-armed and one pair of acrocentric autosomes (Arslan & Zima 2013).

Description locality

Ovacık, Tunceli Province, eastern Anatolia, Turkey (Coşkun 2004a).

Distribution

The Erzincan and Tunceli Provinces in eastern Anatolia (Coşkun 2004a, Coşkun et al. 2010b, Arslan & Zima 2013). It occurs on the left bank of the River Karasy, a right-side tributary of Euphrates (Coşkun et al. 2010b).

Additional information

Coşkun (2004a) recognized this race as a separate species, *Nannospalax munzurii*.

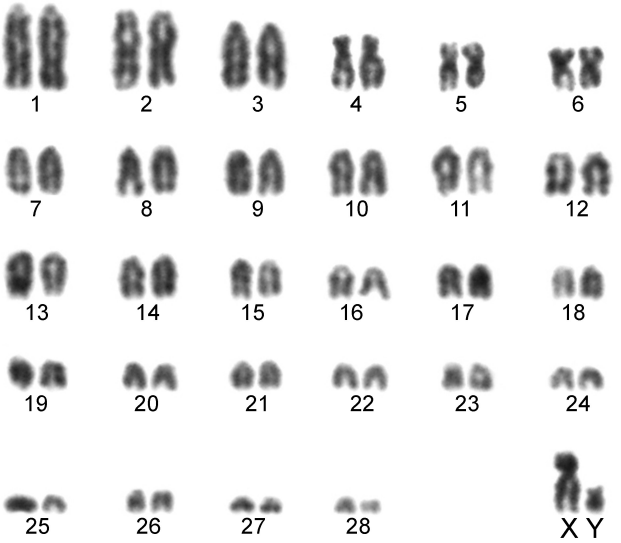

Fig. 20. Karyotype of the Munzurii race (2n = 58, NF = 66) from Kemaliye, Erzincan, in Turkey.

49. Cilicicus (Fig. 21)

2n = 58, NFa = 68-71, NF = 72-75

The complement includes six to eight bi-armed and 22 or 20 pairs of acrocentric autosomes. Descriptions

of the karyotype of a population from Ereğli (Konya Province) by Sözen et al. (2006a) and Arslan et al. (2011a) differ in the proportion of bi-armed to acrocentric autosomes. Arslan et al. (2011a) reported a heteromorphic autosomal pair in this population (NFa = 71). The X chromosome is a medium-sized submetacentric, the Y chromosome is acrocentric (Sözen & Kıvanç 1998b, Sözen et al. 2006a) or submetacentric (Arslan et al. 2011a).

Arslan et al. (2011a) described the C-banding pattern and the distribution of NORs in Ereğli. Dark C-bands are present in the pericentromeric areas of all bi-armed autosomes, with the exception of a small subtelocentric pair. C-heterochromatin is localized in centromeric areas of both homologues of the heteromorphic pair. Distinct dark centromeric C-bands are also apparent in four acrocentric autosomal pairs, whereas faint C-positive bands are visible in other acrocentric autosomes. The sex chromosomes possess pericentrometric C-bands. The active Ag-NOR regions are located in the telomeric area of the short arm of four bi-armed autosomal pairs of medium size. In the heteromorphic pair, a NOR occurs on the bi-armed autosome, but not on its acrocentric homologue (Arslan et al. 2011a).

Description locality

Madenköy, Niğde Province, Anatolia, Turkey (Sözen & Kıvanç 1998b).

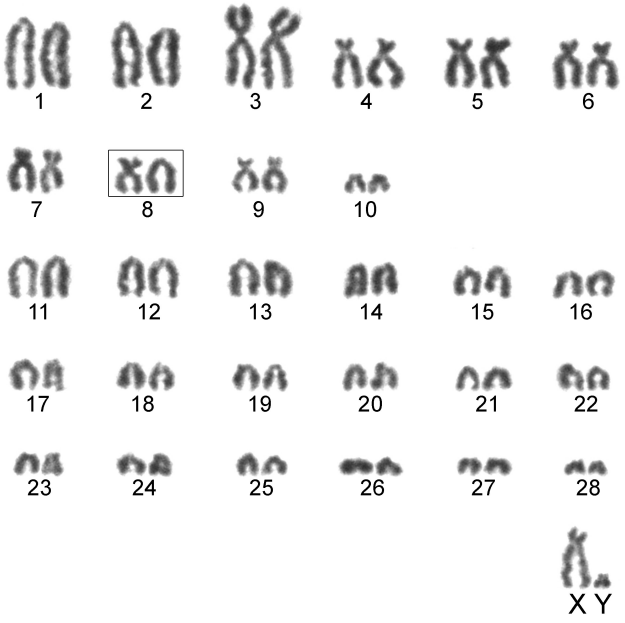

Fig. 21. Karyotype of the Cilicus race (2n = 58, NF = 75) from Ereğli, Konya, in Turkey. The chromosome pair in the frame is heteromorphic.

Distribution

The Konya, Niğde and Adana Provinces in central parts of southern Anatolia (Sözen & Kıvanç 1998b, Sözen et al. 2000b, 2006a, 2015, Arslan et al. 2011a).

Additional information

This race was first described from the type locality of *S. leucodon cilicicus*. Sözen et al. (2015) designated populations from the Niğde Province as 58S. Populations with 58 chromosomes were included in *Nannospalax labaumei* by Kankılıç & Gürpınar (2014) and Kankılıç et al. (2014), but Kankılıç et al. (2015) recognized them as *N. cilicicus*.

50. Sarıkavak

2n = 58, NFa = 74, NF = 78

The complement includes nine pairs of bi-armed and 19 pairs of acrocentric autosomes. The X chromosome is submetacentric, the Y chromosome is acrocentric (Sözen 2004).

Description locality

Sarıkavak, Ankara Province, central Anatolia, Turkey (Sözen 2004).

Distribution

The finding is based on examination of a single specimen and the collection site was completely surrounded by populations with 2n = 60 (Vasvarii race).

Additional information

This race was designated as 58N (Sözen 2004).

51. Taşköprü

2n = 58, NFa = 70-71, NF = 74-75

The complement includes seven bi-armed and 21 acrocentric pairs of autosomes. A submetacentric autosomal pair is the largest in the set, the other bi-armed autosomes are distinctly smaller, submetacentric or subtelocentric. A pair of autosomes may occur in heteromorphic state and it consists of a submetacentric and an acrocentric chromosome (NFa = 71: Sözen et al. 2006b). The X chromosome is medium-sized submetacentric, the Y chromosome is either acrocentric (Kastamonu populations, Sözen et al. 2006b) or subtelocentric (Kargi Plateau in the Çorum Province, Sözen et al. 2011).

Matur et al. (2013) studied the C- and G-banding chromosome patterns. Both sex chromosomes possess centromeric dark bands.

Within the 58 chromosome populations reported from Turkey, two groups can be recognized differing by the presence or absence of a large submetacentric autosomal pair. The populations possessing this marker chromosome occur in central-southern and northern Anatolia (the Cilicicus, Sarıkavak and Taşköprü

races), whereas populations from eastern Anatolia (the Munzurii race) have no similar chromosome in their karyotype (Arslan & Zima 2013).

Description locality

2 km W of Taşköprü, east of Kastamonu, Anatolia, Turkey (Sözen et al. 2006b).

Distribution

Vicinity of Kastamonu and northern parts of the Çorum Province in northern Anatolia (Sözen et al. 2006b, 2011, Matur et al. 2013). The geographic distance (about 400 km) between the areas of occurrence of the 2n = 58 races in northern, central and eastern Anatolia is considerable, thus these populations are widely allopatric and separated by races with different chromosomal numbers.

Additional information

This race was designated as 58N by Matur et al. (2013).

Populations with 60 chromosomes in Anatolia

Most of the area of central Anatolia is inhabited by populations possessing 60 chromosomes in their complements. The position of these populations is particularly difficult to be assessed for several reasons. In spite of the uniform number of chromosomes, individual populations may differ in chromosome morphology and these differences are mainly manifested in the varying proportion of uni-armed to bi-armed autosomes, which can be quantified in the number of autosomal arms (NFa). The mechanisms of this variation are not always obvious and various types of chromosomal re-arrangements can be involved.

Even the karyotypes with the same number of bi-armed autosomes may not be identical, because the individual autosomal pairs are not homologous across populations (Ivanitskaya et al. 2008). Furthermore, differences in the reported values of NFa might originate also from the subjective assessment of chromosome morphology by individual authors. Ivanitskaya et al. (2008) suggested that wide geographical variation in the number of chromosomal arms among populations with 2n = 60 could be explained also by different chromosomal condensation or technical interferences. They assumed that the properly documented variation, originating from heterochromatin amplification or deletion in short arms, was evidenced only in the first and second autosomal pairs (NFa = 74-78).

The resulting pattern of geographic distribution of karyotypically distinct populations with 60 chromosomes is rather confusing. Populations with individual NFa values are not distributed in a parapatric or allopatric pattern, as are the races with varying chromosome numbers. On the contrary, 2n = 60 populations are geographically mixed in a complicated mosaic pattern and defining ranges of individual races is difficult or even impossible. The current knowledge about the populations possessing a high chromosome number in Anatolia is also complicated by previous records of populations with 62 chromosomes (Nevo et al. 1994b, 1995). These findings are probably related to the incidence of supernumerary (B) chromosomes (Ivanitskaya et al. 2008). Therefore, distinguishing of individual races among 60 chromosome populations is puzzling and our simplified concept should be regarded as tentative and preliminary.

52. Kastamonu

2n = 60, NFa = 70-74-75, NF = 74-78-79

The complement includes six to eight pairs of subtelocentric and 23 or 21 pairs of acrocentric autosomes. The 2nd autosomal pair may be heteromorphic, acrocentric or subtelocentric. The X chromosome is a medium-sized submetacentric, the Y chromosome a small acrocentric (Sözen et al. 2000b, Ivanitskaya et al. 2008).

Distinct dark centromeric C-bands are present in most of the bi-armed autosomes and in several acrocentric autosomes. Short arms of some bi-armed autosomes comprise C-heterochromatin. Both sex chromosomes bear centromeric dark bands. The active Ag-NOR are located in the telomeric region of the short arms of subtelocentric autosomes and their number varies (Ivanitskaya et al. 2008). The karyotype of a single female showed 1-3 B chromosomes with the mean number of 0.5 per cell (Ivanitskaya et al. 2008).

Ivanitskaya et al. (2008) distinguished two basic types of cytotypes within the 60 chromosome populations; the 60W (wide distribution) and 60R (restricted distribution). The two cytotypes have different identity of bi-armed autosomal pairs: pairs 3-6, 8, 9, 13, 15 were identified in 60W, whereas pairs 6, 8, 10, 12, 13, 14, 16, 18 occurred in 60R. Ivanitskaya et al. (2008) recognized the originally described karyotype from Ağlı as 60W, but their survey revealed also the presence of the 60R cytotype in the same area. Based on G- and C-banding comparisons Matur et al. (2013) assumed considerable chromosomal divergence, resulting from 10 deletions and four centromeric shifts between the Kastamonu and the central 2n = 60 cytotypes.

Description locality

Ağlı, Kastamonu Province, northern Anatolia, Turkey (Sözen et al. 2000b).

Distribution

The Kastamonu Province in northern Anatolia. It is obviously the northernmost blind mole rat population with 2n = 60 in Anatolia but its range does reach the Black Sea coast (Sözen et al. 2000b, 2006b, Ivanitskaya et al. 2008). The sole reason for distinguishing this race from other 2n = 60 populations in central Anatolia is its complete geographic isolation.

Additional information

Sözen et al. (2000b) designated this race as 60N. Karyotypes with a similar number of autosomal arms, which were recorded in northern and central parts of western Anatolia, at the northern edges of Ankara (Sözen 2004) and in the Provinces of Bursa, Kütahya and Denizli (Sözen et al. 2013), are included in the next race.

53. Vasvarii (Figs. 22-27)

2n = 60, NFa = 68-70-73-74-75-78-79-80, NF = 72-74-78-79-80-82-84

With the exception the Kastamonu race, all the other populations with 2n = 60 are provisionally placed in the Vasvarii race. The number of bi-armed autosomes may vary from five to eleven pairs and, most frequently, the karyotypes contain from six to eight bi-armed autosomal pairs (NFa = 70-74). Variation in the centromeric position, resulting in acrocentric/subtelocentric heteromorphism, is particularly often found in the two largest autosomal pairs (Ivanitskaya et al. 2008), but it may also occur in other autosomal pairs. For instance, Arslan et al. (2011a) recorded variation in the number of chromosomal arms in a small autosomal pair in populations from the Konya Province. The X chromosome is usually reported as a medium-sized submetacentric element. The Y chromosome is apparently varying in size and usually appears as a small metacentric, subtelocentric or acrocentric. A female with the X0 sex chromosome constitution was recorded in the southernmost locality Kızlar Sivrisi – Elmalı in the Antalya Province (Sözen et al. 2013).

Nevo et al. (1994b, 1995) reported populations with 2n = 62 from various sites in central Anatolia (Afyon, Ankara, Konya, Kayseri, Havza, Sivas, Susheri). This diploid chromosome number has never been recorded again and its existence is therefore regarded as doubtful (Sözen et al. 2006b, Coşkun et al. 2010b). The diploid number of 62 chromosomes should thus be eliminated from the list of Turkish cytotypes and the records of the higher diploid numbers of chromosomes should be attributed to the presence of B chromosomes. Ivanitskaya et al. (2008) observed the presence of

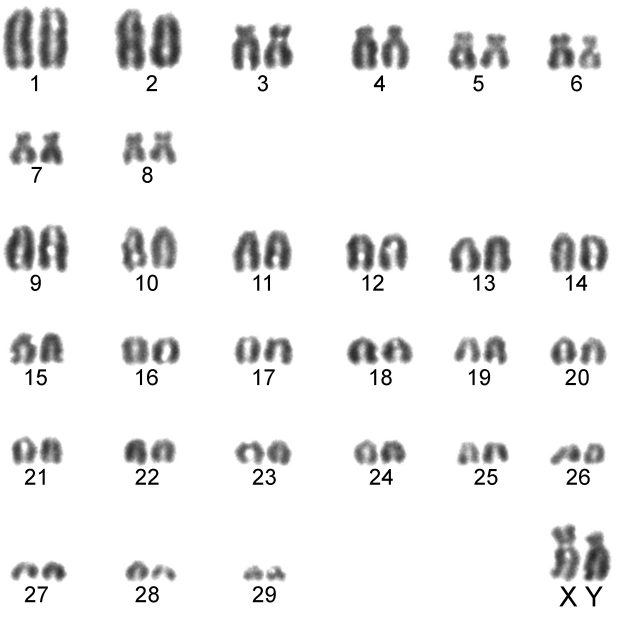

Fig. 22. Karyotype of the Vasvarii race (2n = 60, NF = 74) from Karatay, Konya, in Turkey.

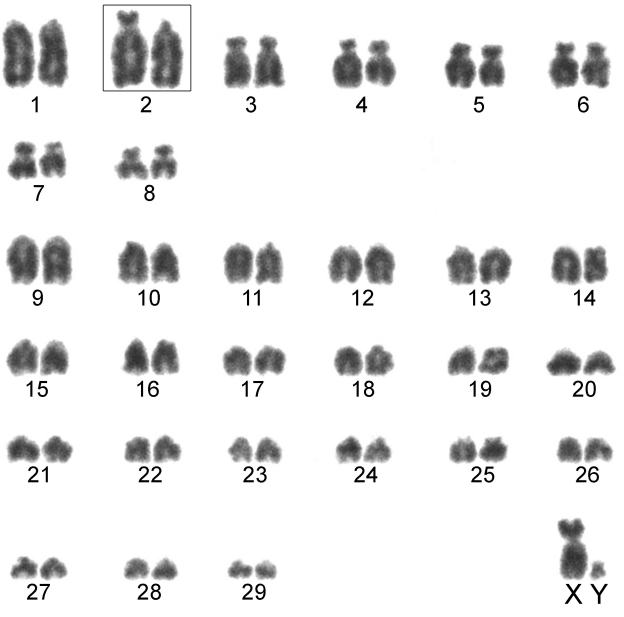

Fig. 23. Karyotype of the Vasvarii race (2n = 60, NF = 75) from Eskil, Aksaray, in Turkey. The chromosome pair in the frame is heteromorphic.

B chromosomes in most studied individuals with the 2n = 60 complement. The B chromosomes show intra-individual variation in number from 0 to 3 and from 15 to 49 percent of mitotic cells carrying these supernumerary chromosomes were reported in individual specimens. The mean number of B chromosomes per cell varies between 0.4 and 0.9. The B chromosomes are similar in size to the smallest autosomes or they are dot-like and stain C-negatively.

C-staining reveals blocks of centromeric or pericentromeric heterochromatin on bi-armed autosomes but most of acrocentric autosomes show the absence of C-heterochromatin. Short C-heterochromatin arms may occur in some subtelocentric and submetacentric autosomes. The short arms of subtelocentric autosomes are comprised by heterochromatin in both 60W and 60R cytotypes. C-staining reveals centromeric and pericentromeric heterochromatin located in all bi-armed chromosomes in 60W and in most subtelocentric autosomes in 60R. The majority of acrocentric autosomes shows absence or only diminutive blocks of centromeric heterochromatin. The acrocentric pairs 3, 4, 5, 9, 15 in the cytotype 60W are free of heterochromatin, whereas their subtelocentric counterparts in the same cytotype have large blocks of upper-centromeric heterochromatin, resulting in almost entirely heterochromatic short arms (Ivanitskaya et al. 2008).

Among populations with the lower NF values, Ivanitskaya et al. (2008) recognized as 60W the karyotype originally described by Sözen et al. (1999) from Akşehir, Matur & Sözen (2005) from Bılecık, by Kankılıç et al. (2007b) from Isparta and Beyşehir and by Kankılıç et al. (2009) from Manisa. Similarly, Ivanitskaya et al. (2008) designated the populations examined in the Cankiri and Bursa Provinces as 60W, whereas the karyotype originally described by Nevo et al. (1995) in Havza (Samsun Province) was recognized as 60R. In populations with the higher NF values, Ivanitskaya et al. (2008) distinguished as 60W the karyotype originally described by Sözen et al. (1999) from Ankara and Burdur, by Nevo et al. (1995) and Tez et al. (2001) from the Sivas Province, by Nevo et al. (1995) and Ivanitskaya et al. (1997) from the Malatya Province and by Nevo et al. (1995) from Karaman, Denizli and Konya.

The sex chromosomes usually show distinct dark C-bands in the centromeric area (Ivanitskaya et al. 1997, 2008, Arslan & Bölükbaş 2010, Arslan et al. 2011a, Matur et al. 2013). Ag-NOR sites are located in telomeric regions of three, four, or five subtelocentric and submetacentric pairs of autosomes (Gülkaç & Küçükdumlu 1999, Ivanitskaya et al. 1997, 2008, Arslan & Bölükbaş 2010, Arslan et al. 2011a, Aşan Baydemir et al. 2013). Ivanitskaya et al. (2008) described the G-banding pattern and studied also fluorochrome staining and fluorescence *in situ* hybridization of telomeric and rDNA probes. The G-banding pattern was also examined by Matur et al. (2013).

Description locality

Malatya in the eastern part of central Anatolia, Turkey: 2n = 60, NFa = 76, NF = 80, X submetacentric, Y subtelocentric (Yüksel 1984).

Distribution

Populations with 60 chromosomes are distributed in a large area of interior central Anatolia. In the west, the range includes sites in the Provinces of Denizli (Nevo et al. 1995, Sözen et al. 2013), Kütahya and Manisa (Sözen et al. 2013). The easternmost populations were recorded in the Provinces of Malatya (Ivanitskaya et al. 1997, Gülkaç & Küçükdumlu 1999, Ulutürk et al.

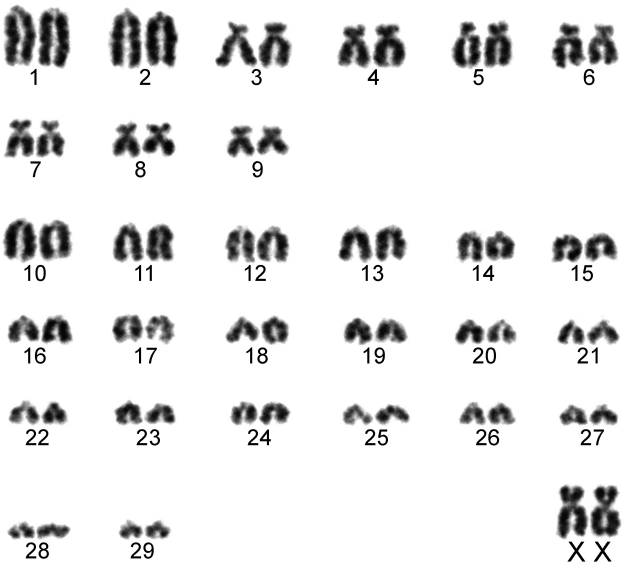

Fig. 24. Karyotype of the Vasvarii race (2n = 60, NF = 76) from Ortaköy, Aksaray, in Turkey.

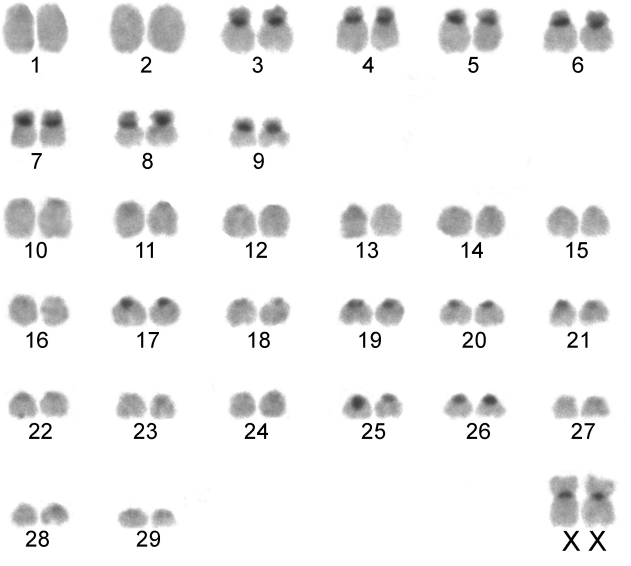

Fig. 25. C-banded karyotype of the Vasvarii race (2n = 60, NF = 76) from Ilgın, Konya, in Turkey.

2009, Coşkun et al. 2010b), Kahramanmaraş (Sözen et al. 2013) and at the right bank of the River Euphrates in the Elazığ Province (Coşkun et al. 2010b). In the north, marginal populations were reported in the Provinces of Karabük (Eskipazar – Sözen et al. 2013, Ovacık – Sözen et al. 2015), Samsun (Sözen et al. 2015) and in the north-east at the Karataş Plateau in the Giresun (Sözen et al. 2015) and Erzincan Provinces (Kankılıç et al. 2014). The southernmost populations with 60 chromosomes were found in the Provinces of Antalya (Sözen et al. 2006a, 2013) and Mersin (Sözen et al. 2015). The karyotype from eastern Anatolia was designated as 60E (east), the one from central Anatolia as 60C (central), and the one from western Anatolia as 60W (west) by Nevo et al. (1994b, 1995).

Populations with the lowest number of autosomal arms (NFa = 68) were reported from the Niğde Province (Sözen et al. 2000b). The most frequently found complement contains from six to eight bi-armed autosomal pairs (NFa = 70-74) and it was recorded in many sites located from the west to the east in the Provinces of Manisa, Uşak, Burdur, Isparta, Antalya, Konya, Karaman, Aksaray, Mersin, Adana, Kayseri, Kahramanmaraş and Malatya, as well as in the northern parts of central Anatolia (the Provinces of Bursa, Bılecık, Kütahya, Eskişehir, Bolu, Karabük, Ankara, Çankırı, Yozgat, Çorum, Amasya, Samsun, Tokat, Sivas, Giresun and Erzincan; Sözen et al. 2000b, 2006b, 2011, 2013, 2015, Tez et al. 2001, Sözen 2004, 2005, Matur & Sözen 2005, Kankılıç et al. 2007b, 2009, 2010, Matur et al. 2013).

The localities north of Bolu indicate the northern border of distribution of the Vasvarii race. In northern Anatolia, some populations with 60 chromosomes may be surrounded by races with lower chromosome number and therefore be separated from other populations with 2n = 60 occurring in central Anatolia. Populations with NFa = 70-74 (occasionally also with nine bi-armed pairs) were found in the Amasya, Samsun and Aksaray Provinces in northern and central Anatolia, Turkey (Sözen et al. 2006a, 2015, Arslan & Bölükbaş 2010).

A complicated situation was reported from the surroundings of Malatya in the eastern parts of central Anatolia, where some populations with a higher number of bi-armed autosomal pairs (9-11) were ascertained (Yüksel 1984, Gülkaç & Yüksel 1989, Nevo et al. 1995, Gülkaç & Küçükdumlu 1999, Ulutürk et al. 2009, Coşkun et al. 2010b). Coşkun et al. (2010b) recorded such a karyotype (NFa = 78, designated as 60a) north of Malatya and proposed that it is separated

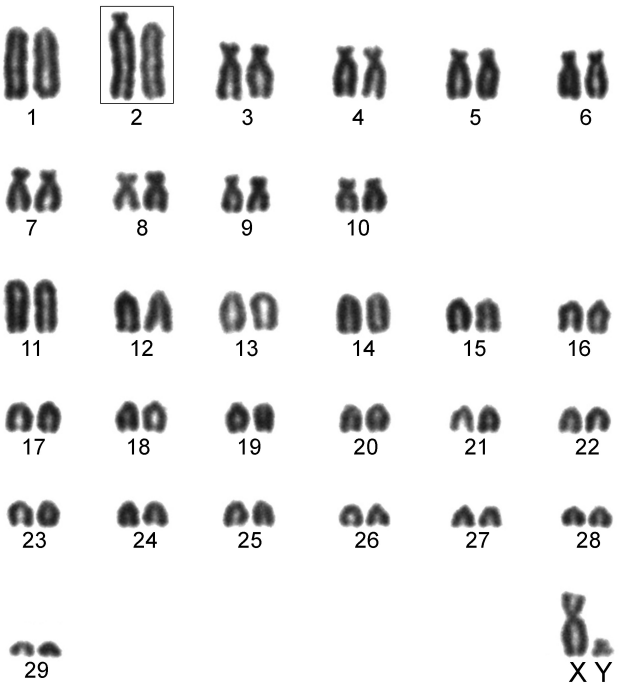

Fig. 26. Karyotype of the Vasvarii race (2n = 60, NF = 79) from Çumra, Konya, in Turkey. The chromosome pair in the frame is heteromorphic.

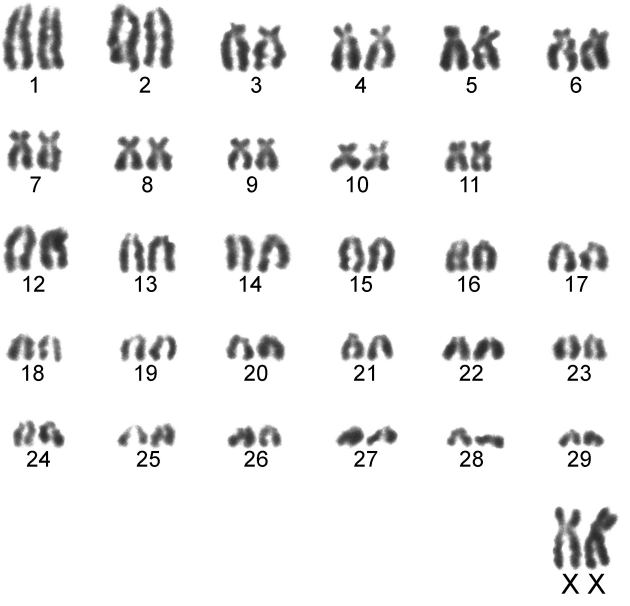

Fig. 27. Karyotype of the Vasvarii race (2n = 60, NF = 80) from Cihanbeyli, Konya, in Turkey.

from populations with a lower number of bi-armed autosomes (NFa = 74, designated as 60b) by the River Tohma, a right-side tributary of Euphrates.

The higher NFa values were found occasionally also in other parts of Anatolia, in the Provinces of Kırşehir, Nevşehir, Kayseri (Yüksel & Gülkaç 1995, Sözen et al. 2015), Ankara, Denizli, Burdur (Sözen et al. 1999, Kankılıç et al. 2010), the Kızılırmak River basin

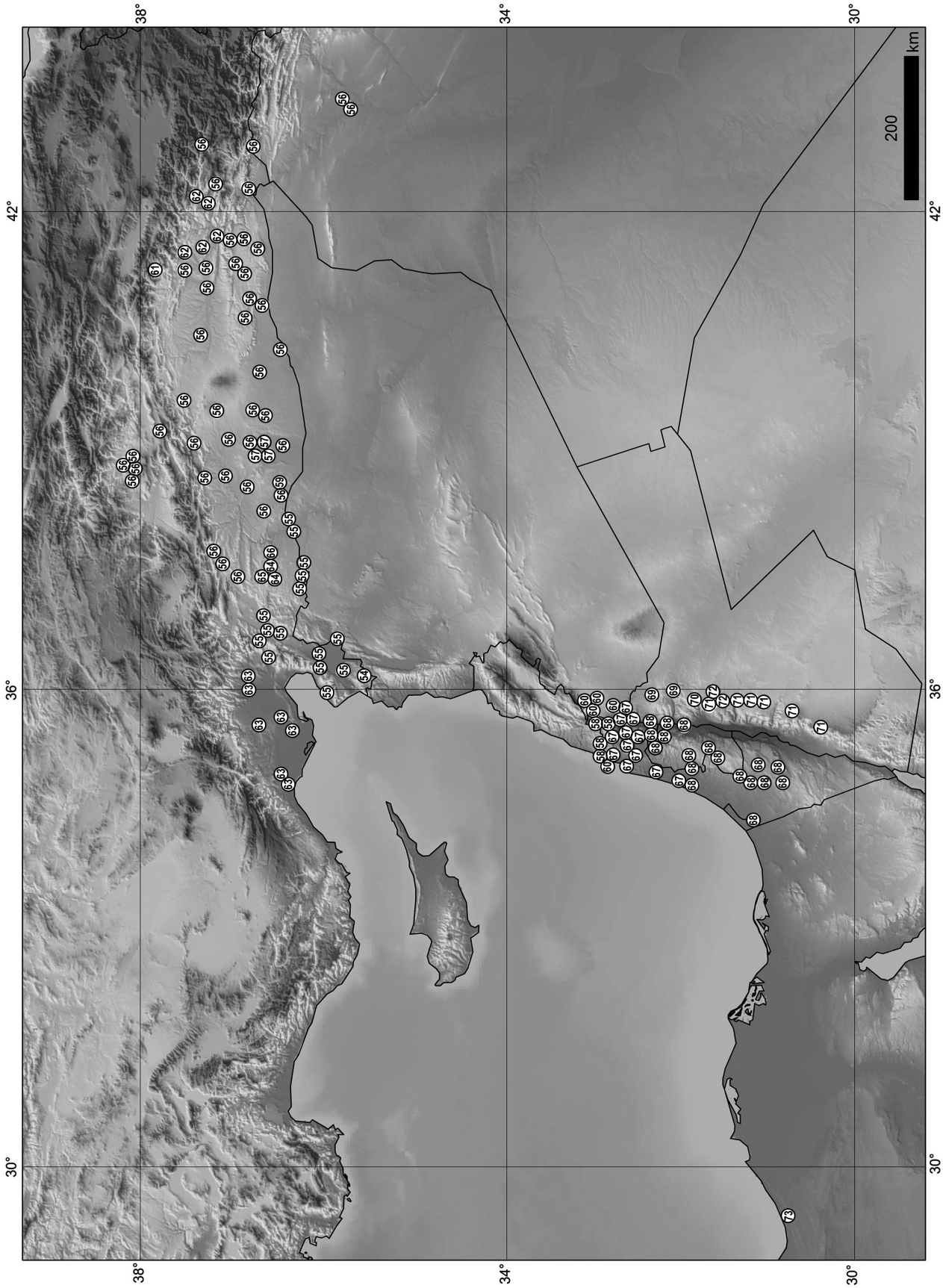

Fig. 28. Distribution map of the chromosomal races recorded within *Nannospalax ehrenbergi*. See text for numbering of the races.

(Yüksel & Gülkaç 2001), the Provinces of Bursa, Kütahya and Antalya (Sözen et al. 2006a, 2013), Yozgat (Kankılıç et al. 2007a), Afyon (Kankılıç et al. 2009), Sivas (Ulutürk et al. 2009), Konya (Arslan et al. 2011a), Çankırı, Çorum (Sözen et al. 2011) and Niğde (Sözen et al. 2015).

Additional information

Kankılıç et al. (2007a, b, 2009) recognized the populations examined in Bılecık, Kütahya, Eskişehir (NFa = 72), Manisa (NFa = 70), Isparta (NFa = 74), Yozgat (NFa = 76) and Afyon (NFa = 78) as *N. leucodon cilicicus*. Hadid et al. (2012) designated the 60 chromosome populations as the "*vasvarii*" lineage because this name was used for specimens from Malatya. Kankılıç & Gürpınar (2014) and Kankılıç et al. (2014) treated the 60 chromosome populations with NFa = 72, 74, 76, 78 and 80 as *N. labaumei*.

Nannospalax ehrenbergi (Fig. 28)

Gülkaç & Küçükdumlu (1999) assumed that the ranges of *N. xanthodon* and *N. ehrenbergi* are isolated by the River Euphrates in southeastern Anatolia but this border is apparently valid only in some regions. Recent views of the geographic range were published by Schlitter et al. (2008) and Kryštufek & Vohralík (2009).

54. Yayladağ

2n = 48, NFa = 69-70, NF = 73-74

The complement includes twelve pairs of bi-armed and eleven pairs of acrocentric autosomes. The X chromosome is metacentric, the Y chromosome was not distinguished (Coşkun 2004b). A heteromorphic autosomal pair, consisting of a subtelocentric and an acrocentric chromosome (NFa = 69) was recorded in two specimens (Arslan & Zima, in press).

Dark C-bands are visible in centromeric or pericentromeric areas of six bi-armed and all acrocentric autosomes. A subtelocentric pair has only one telomeric C-band on the short arm and an acrocentric pair has an interstitial C-band on the long arm. The subtelocentric element from the heteromorphic autosomal pair is almost entirely C-positive, except for a narrow distal region on the long arm, but only a centromeric dark C-band occurs on its homologue. The X chromosome reveals no positive band and the Y chromosome has a dark centromeric C- band. NORs are located in telomeric regions of the C-heterochromatic short arms of two bi-armed and one acrocentric pair of autosomes. The acrocentric homologue of the heteromorphic pair shows no Ag-NOR positive staining (Arslan & Zima, in press).

Description locality

Yayladağ 10 km N, Hatay (Antakya) Province, southern Anatolia, Turkey (Coşkun 2004b).

Distribution

The southernmost parts of Asiatic Turkey near the Syrian border and the coast of the Mediterranean Sea (Coşkun 2004b, Arslan & Zima, in press).

55. Intermedius (Fig. 29)

2n = 52, NFa = 70, NF = 74

The complement includes ten pairs of bi-armed and 15 pairs of acrocentric autosomes. The X chromosome is a medium-sized submetacentric or metacentric, the Y chromosome is a small acrocentric (Coşkun 1999, Arslan & Zima 2015a).

Distinct dark C-bands occur in centromeric areas of the bi-armed autosomes except for one smaller pair and also in three acrocentric pairs of autosomes. Tiny positive centromeric bands are apparent also in some other acrocentric pairs. The sex chromosomes have distinct centromeric C-positive bands (Arslan & Zima 2015a). This pattern of C-band distribution examined in a population from Fevzipaşa in the Gaziantep Province by Arslan & Zima (2015a) is similar to that reported in populations of *N. xanthodon* rather than of *N. ehrenbergi* (cf. Ivanitskaya et al. 1997). NORs are located in telomeric regions of the short arms of four bi-armed autosomes and in a smaller acrocentric autosome (Arslan & Zima 2015a).

Description locality

Kilis 7 km E, southern Anatolia, Turkey (Coşkun 1999).

Distribution

The Hatay, Kilis, Osmaniye and Gaziantep Provinces in south-eastern Anatolia (Coşkun 1999, 2004b,

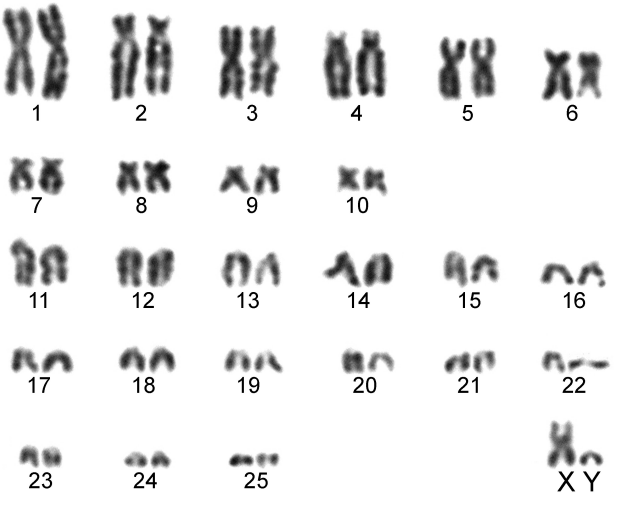

Fig. 29. Karyotype the Intermedius race (2n = 52, NF = 74) from Fevzipaşa, Gaziantep, in Turkey.

Sözen et al. 1999, Coşkun et al. 2006, Arslan & Zima 2015a).

Additional information

Coşkun et al. (2006) named this cytotype as the Hatay population and the specimens examined in their study were collected from the type locality of *S. intermedius*.

56. Elazığ

2n = 52, NFa = 72, NF = 76

The complement includes six pairs of metacentric, five pairs of subtelocentric and 14 pairs of acrocentric autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome is acrocentric or subtelocentric (Yüksel 1984).

Telomeric dark C-bands appear on the short arm of two subtelocentric pairs and distinct dark pericentromeric bands in other subtelocentric pairs. Dark centromeric C-bands are not distinct in most of bi-armed autosomes. The C-banding pattern in some subtelocentric autosomes may differ between populations. All acrocentric autosomes have pronounced pericentromeric heterochromatin blocks. The specimens from Elazığ differ from those collected in Birecik and Diyarbakir in the absence of dark C-bands on two large subtelocentric autosomes (Ivanitskaya et al. 1997). The X chromosome has a distinct centromeric C-band, the Y is almost entirely C-heterochromatic. In Turkish populations, NORs were reported in telomeres of the short arms of two subtelocentric and one submetacentric pair (Ivanitskaya et al. 1997), but Gülkaç & Küçükdumlu (1999) recognized NORs on two pairs of large subtelocentrics, always in distal regions of the short arms. Coşkun et al. (2014) studied the AgNOR distribution in specimens from Iraqi populations and located NORs in three autosomal pairs. Ivanitskaya et al. (1997) described the G-banding pattern.

Evident differences between this race and the Israeli races appear in the C-heterochromatin distribution, which were specified by Ivanitskaya et al. (1997). Telomeric C-bands in the bi-armed autosomes were not detected in the Israeli cytotypes. On the other hand, all bi-armed autosomes in groups A and B of the Israeli races possess large pericentromeric or interstitial blocks of heterochromatin. In contrast to the Israeli cytotypes, which have widely distributed size polymorphism of both arms in the largest subtelocentric autosomes, Turkish races do not reveal this type of variation (Ivanitskaya et al. 1997).

Description locality

Elazığ, eastern part of central Anatolia, Turkey (Yüksel 1984).

Distribution

This is the most widespread chromosome race in south-eastern Anatolia (Yüksel 1984, Yüksel & Gülkaç 1992, Kılıç 1995, Gülkaç & Küçükdumlu 1999, Coşkun et al. 2006, 2010b), being recorded in the regions of Şırnak, Siirt, Batman, Mardin, Diyarbakır, Elazığ, Adıyaman, Gaziantep, Şanlıurfa and Kahramanmaraş. It occurs on the left bank of Euphrates, in the river bend between the Keban Dam Lake and the Karakaya Dam Lake (Coşkun et al. 2010b) and was found also in the Mosul Province of Iraq (Coşkun et al. 2012a, 2014).

Gülkaç & Küçükdumlu (1999) assume that the ranges of *N. xanthodon* and *N. ehrenbergi* are separated by the River Euphrates in southeastern Anatolia, but mole rats of the Elazığ race are found at both the eastern and the western bank (Ivanitskaya et al. 1997). Euphrates evidently does not pose a zoogeographical barrier since other races of *N. ehrenbergi* were also recorded on the right (western) bank of the river.

Additional information

Nevo et al. (1994b, 1995) designated this race as 52E (east). Yüksel & Gülkaç (1992) recognized populations with the same karyotype as two distinct subspecies: those from the province of Şanlıurfa east of the River Euphrates were attributted to *Spalax ehrenbergi kirgisorum*, while those from the Provinces Adiyaman and Gaziantep on the west bank were recognized as *S. e. intermedius*.

57. Şanlıurfa

2n = 52, NFa = 76-78, NF = 80-82

The complement includes eight pairs of metacentric and submetacentric, five pairs of subtelocentric (two subtelocentric pairs are very large) and 12 pairs of acrocentric autosomes (NFa = 76). The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric (Ivanitskaya et al. 1997). A different karyotype with NFa = 78 was reported from a site near Şanlıurfa (Nevo et al. 1995). NORs are located in the telomeres of short arms of two subtelocentric and one submetacentric pairs (Ivanitskaya et al. 1997).

The complement is similar in morphology with the Galili race (2n = 52, NF = 84) from Israel (Nevo et al. 1995), but Ivanitskaya et al. (1997) noted general differences in the karyotype structure between the Turkish and Israeli cytotypes.

Description locality

Şanlıurfa, south-eastern Anatolia, Turkey (Ivanitskaya et al. 1997).

Distribution

Şanlıurfa and its surroundings (Nevo et al. 1995, Ivanitskaya et al. 1997).

Additional information

This race has a similar karyotype as the previous one and the difference is restricted only to the number of bi-armed autosomes. However, Ivanitskaya et al. (1997) noted that no intrapopulational variation in NF was found in the area studied and no hybrid individuals were recorded, in spite of relatively dense sampling. In this area, several other cytotypes were also found. Yüksel & Gülkaç (1992) reported the karyotype with 2n = 54 and NFa = 72 from the eastern banks of the River Euphrates in the Şanlıurfa Province, which is included here within the Suruç race.

58. Galili

2n = 52, NFa = 80, NF = 84

In the original description of this race (Wahrman et al. 1969a, b), 16 bi-armed and ten acrocentric pairs were reported in the complement, but the number of autosomal arms may vary and even exceeds 80 in some individuals. The X chromosome was identified as one of the submetacentrics, the Y chromosome as a small acrocentric.

Wahrman et al. (1969a, b) proposed that the differences between the Israeli races of mole rats are due to Robertsonian re-arrangements and pericentric inversions. The chromosomes can be divided into three groups: group A is composed of the unchanged, mostly submetacentric chromosomes, which are shared in the complements of all the races. Group B includes bi-armed and uni-armed autosomes presumably involved in the Robertsonian re-arrangements. The bi-armed autosomes in groups A and B possess large pericentromeric or interstitial blocks of C-heterochromatin. This contrasts the karyotype structure in Turkish races of *N. ehrenbergi*, which frequently show only telomeric C-bands or whole C-heterochromatic arms in similar bi-armed autosomes. Group C includes smaller acrocentric and subtelocentric chromosomes presumably affected by pericentric inversions. In this group, certain pairs are occasionally heterozygous due to an inversion and this polymorphism is assumed to reflect recent evolutionary dynamics.

The NOR distribution pattern may vary (Wahrman et al. 1985). Four chromosomes carry NORs, one of them in a distal position. The short arm of autosome 1 bears a terminal nucleolus organizer region, which varies in size. Widely distributed size polymorphism of the short and the long arm in this chromosome is reported. The C-negative segment between the centromere and the NOR is also variable in length and it replicates later than the rest of the chromosome. The long arm of autosome 1 has a heteropycnotic C-negative modification in the area near the centromere, which may be of varying length. This polymorphism is widespread across all four chromosome races reported from Israel and occurs also intra-individually (Wahrman et al. 1985, Nevo et al. 1988a, Ivanitskaya et al. 2005). Turkish populations do not reveal such a type of variation (Ivanitskaya et al. 1997).

Variation in the quantity and distribution of constitutive heterochromatin may also occur on other chromosomes. Ivanitskaya et al. (2005) studied the distribution of C-bands and base-specific fluorochrome staining and performed comparative genomic hybridization between 52 and 60 chromo-some Israeli races. C-positive centromeric hetero-chromatin and some telomeric sites comprise GC-rich DNA sequences and slight qualitative differences in highly repetitive sequences were observed between the two races. The high level of homology in the composition of heterochromatin may relate to the recent divergence of Israeli mole rats. Nevo et al. (2001) described chromosome C- and G-banding pattern.

The natural hybrids with other chromosome races are partly fertile but their fitness appears lower than that of the parents (Nevo & Bar-El 1976). Wahrman et al. (1969a) found two individuals with 53 chromosomes, which were assumed to originate from hybridization with the 2n = 54 race. Ivanitskaya et al. (2010) studied chromosomes in a hybrid zone between races with 2n = 52 and 2n = 58, in relation to incidence of chromosomal novelties and the level of meiotic and mitotic abnormalities. Among 149 specimens studied, 82 were hybrids with 64 different karyotypes, ranging in diploid numbers from 50 to 60 chromosomes. Nine hybrid specimens were mosaics for the chromosome numbers, due to the occurrence of specific cell lines and six specimens possessed variable number of B chromosomes. B chromosomes have not been found in other Israeli populations. Mosaicism of B chromosomes was reported also in meiotic cells, however abnormal chromosome pairing during meiosis occurrs very rarely. The Y chromosome has a different structure in both hybridizing races.

Greenbaum et al. (1990) studied synaptonemal complex in meiosis of hybrids between the 52 and 58 chromosome races. Zuccotti et al. (1995) studied spermatogenesis in natural hybrids between races with 2n = 52 and 58 and found impaired development, even though the production of sperm was not affected.

Description locality
Kerem Ben Zimra, Upper Galilee Mountains, extreme north of Israel (Wahrman et al. 1969a, b).
Distribution
The Upper Galilee Mountains (Wahrman et al. 1969a, b, Wahrman et al. 1985, Nevo et al. 1988a).
Additional information
Nevo et al. (2001) described this race as *Spalax galili*. The geographic distribution of the four races reported from Israel is significantly correlated with four climatic regimes characterized by a combination of humidity and temperature. The races are distributed parapatrically along a north-south ecological gradient of increasing aridity and narrow hybrid zones are formed in the areas of geographical contact (Nevo et al. 2001, Nevo 2013). Nevo et al. (1988a) investigated polymorphism in chromosome 1 and found that this polymorphism (particularly variation affecting the short arm) is correlated with water availability and temperature. Hadid et al. (2013) proposed a possible incipient sympatric adaptive ecological speciation in the Galili race, related to adaptation of populations to different soils.

59. Suruç
2n = 54, NFa = 72, NF = 76
The complement includes 10 pairs of bi-armed and 16 pairs of acrocentric autosomes. The X chromosome is metacentric, the Y chromosome is subtelocentric (Yüksel & Gülkaç 1992).
Description locality
Suruç, Şanlıurfa Province, south-eastern Anatolia, Turkey (Yüksel & Gülkaç 1992).
Distribution
The race is known from two close localities in the Şanlıurfa Province near the Syrian border (Yüksel & Gülkaç 1992).
Additional information
Yüksel & Gülkaç (1992) recognized populations with this karyotype as *S. ehrenbergi kirgisorum*.

60. Golani
2n = 54, NFa = 78, NF = 82
In the original description of this race (Wahrman et al. 1969a, b), 14 bi-armed and 13 acrocentric pairs were reported in the complement and it was noted that the number of autosomal arms is variable. The X chromosome was identified as one of the submetacentrics, the Y chromosome as a small acrocentric. Nevo et al. (2001) described chromosome banding patterns.
Wahrman et al. (1969a) found two individuals with 53 chromosomes, recognized as hybrids with the 2n = 52 race. Greenbaum et al. (1990) studied synaptonemal complex in meiosis of hybrids between the 54 and 58 chromosome races.
Description locality
Quneitra, Golan Heights, north-eastern Israel (Wahrman et al. 1969a, b).
Distribution
The Golan Heights (Wahrman et al. 1969a, b, Nevo & Bar-El 1976, Wahrman et al. 1985, Nevo et al. 1988a, 2001).
Additional information
Nevo et al. (2001) described this race as *Spalax golani*.

61. Kulp
2n = 56, NFa = 58, NF = 62
The karyotype comprises two pairs of meta- and submetacentric and 25 pairs of acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome a medium-sized acrocentric (Coşkun et al. 2015).
C-banding reveals pericentromeric constitutive heterochromatin in one submetacentric and seven acrocentric autosome pairs. Two acrocentric autosome pairs and another acrocentric chromosome with a secondary constriction show interstitial C-positive bands on their long arms. A secondary constriction occurs on the Y chromosome. NORs are located in one medium-sized metacentric and four acrocentric pairs of autosomes (Coşkun et al. 2015).
Description locality
Özbek village, Kulp, north-east of Diyarbakır, southern Anatolia, Turkey (Coşkun et al. 2015).
Distribution
Known only from the locality of original description.

62. Siirt
2n = 56, NFa = 62, NF = 66
The complement includes four pairs of bi-armed (metacentric and submetacentric) and 23 pairs of acrocentric autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric (Coşkun 2004c).
Description locality
Kurtalan-İncirlik village, Siirt Province, south-eastern Anatolia, Turkey (Coşkun 2004c).
Distribution
This race was recorded in the Siirt and Batman Provinces, in the easternmost parts of southern Anatolia near the borders with Syria and Iraq (Coşkun 2004c, Coşkun et al. 2006).

63. Ceyhanus

2n = 56, NFa = 64-68, NF = 68-72

The complement includes three pairs of metacentric or submetacentric (two large and one very small), four pairs of subtelocentric (a large and three small) and 20 pairs of acrocentric autosomes (NFa = 68). The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric (Ivanitskaya et al. 1997). Coşkun et al. (2006) recorded in two specimens from Kozan Pekmezci, in the Adana Province, a complement that included five pairs of bi-armed and 22 pairs of acrocentric autosomes (NFa = 64). We found the same karyotype in the Osmaniye Province (Fig. 30). Heterochromatin is absent from most meta- and submetacentric autosomes, but telomeric dark blocks of C-heterochromatin occur on the short arm of two subtelocentric pairs. Almost all acrocentric autosomes reveal pericentromeric heterochromatin block. The X chromosome has a pericentromeric dark C-band. NORs are located in telomeres of the short arms of three subtelocentric pairs (Ivanitskaya et al. 1997). Ivanitskaya et al. (1997) described the G-banding pattern.

Description locality

Tarsus 3 km N, Mersin Province, south-eastern Anatolia, Turkey (Ivanitskaya et al. 1997).

Distribution

The Mersin, Osmaniye and Adana Provinces in south-eastern Anatolia (Nevo et al. 1995, Coşkun et al. 2006, Sözen et al. 2006a, 2015).

Additional information

Coşkun et al. (2010a) suggested that *Nannospalax ehrenbergi ceyhanus* may be the available name for populations distributed in the warm and dry environs of Adana and Tarsus. Sözen et al. (2015) designated the population examined from Kadirli as 56eh (*ehrenbergi*).

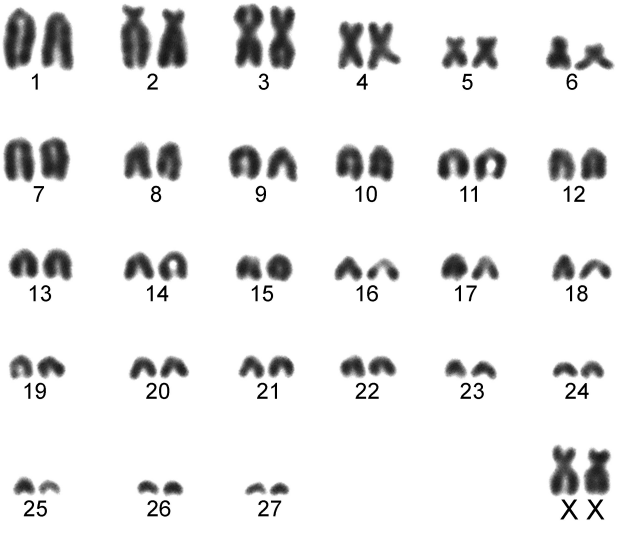

Fig. 30. Karyotype of the Ceyhanus race (2n = 56, NF = 68) from Kadirli, Osmaniye, in Turkey.

64. Gaziantep A

2n = 56, NFa = 78, NF = 82

The complement includes seven pairs of metacentric, five pairs of submetacentric or subtelocentric and 15 pairs of acrocentric autosomes. The X chromosome is a medium-sized metacentric, the Y chromosome a small subtelocentric (Ivanitskaya et al. 1997).

Two subtelocentric autosomes have dark telomeric C-blocks on the short arms, whereas the remaining bi-armed autosomes are C-negatively stained. Most acrocentric autosomes bear distinct blocks of pericentromeric heterochromatin. C-banding heteromorphism was recorded in the first acrocentric pair of a single male. NORs are situated in telomeres of the short arms of three subtelocentric pairs and in the telomeric region of the long arm of an acrocentric autosomal pair (Ivanitskaya et al. 1997). Ivanitskaya et al. (1997) described the G-banding pattern.

This race differs from the specimens examined from the same area in the arm number (Gaziantep B, Yüksel & Gülkaç 1992) and/or in the diploid number (Gaziantep C, Nevo et al. 1995).

Description locality

Gaziantep, south-eastern Anatolia, Turkey (Ivanitskaya et al. 1997).

Distribution

Type locality.

Additional information

Coşkun (1996b) described a new taxon *Spalax nehringi nevoi* from Sarıgüllük, 6 km from Gaziantep, but did not provide any karyotypic data.

65. Gaziantep B

2n = 56, NFa = 86, NF = 90

The complement includes 16 pairs of bi-armed and 11 pairs of acrocentric autosomes. The X chromosome is submetacentric (Yüksel & Gülkaç 1992).

Description locality

Gaziantep, south-eastern Anatolia, Turkey (Yüksel & Gülkaç 1992).

Distribution

Gaziantep and Adıyaman Provinces, south-eastern Anatolia (Yüksel & Gülkaç 1992).

Additional information

Yüksel & Gülkaç (1992) recognized populations with this karyotype from the Provinces Adıyaman and Gaziantep on the west bank of the River Euphrates as *S. ehrenbergi intermedius*.

66. Gaziantep C

2n = 58, NFa = 78, NF = 82

The complement includes three pairs of metacentric, three pairs of smaller submetacentric, five pairs of subtelocentric and 17 pairs of acrocentric autosomes. The X chromosome is a medium-sized submetacentric, the Y chromosome was not identified (Nevo et al. 1995). The karyotype of this race is similar in morphology to the Carmeli race from Israel (Nevo et al. 1995).

Description locality

Gaziantep 10 km E, south-eastern Anatolia, Turkey (Nevo et al. 1995).

Distribution

Vicinity of Gaziantep (Nevo et al. 1995).

Additional information

One might suggest that the Gaziantep races merge into one, however, Ivanitskaya et al. (1997) noted that no intrapopulational chromosomal variatian in 2n was found in the area studied and no hybrid individuals were recorded in spite of relatively dense sampling. The sympatric or nearly sympatric occurrence of different races could thus be assumed in the area and a thorough revision of the pattern is desirable.

67. Carmeli

2n = 58, NFa = 72, NF = 76

Wahrman et al. (1969a, b) recognized in the complement nine bi-armed and 20 acrocentric chromosomal pairs. The X chromosome was identified as a submetacentric, the Y chromosome as a small acrocentric. Nevo et al. (2001) described chromosome banding patterns.

Ivanitskaya et al. (2010) studied chromosomes in a hybrid zone between races with 52 and 58 chromosomes. Greenbaum et al. (1990) described the synaptonemal complex in meiosis of hybrids between the races with 52 and 58 chromosomes and 54 and 58 chromosomes. Zuccotti et al. (1995) studied spermatogenesis in natural hybrids between the races possessing 52 and 58 chromosomes.

Description locality

Muhraka, Mt. Carmel, northern Israel (Wahrman et al. 1969a, b).

Distribution

The Lower Galilee Mountains and central Yizreel and Coastal Plain in Israel (Wahrman et al. 1969a, b, Nevo & Bar-El 1976, Wahrman et al. 1985, Nevo et al. 1988a, 2001).

Additional information

Nevo et al. (2001) described this race as *Spalax carmeli*, however, the holotype of *S. ehrenbergi* comes from Jaffa, a place located in a hybrid zone between *S. carmeli* (2n = 58) and *S. judaei* (2n = 60). Nevo et al. (2001) reserved *ehrenbergi* to designate the superspecies but recognized no species per se (Musser & Carleton 2005).

68. Judaei

2n = 60, NFa = 72, NF = 76

Wahrman et al. (1969a, b) distinguished in the complement eight bi-armed and 22 acrocentric chromosomal pairs. The X chromosome was identified as one of the submetacentrics, the Y chromosome as a small acrocentric.

Nevo et al. (2001) described chromosome banding patterns and Ivanitskaya et al. (2005) studied the distribution of C-bands and base-specific fluorochrome staining and performed comparative genomic hybridization.

Several hybrids between the 2n = 58 and 60 races were reported in Samaria (Wahrman et al. 1969a, b). Ivanitskaya et al. (2005) recorded hybrids between the Galili (2n = 52) and the Judaei races (2n = 60). Zuccotti et al. (1995) studied spermatogenesis in natural hybrids with the Carmeli race (2n = 58).

Description locality

Lahav, Judean Mts., central Israel (Wahrman et al. 1969a, b)

Distribution

Mountains of Samaria and Judea, the Jordan valley, the southern Coastal Plain and northern Negev Desert in Israel (Wahrman et al. 1969a, b, Nevo & Bar-El 1976, Wahrman et al. 1985, Nevo et al. 1988a, 2001).

Additional information

Nevo et al. (2001) described this race as *Spalax judaei*.

69. Irbid

2n = 60, NFa = 74, NF = 78

The complement includes eight pairs of bi-armed and 21 pairs of acrocentric autosomes. The largest autosome is subtelocentric with relatively large short arms. Autosomal pairs 7 and 29 are bi-armed. The X chromosome is a medium-sized submetacentric, the Y chromosome a small acrocentric (Ivanitskaya & Nevo 1998, Nevo et al. 2000).

Nevo et al. (2000) found that blind mole rats from Jordan possess two different diploid numbers of chromosomes (2n = 60 and 62) and individual populations may differ in the centromere position on four autosomes, which can be either acrocentric or bi-armed (numbered 1, 7, 26 and 29). Two of these pairs (26 and 29) belong to group C that includes inversion chromosomes, which are not considered

responsible for speciation of blind mole rats in Israel (Wahrman et al. 1969a, b, 1985). Changes of the centromeric position in the 1st and 7th pairs from group A are the principal rearrangements that separate Israeli and Jordan 2n = 60 cytotypes. Chromosome pair 7, which is invariably submetacentric in all Israeli populations is acrocentric in most Jordanian karyotypes, as is the case in Turkish populations. Rearrangements of these four pairs produce variation in the number of chromosomal arms (NF = 72-78) and four basic cytotypes were distinguished in Jordan (Nevo et al. 2000). Comparative analysis of G-banded chromosomes indicates that differentiation of bi-armed and uni-armed autosomes is due to pericentric inversions or centromeric shifts. Two of the Jordan populations (Madaba, Mt. Nebo) are karyotypically polymorphic.

Ivanitskaya & Nevo (1998) and Nevo et al. (2000) described the C- and G- banding pattern and the distribution of NORs. All examined cytotypes in Jordan have a similar distribution of heterochromatin material, except for the four variable autosomal pairs. Acrocentric autosomes have blocks of pericentromeric C-heterochromatin of variable size, bi-armed autosomes are usually C-negative, except for the first pair. The length of the C-negative short arm in the first autosomal pair varies among geographic populations from Jordan and this variation is related to the C-positive pericentromeric region. The X chromosome possesses a tiny centromeric block of heterochromatin, the Y chromosome is C-negative (Ivanitskaya & Nevo 1998, Nevo et al. 2000).

The NORs are located on the subtelocentric variant of autosome 1 and on another metacentric autosome. The number of NORs is associated with the morphology of the first pair (Ivanitskaya & Nevo 1998). The cytotypes with subtelocentric chromosomes of this pair (NFa = 70, 72, 74) have two NOR-bearing pairs (telomeric regions of pairs 1 and 5) and the cytotype with NFa = 68 (the acrocentric variant of autosome 1) showed only one NOR- bearing pair (pair 5).

Description locality

Irbid, Jordanian mountain ridge, Jordan (Nevo et al. 2000).

Distribution

Gilead and Ammon mountains in north-western Jordan (Ivanitskaya & Nevo 1998, Nevo et al. 2000).

Additional information

We follow here the pattern of differentiation of cytotypes proposed by Nevo et al. (2000). The delimitation of four cytotypes in Jordan is only partly supported by the divergence pattern obtained by an analysis of 32 allozyme gene loci and karyotype characteristics alone were not sufficient for putative species identification. Based on allozyme-derived genetic distances, the Jordanian 2n = 60 populations preceded the Israeli ones with the same diploid number. Nevo et al. (2000) interpreted the Irbid race as a link of colonization of blind mole rats in the region between southern Turkey and North Africa. The Jordanian races still retain footprints of their Turkish origins (Nevo et al. 2000).

70. Naur

2n = 60, NFa = 72, NF = 76

The complement includes seven pairs of bi-armed and 22 pairs of acrocentric autosomes. The largest autosomal pair 1 is subtelocentric and pair 26 is bi-armed. The X chromosome is a medium-sized submetacentric, the Y chromosome is an acrocentric (Ivanitskaya & Nevo 1998, Nevo et al. 2000).

Ivanitskaya & Nevo (1998) and Nevo et al. (2000) described the C- and G- banding pattern and the distribution of NORs. C-positive short arms occur on some bi-armed autosomes. The NORs are located on two bi-armed autosomes.

Description locality

Naur, 25 km N of Madaba, Ammon Mountains, Jordan (Ivanitskaya & Nevo 1998, Nevo et al. 2000)

Distribution

Ammon and Northern Moav Mts. in the region situated south-east of Amman (Ivanitskaya & Nevo 1998, Nevo et al. 2000).

Additional information

The sample from Mount Nebo includes specimens possessing the karyotype of this race, but also specimens with NFa = 70. The conventionally stained karyotype of this race is seemingly identical to the Israeli race with 2n = 60, but G-banding comparison indicates differences in the centromere position in two autosomal pairs (Nevo et al. 2000).

71. Ariha

2n = 60, NFa = 70, NF = 74

Most specimens studied within this race have identical karyotype with six bi-armed and 23 acrocentric autosome pairs. The largest autosome is subtelocentric and the length of its short arm is geographically variable. The karyotypes of populations distributed north of Wadi Hasa (Ariha, Karak and Mazar) have almost invisible short arms of the first pair, whereas those found in populations south of Wadi Hasa (Tafila, Wadi Musa) have distinct short arms on this pair (Nevo et al. 2000). The X chromosome is a medium-

sized submetacentric, the Y chromosome is a small acrocentric.
Ivanitskaya & Nevo (1998) described the C- and G-banding pattern and the distribution of NORs. NORs are located in two autosomal pairs.
Description locality
Ariha, 5 km S of Wadi Mujib, southern Moav Mountains, Jordan (Ivanitskaya & Nevo 1998, Nevo et al. 2000).
Distribution
Southern Moav and Edom Mts., central and southern Jordan (Ivanitskaya & Nevo 1998, Nevo et al. 2000). This race is geographically separated from the previous one by the canyon of Wadi Mujib (Nahal Arnon), although the same karyotype was found in two animals collected north of the canyon in the Mt. Nebo polymorphic population. The large canyon of Wadi Hasa has separated this race into two groups.

72. Madaba
2n = 60, NFa = 68, NF = 72 and 2n = 62, NFa = 70, NF = 74
This race includes two cytotypes, with 2n = 60 and 2n = 62. The complement with 62 chromosome was recorded in two specimens only. Seven other specimens examined in this site possessed the standard karyotype with 60 chromosomes (Nevo et al. 2000). The karyotype includes five bi-armed autosomal pairs, the other autosomes are acrocentric. Autosomal pairs 1, 7, 26 and 29 are always acrocentric. The karyotype with 62 chromosomes contains an additional pair of small acrocentric chromosomes and it was only found in the polymorphic sample from Madaba. The additional autosomes seem to be the smallest in the set and their C-banding pattern is similar as in other acrocentric autosomes (Nevo et al. 2000). The first autosomal pair is acrocentric in both types (after partial deletion of the short arms followed by pericentric inversion). The X chromosome is a medium-sized submetacentric, the Y chromosome is a small acrocentric (Ivanitskaya & Nevo 1998, Nevo et al. 2000).
Ivanitskaya & Nevo (1998) and Nevo et al. (2000) described the C- and G- banding pattern and the distribution of NORs. Only one pair of autosomes bearing NOR was observed.
Description locality
Madaba 6 km S (near Amman), northern Moav Mountains, Jordan (Nevo et al. 2000)
Distribution
Northern Moav Mts. in central Jordan (Ivanitskaya & Nevo 1998, Nevo et al. 2000).

73. Aegyptiacus
2n = 60, NFa = 72, NF = 76
The complement includes seven pairs of bi-armed autosomes (each pair is individually identifiable) and 22 pairs of acrocentric autosomes. The X chromosome is a large submetacentric, the Y chromosome is a minute element. Apparent heteromorphism in the length of the short arm of the largest pair of bi-armed autosomes was recorded in four specimens (Lay & Nadler 1972).
Description locality
Burg el-Arab, El-Hammam, Matruh Governate, coast of the Mediterranean Sea, Egypt (Lay & Nadler 1972).
Distribution
The karyotype was examined only from the locality of description in Egypt.
Additional information
Nevo et al. (1991, 1994a) considered this population as a new unnamed species and Hadid et al. (2012) recognized it as *N. aegyptiacus*.

Spalax (Fig. 31)
The range of the genus includes parts of south-eastern Europe in Romania, Ukraine and southern Russia up to western Kazakhstan (IUCN 2014).

74. *Spalax antiquus*
2n = 62, NFa = 120, NF = 124
The complement includes five pairs of small metacentric, 12 pairs of submetacentric and 13 pairs of subtelocentric autosomes. The X chromosome is a large metacentric, the Y chromosome a small subtelocentric (Raicu et al. 1968).
Description locality
Boju, Transylvania, Romania (Raicu et al. 1968).
Distribution
Transylvania in Romania.
Additional information
Raicu et al. (1968) recognized the population under study as *Spalax microphthalmus*. Németh et al. (2013a) separated the isolated populations in Romanian Transylvania as a distinct species, *Spalax antiquus*. Another species, *S. istricus*, was distinguished in the southern distribution isolate in Oltenia (near Craiova, Romania) but no recent record of the occurrence of blind mole-rats are known from this region. Conservation measures were suggested by Csorba et al. (2015).

75. *Spalax graecus*
2n = 62, NFa = 120, NF = 124
The complement is identical with that of the previous species (Raicu et al. 1968).

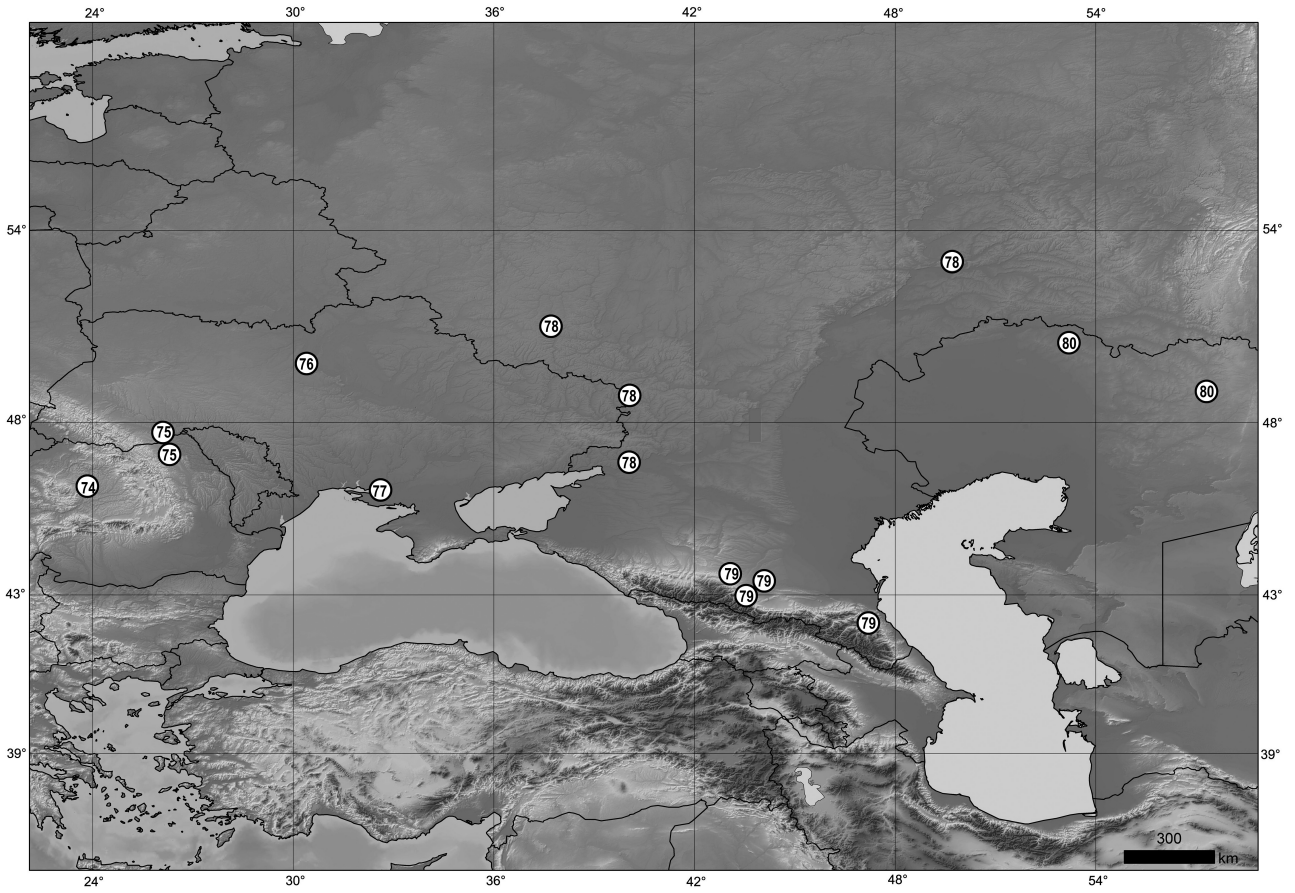

Fig. 31. Distribution map of the karyologically studied populations of the *Spalax* species. See text for numbering of the species.

Description locality
Suceava in Romanian Moldavia (Raicu et al. 1968).
Distribution
Romanian Moldavia (Raicu et al. 1968), Bukovina in western Ukraine (Lyapunova et al. 1974, Martynova et al. 1975).
Additional information
The karyotype was originally described under the name *Spalax microphthalmus*. Taxonomic problems of this species were discussed by Németh et al. (2013a) and Chişamera et al. (2014). The allopatric populations separated by the Carpathians from the Transylvanian Plain and from Oltenia and Muntenia in Romania were recognized as valid species, *Spalax antiquus* and *Spalax istricus*, respectively. Both species seem to be critically endangered and possibility of extiction is considered real in the latter one (Németh et al. 2013a, Csorba et al. 2015).

76. *Spalax zemni*
2n = 62, NFa = 120, NF = 124
The complement is identical with that of *S. graecus* (Martynova et al. 1975).
Description locality
Vicinity of Kiev, Ukraine (Martynova et al. 1975).
Additional information
The karyotype was described under the name of *Spalax podolicus* Trouessart, 1897.

77. *Spalax arenarius*
2n = 62, NFa = 120, NF = 124
The complement includes five pairs of small metacentric, 12 pairs of submetacentric and 13 pairs of subtelocentric autosomes. The last pair of the submetacentric – subtelocentric group of autosomes is distinctly small. The X chromosome is a large metacentric, the Y chromosome a small subtelocentric (Lyapunova et al. 1974).
Description locality
Eastern bank at the mouth of the River Dnieper, south-eastern Ukraine (Lyapunova et al. 1974).
Distribution
Sand habitats along the lower course and the mouth of the River Dnieper (Lyapunova et al. 1974, Martynova et al. 1975).

78. *Spalax microphthalmus*

2n = 60, NFa = 116, NF = 120

The complement includes five pairs of metacentric, 11 pairs of submetacentric and 13 pairs of subtelocentric autosomes. The X chromosome is a large metacentric, the Y chromosome a small acrocentric (Lyapunova et al. 1974). In another study, some of the subtelocentric autosomes were evaluated as acrocentric and the number of chromosomal arms subsequently decreased (NFa = 110-112). Puzachenko & Baklushinskaya (1997) described chromosome banding patterns in populations from Streletskaya and Kazatskaya steppes in the Kursk region, Russia. Animals heterozygous for a complex chromosome rearrangement, resulting in the increased chromosome size and altered location of the centromere, were revealed in this paper.

Description locality

Streleckaya Steppe Reserve, Luhansk Region, Ukraine (Lyapunova et al. 1974).

Distribution

Western Ukraine and southern Russia (Lyapunova et al. 1974, Martynova et al. 1975, Belyanin et al. 1976, Puzachenko & Baklushinskaya 1997).

Additional information

Populations from northern Caucasus probably belong to *S. giganteus* (Dzuev & Shogenov 2003, Zagorodniuk in litt.).

79. *Spalax giganteus*

2n = 62, NFa = 120, NF = 124

The complement includes five pairs of small metacentric, 12 pairs of submetacentric and 13 pairs of subtelocentric autosomes. The X chromosome is a large submetacentric or subtelocentric, the Y chromosome is a small subtelocentric (Lyapunova et al. 1974).

Description locality

Daghestan, not specified (Lyapunova et al. 1974).

Distribution

Daghestan, possibly central parts of the northern Caucasus Mts., Russia.

Additional information

The populations from northern Caucasus, previously recognized as *S. microphthalmus*, revealed the same karyotype (Dzuev & Shogenov 2003).

80. *Spalax uralensis*

2n = 62, NFa = 120, NF = 124

The complement is identical with that of *S. giganteus* (Lyapunova et al. 1974).

Description locality

The eastern bank of the River Ural, Kazakhstan (Lyapunova et al. 1974).

Distribution

Western Kazakhstan. The karyotypes were studied in two sites at the eastern bank of the River Ural (Lyapunova et al. 1974).

Additional information

Previously synonymized with *S. giganteus*. The allopatric populations to *S. giganteus* in western Kazakhstan distributed between the Rivers Ural and Emba were recognized as a separate species, i.e. *S. uralensis* (Musser & Carleton 2005).

Discussion

Cytogenetic research efforts in blind mole rats have been rather extensive and the present review summarizes almost 100 papers reporting and describing karyotypic features of these animals across their distribution range. It is difficult to determine exactly the actual number of studied individuals and populations because relevant information is not reported in all papers, and/or is not clear if the same material was included in several different articles. Nevertheless, we estimate that karyotype examination has been performed in more than 2300 specimens originating from about 635 individual sites.

This huge material provides a large dataset of information confirming wide variation in the diploid number and chromosomal morphology. On the other hand, it is also obvious that our understanding of major evolutionary mechanisms of this variation is still insufficient. Important questions still remain open related to chromosomal evolution, adaptive significance of chromosomal changes, taxonomic implications of chromosomal variation and phylogenetic pathways.

Chromosomal evolution

Evolution of the karyotype is obviously complex in blind mole rats and has involved chromosomal re-arrangements of various types. Robertsonian re-arrangements (fusions and fissions), pericentric inversions, centromeric shifts and changes in C-heterochromatin content (including the occasional incidence of B chromosomes) are usually implicated as the mechanisms of chromosomal evolution in this group. Ivanitskaya et al. (1997) also assumed the occurrence of euchromatin deletions or even loss of whole chromosomes. An important role in evolution can also be expected from positional changes of the NOR sites (Ivanitskaya et al. 1997, 2008, Nevo et al. 2000, Arslan et al. 2014a, Arslan & Zima 2015a, b). Unfortunately, comparative studies aimed at examining chromosomal banding pattern

and/or applications of FISH techniques are still rare (Wahrman et al. 1985, Ivanitskaya et al. 1997, 2005, 2008, Ivanitskaya & Nevo 1998, Nevo et al. 2000, Arslan et al. 2011a, 2014a, Matur et al. 2013, Arslan & Zima 2015a, b) and our knowledge on the detailed mechanisms of chromosomal change in blind mole rats remains insufficient. The best evidence about re-arrangements involved in chromosomal evolution has hitherto been obtained in the Israeli and other races from the Middle East (Wahrman et al. 1985, Nevo et al. 2000, Ivanitskaya et al. 2010).

A general opinion suggests that the Robertsonian re-arrangements are the major mechanism of the change in the diploid number of chromosomes in blind mole rats and that divergent processes were presumably peripatric, through fixation of Robertsonian re-arrangements in small isolated marginal populations. However, the direction of this change is controversial. Savić & Soldatović (1979b, 1984) proposed that the evolution of karyotypes in the Balkan blind mole rats most probably took the form of a decrease in the number of acrocentric autosomes and lowering in the diploid number of chromosomes. In their scenario, the ancestral karyotype might have consisted of 60 mostly acrocentric chromosomes and similar changes could have happened independently in various separate lineages. This opinion was supported also by Ivanitskaya et al. (2005) and Matur et al. (2013). On the contrary, Nevo (1991) and Nevo et al. (1994b, 1995, 2000) proposed the increase of chromosome numbers by fissions of bi-armed to acrocentric chromosomes as the major initial mechanism of chromosomal evolution in blind mole rats. The ancestral spalacine karyotype was thus presumably 2n = 38 and increased gradually in various lineages. It is difficult to decide, which of these hypotheses is correct. The presence of high diploid numbers (2n = 60 or 62) in species of the genus *Spalax* seems to support the fusion scenatio. The populations with 60 chromosomes are distributed in the marginal areas of the subfamily range, i.e. in south-eastern Europe and northern Africa. The fission hypothesis was also not supported in molecular phylogenies where the populations with lower chromosome numbers did not hold basal positions but rather appeared in internal branches of the resulting trees (Reyes et al. 2003, Hadid et al. 2012, Kandemir et al. 2012, Kryštufek et al. 2012). The role of other types of re-arrangements is usually not appreciated. Nevo et al. (2000) interpreted pericentric inversions as local chromosomal adaptations within species rather than iniciators of speciation.

It is difficult to find any universal chromosomal differences that can be used to distinguish the currently recognized taxa of blind mole rats. In the karyotype of the species classified in the genus *Spalax*, almost all autosomal pairs are usually distinguished as bi-armed (with the exception of *S. microphthalmus*), whereas complements of the populations with 60 chromosomes classified within *Nannospalax* include mostly acrocentric autosomes. Similarly, little chromosomal differentiation can be observed that could be applied to distinguish the *Nannospalax* species. The karyotype of most of populations of *N. leucodon* in south-eastern Europe includes two or three distinctly large subtelocentric autosomal pairs, with possible exceptions of the Varna, Bulgaricus and Srebarnensis races (Savić & Soldatović 1984). On the contrary, such marker chromosomes are lacking in most populations classified in *N. xanthodon* and *N. ehrenbergi*, except for two races from western Anatolia (Xanthodon and Anatolicus, Arslan et al. 2013), and possibly also from south-eastern Anatolia (race Şanlıurfa, Ivanitskaya et al. 1997). Certain differences in the distribution of NORs and C-bands were found between population of *N. xanthodon* and *N. ehrenbergi* from south-eastern Anatolia (Ivanitskaya et al. 1997, Arslan et al. 2015a). Examples of chromosomal divergence have been reported between intraspecific population groups. The populations of *N. ehrenbergi* from Turkey and other parts of the Middle East differ in the presence or absence of polymorphism in the 1st autosomal pair as well as in the character of the occurrence of telomeric C-bands and heterochromatic short arms (Ivanitskaya et al. 1997, Nevo et al. 2000). Nevertheless, consistent chromosomal differences are usually not apparent between the recognized taxa, in contrast to frequently distinct differentiation between the races.

The amazing variety of karyotypes within blind mole rats provokes the question of hybridization between individual chromosome forms and races. Surprisingly, hybrids have been found only occasionally and they are seemingly absent in large parts of the distribution range. No hybrids were detected in the Balkan populations and their absence was confirmed even in contact zones or rare areas of parapatric occurrence of various chromosome races (Savić & Soldatović 1984). Hybrids seem to be lacking or be extremely rare in Turkey (e.g. Nevo et al. 1995, Ivanitskaya et al. 1997, Sözen 2004, Sözen et al. 2006a, 2013) and the sole exception is the finding of three heterozygous individuals from central-eastern Anatolia (Coşkun et al. 2010b) with a presumably hybrid karyotype (2n = 49). The only geographic area, in which hybridization

between races has regularly been reported, is Israel (Wahrman et al. 1969a, b, Ivanitskaya et al. 2010). Only few studies have addressed the fitness of hybrids in experimental breeding colonies. Savić & Soldatović (1984) attempted experimental crossbreeding of various races but not even copulation occurred in some cases. This suggests a strong pre-copulatory barrier between populations with different karyotypes. Fitness of natural hybrids appeared lower than of their parents also in the study by Nevo & Bar-El (1976). Zuccotti et al. (1995) found impaired development during spermatogenesis in natural hybrids between Israeli races, but sperm production seemed not to be affected. Greenbaum et al. (1990) studied meiosis and synaptonemal complex in hybrids between Israeli races with respect to structural polymorphisms in the largest chromosomal pair. The involved region underwent adjustment resulting in a fully paired, mid-pachytene synaptonemal complex and the data suggested no reproductive detriment associated with chromosome 1 heterozygosity.

We should, thus, admit that our knowledge about the mechanisms of reproductive isolation produced by chromosomal changes is still quite limited in blind mole rats. There are only few indications of the existence of possible pre-copulatory mechanisms of isolation (Nevo & Bar-El 1976, Nevo & Heth 1976, Savić & Soldatović 1984).

Adaptive nature of chromosomal change

It is assumed that extensive re-arrangements of the karyotype promote accelerated divergent evolution and positively selected changes should accumulate in chromosomes that present fixed structural differences (Navarro & Barton 2003). Therefore, the role of chromosome change in adaptive speciation processes in the blind mole rats should be seriously considered. Nevo (1993) and Nevo et al. (1994b) proposed that chromosomal speciation and adaptive radiation of mole rats in Asia Minor and Israel is correlated with increased ecological stress. They assumed an evolutionary model of positive association of the diploid chromosome number and genetic diversity with aridity stress in blind mole rats. This is based on the assumption that Robertsonian fissions of metacentric chromosomes considerably increase haplotype diversity. This haplotype diversity may enhance population adaptation to climatic stress and ecological unpredictability in space and time. This hypothesis was extended to the entire subfamily in a conclusion that the trends of chromosome evolution in blind mole rats involve increase in the diploid number of chromosomes along gradients of increased aridity (e.g. Nevo et al. 2000). This indicates that evolution of blind mole rats might be determined by climate oscillations and other environmental (namely tectonic) changes in the past (Hadid et al. 2012, Németh et al. 2013a).

Nevo (2013) underlined that environmental stress played a major role in the evolution of blind mole rats, affecting their adaptive evolution and ecological speciation underground. Spending their entire life underground, the blind mole rats are safeguarded against aboveground climatic fluctuations and predators. However, they encounter multiple stresses in their underground burrows including darkness, energy demands, hypoxia, hypercapnia, food scarcity and pathogenicity. Consequently, adaptive genomic, proteomic and phenomic complexes have evolved to cope with these stresses (Fang et al. 2014). A possible case of incipient sympatric adaptive ecological speciation in *Spalax galili* (2n = 52) was reported by Hadid et al. (2013). The frequency of all major haplotype clusters was highly soil-based in populations studied and up to 40 % of the mtDNA diversity was edaphically dependent, suggesting constrained gene flow.

Taxonomic implications

Current taxonomic treatment of the subfamily Spalacinae seems to converge into recognition of two extant genera, *Spalax* and *Nannospalax* (Hadid et al. 2012, Chişamera et al. 2013). Traditionally, six or seven extant species have been recognized within *Spalax* (Musser & Carleton 2005, Korobchenko & Zagorodniuk 2009, Németh et al. 2013a) and three species within *Nannospalax* (Musser & Carleton 2005, Puzachenko 2006, Kryštufek & Vohralík 2009). Taxonomy of *Spalax* has been more stable in time and relatively few changes have been suggested. The status of populations from northern Caucasus is not clear (*S. microphthalmus* or *S. giganteus*; Dzuev & Shogenov 2003). Molecular and morphological findings indicated an independent status of two additional allopatric, possibly extinct or at least seriously endangered, species (*S. antiquus*, *S. istricus*) from Romania (Németh et al. 2013a). Numerous taxonomic and nomenclatural changes have been proposed within the subgenus *Nannospalax*. Savić & Soldatović (1984) attempted to propose a detailed taxonomic solution for the Balkan races and populations and recognized 13 species in south-eastern Europe (*Nannospalax montanoserbicus*, *N. syrmiensis*, *N. hercegovinensis*, *N. turcicus*,

N. bulgaricus, *N. hellenicus*, *N. makedonicus*, *N. hungaricus*, *N. leucodon*, *N. montanosyrmiensis*, *N. monticola*, *N. serbicus* and *N. rhodopiensis*). This approach was partly followed in some later papers (Hadid et al. 2012, Csorba et al. 2015). However, genetic divergences among the European cytotypes are low and two of these supposed species (*serbicus* and *makedonicus*) clustered together in a mitochondrial tree (Kryštufek et al. 2012). Formal nomenclatoric problems associated with the taxonomic treatment proposed by Savić & Soldatović (1984) were emphasized by Kryštufek (1997) as previously mentioned in brief.

Nevo et al. (1994b) emphasized the need of a substantial revision of the phylogeny and systematics of blind mole rats and suggested that about 50 biological species can be distinguished based on karyotype variation. Consequently, Nevo et al. (2001) described the Israeli chromosomal races as new species *Spalax galili*, *S. golani*, *S. carmeli* and *S. judaei*. The formal problem of this description is related to the nomenclatural fact, that the type locality of *N. ehrenbergi* is apparently situated inside the range of one of the new species (Musser & Carleton 2005). Furthermore, the monophyletic nature of these individual new species was not convincingly supported in molecular phylogenies (Reyes et al. 2003, Kandemir et al. 2012). Other putative species were proposed to occur in Egypt and Jordan (Nevo et al. 1991, 2000). Numerous names introduced in older papers are available in Anatolia. We should consider that the type localities of certain nominal taxa are the same or geographically very close (e.g. *xanthodon* and *anatolicus* in the İzmir Province or *nehringi* and *armeniacus* in the Kars Province). This complicates the nomenclatural solutions considerably.

Savić & Soldatović (1984) proposed the name *N. nehringi anatolicus* for populations with the low diploid number from regions along the Aegean coast in western Anatolia. Sözen & Kıvanç (1998b) recognized a population studied near Ulukışla in central Anatolia as *N. leucodon cilicicus*. *N. leucodon nehringi*, *N. l. armeniacus* and *N. l. intermedius* were considered as possible names for populations in eastern Anatolia. Coşkun (1996a, b) described two new subspecies (*N. nehringi tuncelicus* and *N. n. nevoi*) from eastern and south-eastern Anatolia, *N. tuncelicus* was treated as a separate species in subsequent papers, along with another new species, *N. munzuri* (Coşkun 2004a). Coşkun et al. (2010a) further proposed that *N. ceyhanus* is an available name for some populations of *N. ehrenbergi* from south-eastern Anatolia (the area east of Adana). Hadid et al. (2012) distinguished the clade *vasvarii* including populations from the Central Anatolian Plateau characterized by the high diploid number of chromosomes (2n = 60-62). This "*vasvarii*" lineage was found to be basal to the "*leucodon*" and "*xanthodon*" lineages, distributed in Europe and the rest of Anatolia, respectively. Finally, Kankılıç & Gürpınar (2014) proposed that four mole rat species live in Anatolia: *N. ehrenbergi* in southeastern Anatolia, *N. nehringi* in eastern Anatolia, *N. xanthodon* in western Anatolia and *N. labaumei* in central Anatolia. Kankılıç et al. (2014) suggested that in addition to these species, some of the other *N. xanthodon* chromosomal races (2n = 36, 38, 40, 52) should be treated as distinct species.

The taxonomic treatment of blind mole rats resulting from all these studies is not providing an easy survey. It is desirable that reliable estimates of genetic distances and gene flow between populations and races are available. The taxonomic and nomenclatural issues should be concluded only after obtaining such data. The available mitochondrial tree (Kryštufek et al. 2012) provides a fairly good basis for species delimitation based on genetic distances. It is evident that there are several species within each nominal taxon distributed in Asia (*xanthodon* and *ehrenbergi*). Populations classified as *leucodon* in south-eastern Europe are, however, genetically rather uniform.

Phylogenetic context

In spite of extensive efforts, a robust resolution of phylogenetic relationships among extant populations, races and species of blind mole rats is still lacking. Nevertheless, certain important findings emerge from the available analyses. The monophyletic character of two major lineages of extant blind mole rats, the genera *Spalax* and *Nannospalax* seem to be confirmed (Topachevskii 1969, Hadid et al. 2012, Chişamera et al. 2014). Within *Nannospalax*, races from south-eastern Europe (the *leucodon* clade) appear monophyletic and distinct from races distributed in Asia. The situation is more complicated in the Asian continent. The existence of two major clades (*xanthodon* and *ehrenbergi*) seems realistic. However, the geographic borders of their ranges and reliable criteria for distinguishing them either morphologically or karyologically should be further elaborated. Both lineages are probably parapatric in south-eastern Anatolia, with *xanthodon* populations occcuring in highlands and *ehrenbergi* populations in lowlands. Hadid et al. (2012) estimated that the altitude of 1500 m separates the populations of both clades.

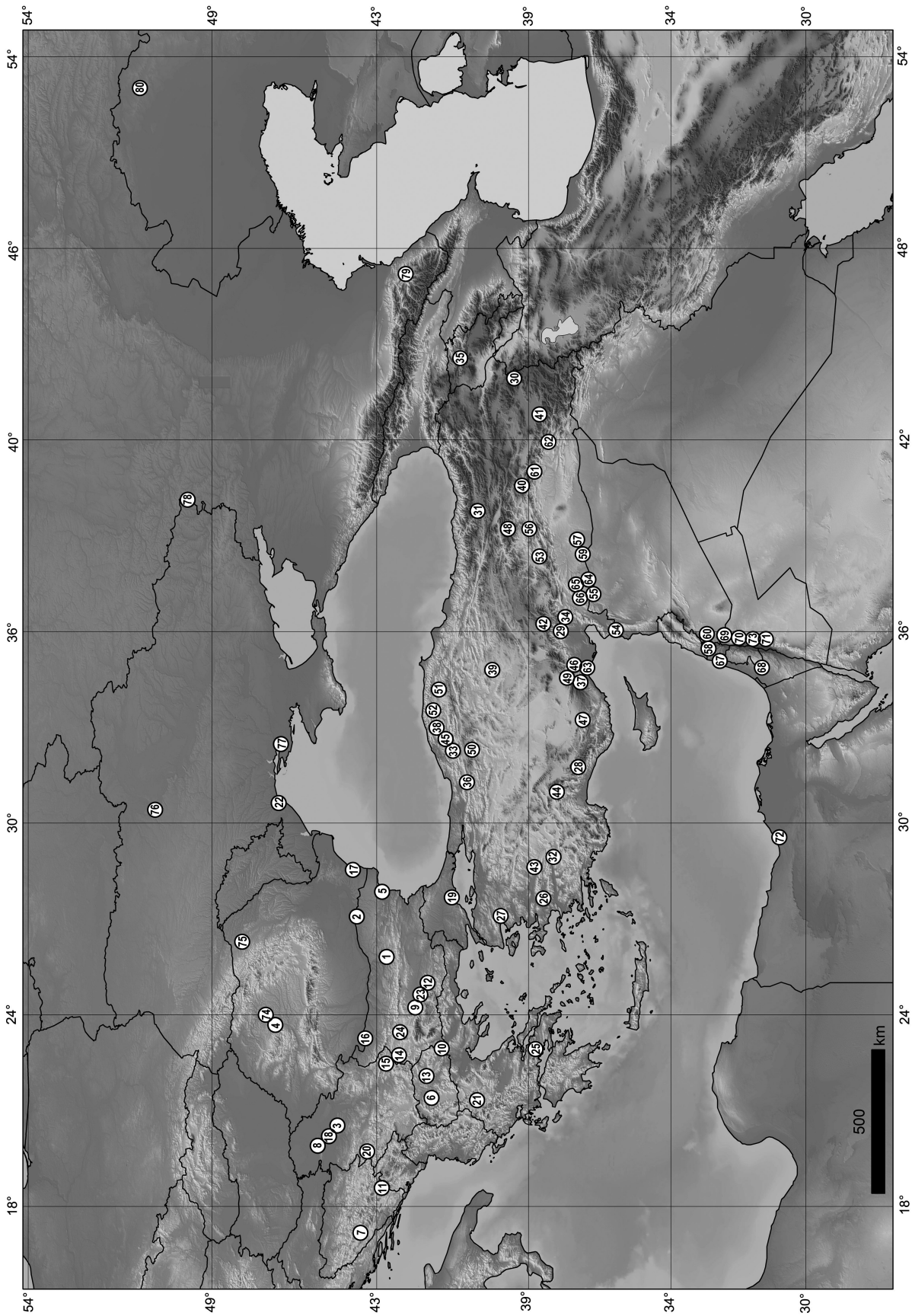

Fig. 32. Distribution map of the description localities of individual chromosomal races and the species of blind mole rats. See text for numbering.

Table 1. Distribution of the chromosome diploid numbers (2n) in blind mole rats. +, the recorded diploid number.

2n	36	38	40	42	44	46	48	50	52	54	56	58	60	62
N. leucodon						+	+	+	+	+	+	+		
N. xanthodon	+	+	+			+	+	+	+	+	+	+	+	+
N. ehrenbergi							+		+	+	+	+	+	+
Spalax													+	+
Spalacinae	+	+	+			+	+	+	+	+	+	+	+	+

Table 2. Distribution of the numbers of chromosomal arms in the female complement (NF) in blind mole rats. +, the recorded number.

NF	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98	120	124
N. leucodon								+	+	+	+	+	+	+	+	+	+	+	+		
N. xanthodon				+	+	+	+	+	+	+	+	+			+						
N. ehrenbergi	+		+	+		+	+	+	+	+	+		+								
Spalax																				+	+
Spalacinae	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

A separate lineage of populations from central Anatolia, possessing a high number of chromosomes, appeared in several molecular phylogenies (Hadid et al. 2012, Kankılıç & Gürpınar 2014). Other separate species will probably be differentiated within the putative major clades of *Nannospalax*, however, some results showed that associations between genetic and chromosomal variation are not widespread and common and, therefore refute the generalization of a "cytotype-equals-species" approach (Kryštufek et al. 2012).

Adaptive significance of chromosomal variation in blind mole rats remains a challenging question. It is quite probable that the past phylogenetic history of this group was deeply influenced by environmental conditions (Nevo et al. 2000, Hadid et al. 2012, Németh et al. 2013a) and understanding of the adaptive nature of chromosomal evolution in blind mole rats can help to comprehend the past events better.

Conclusions

The seven extant species of Spalax revealed rather uniform karyotype. Within the traditional species classified in the *Nannospalax* genus, 25 races can be distinguished within *N. leucodon*, 28 races within *N. xanthodon* and 20 races within *N. ehrenbergi*. The present review describes the existence of 73 distinct chromosome races recorded in blind mole rats. In total, 12 distinct diploid numbers of chromosomes were found (2n = 36-62) and variation in chromosome morphologies was observed between populations with the same diploid number of chromosomes (NF = 62-124). A distribution map of the description localities of individual chromosomal races and the species of blind mole rats is shown in Fig. 32. The extent of variation in the diploid number and the number of chromosomal arms in individual major lineages is shown in Tables 1 and 2. The general scarcity of hybrids between individual races indicates that some of the races represent actually separate biological species. Further research aimed to reinforce phylogenetic resolution as well as knowledge of gene flow between populations is needed to achieve definitive nomenclatural conclusions about the taxonomic status of extant populations.

Nannospalax leucodon

1. Bulgaricus 2n = 46, NFa = 72, NF = 76
2. Srebarnensis 2n = 48, NFa = 74, NF = 78
3. Hungaricus 2n = 48, NFa = 80, NF = 84.
4. Transsylvanicus 2n = 50, NFa = 80, NF = 84
5. Varna 2n = 52, NFa = 76, NF = 80
6. Makedonicus 2n = 52, NFa = 82, NF = 86
7. Monticola 2n = 54, NFa = 80, NF = 84
8. Montanosyrmiensis 2n = 54, NFa = 82, NF = 86
9. Pazardzhik 2n = 54, NFa = 82, NF = 86
10. Strumiciensis 2n = 54, NFa = 84, NF = 88
11. Hercegovinensis 2n = 54, NFa = 86, NF = 90
12. Rhodopiensis 2n = 54, NFa = 88, NF = 92
13. Ovchepolensis 2n = 54, NFa = 90, NF = 94
14. Tranensis 2n = 54, NFa = 92, NF = 96
15. Serbicus 2n = 54, NFa = 94, NF = 98
16. Lom 2n = 54, NFa = 94, NF = 98
17. Dobrudzha 2n = 54-56, NFa = 74-80, NF = 78-84
18. Syrmiensis 2n = 54-56, NFa = 86-90, NF = 90-94
19. Turcicus 2n = 56, NFa = 72-74, NF = 76-78
20. Montanoserbicus 2n = 56, NFa = 76-78, NF = 80-82

21. Epiroticus 2n = 56, NFa = 80, NF = 84
22. Leucodon 2n = 56, NFa = 80, NF = 84
23. Thracius 2n = 56, NFa = 84, NF = 88
24. Sofiensis 2n = 56, NFa = 86, NF = 90
25. Hellenicus 2n = 58, NFa = 84, NF = 88

Nannospalax xanthodon
26. Xanthodon 2n = 36, NFa = 66, NF = 70
27. Anatolicus 2n = 38, NFa = 70, NF = 74
28. Beyşehir 2n = 40, NFa = 68, NF = 72
29. Yirce 2n = 46, NFa = 66, NF = 70
30. Van 2n = 48, NFa = 64-68, NF = 68-72
31. Gümüşhane 2n = 48, NFa = 66-67, NF = 70-71
32. Pamukören 2n = 50, NFa = 68-70, NF = 72-74
33. Keltepe 2n = 50, NFa = 66, NF = 70
34. Andırın 2n = 50, NFa = 66-67, NF = 70-71
35. Nehringi 2n = 50, NFa = 66-68, NF = 70-72
36. Abant 2n = 52, NFa = 66-68, NF = 70-72
37. Sebil 2n = 52, NFa = 68, NF = 72
38. Eflani 2n = 54, NFa = 68-70, NF = 72-74
39. Yozgat 2n = 54, NFa = 70-71, NF = 74-75
40. Tuncelicus 2n = 54, NFa = 70, NF = 74
41. Bitlis 2n = 54, NFa = 70, NF = 74
42. Adana 2n = 54, NFa = 70, NF = 74
43. Kula 2n = 56, NFa = 68-70, NF = 72-74
44. Isparta 2n = 56, NFa = 68, NF = 72
45. Safranbolu 2n = 56, NFa = 68-70, NF = 72-74
46. Gülek 2n = 56, NFa = 66-68, NF = 70-72
47. Karaman 2n = 56, NFa = 66, NF = 70
48. Munzurii 2n = 58, NFa = 62-64, NF = 66-68
49. Cilicicus 2n = 58, NFa = 68-71, NF = 72-75
50. Sarıkavak 2n = 58, NFa = 74, NF = 78
51. Taşköprü 2n = 58, NFa = 70-71, NF = 74-75
52. Kastamonu 2n = 60, NFa = 70-74-75, NF = 74-78-79
53. Vasvarii 2n = 60, NFa = 68-70-73-74-75-78-79-80, NF = 72-74-78-79-80-82-84

Nannospalax ehrenbergi
54. Yayladağ 2n = 48, NFa = 69-70, NF = 73-74
55. Intermedius 2n = 52, NFa = 70, NF = 74
56. Elazığ 2n = 52, NFa = 72, NF = 76
57. Şanlıurfa 2n = 52, NFa = 76-78, NF = 80-82
58. Galili 2n = 52, NFa = 80, NF = 84
59. Suruç 2n = 54, NFa = 72, NF = 76
60. Golani 2n = 54, NFa = 78, NF = 82
61. Kulp 2n = 56, NFa = 58, NF = 62
62. Siirt 2n = 56, NFa = 62, NF = 66
63. Ceyhanus 2n = 56, NFa = 64-68, NF = 68-72
64. Gaziantep A 2n = 56, NFa = 78, NF = 82
65. Gaziantep B 2n = 56, NFa = 86, NF = 90
66. Gaziantep C 2n = 58, NFa = 78, NF = 82
67. Carmeli 2n = 58, NFa = 72, NF = 76
68. Judaei 2n = 60, NFa = 72, NF = 76
69. Irbid 2n = 60, NFa = 74, NF = 78
70. Naur 2n = 60, NFa = 72, NF = 76
71. Ariha 2n = 60, NFa = 70, NF = 74
72. Madaba 2n = 60 or 62, NFa = 68 or 70 NF = 72 or 74
73. Aegyptiacus 2n = 60, NFa = 72, NF = 76

Spalax
74. *Spalax antiquus* 2n = 62, NFa = 120, NF = 124
75. *S. graecus* 2n = 62, NFa = 120, NF = 124
76. *S. zemni* 2n = 62, NFa = 120, NF = 124
77. *S. arenarius* 2n = 62, NFa = 120, NF = 124
78. *S. microphthalmus* 2n = 60, NFa = 116, NF = 120
79. *S. giganteus* 2n = 62, NFa = 120, NF = 124
80. *S. uralensis* 2n = 62, NFa = 120, NF = 124

The fascinating pattern of chromosomal variation found in the blind mole rats provides a scholarly model for various studies. Chromosomal evolution in blind mole rats is related to their distribution pattern, population structure and reproductive strategy, as well as to external factors from their underground environment, including climatic and tectonic alterations.

Threats, resulting from agricultural development, urbanization, habitat degradation and shrinking of the distribution area of blind mole rats are of extreme importance. Population decline is apparent, particularly in the European part of the range and some populations or races probably became extinct, therefore conservation action is highly desirable (Csorba et al. 2015). The recently emerging knowledge about various unique features of blind mole rats is another reason for continuing scientific investigations of this remarkable group.

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