A GENETIC INVESTIGATION ON THE EVOLUTION AND TAXONOMY OF THE
GENUS *NANNOSPALAX* IN TURKEY

by

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BS. in Biology, Balıkesir University, 2008

Submitted to the Institute of Environmental Sciences in partial fulfillment of

the requirements for the degree of

Master of Science

in

Environmental Sciences

Boğaziçi University

2014

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DATE OF APPROVAL   28/01/2014

ACKNOWLEDGEMENTS

Foremost, I would like to express my deepest gratitude to my supervisor Assoc. Prof. Raşit Bilgin for his priceless guidance, patience and encouragement. I could not have imagined having a better supervisor and mentor for my study.

I would also like to offer my sincere appreciation to Teoman and Tolga Kankılıç for providing the samples of the present thesis and for the valuable constructive criticism.

Besides, I would like to thank the rest of my thesis comittee: Assist. Prof. Ulaş Tezel and Assist. Prof. Baki Yokeş for their useful comments, remarks and engagement.

My special thanks goes to my friends Evrim Kalkan and Öncü Maracı for teaching me everything about laboratory work and for recueing me whenever I got into trouble and for all the fun we have had in the last three years. I also thank Emrah Çoraman for technical help on my thesis, and Ayşe Mergenci for reviewing earlier drafts.

I am deeply indepted to my friends Gökhan Dursun, Mustafa Tezcan and Zerrin Tezel for listening and solving my issues and supporting me spiritually.

I also thank my family: my mother Hasibe Karaman, my father Olgun Karaman and my sister Şeyma Nur Karaman for their support, both financially and emotionally during my thesis.

Finally, and most importantly, my special words of thanks must go to my husband Mehmet Arslan for standing by my side. His support, understanding and love always give me strength.

A GENETIC INVESTIGATION ON THE EVOLUTION AND TAXONOMY OF THE GENUS *NANNOSPALAX* IN TURKEY

Currently there is no consensus over the details of evolutionary history and taxonomical classification of the genus *Nannospalax* in Turkey. This includes the geographical distribution of the different cytotypes, their relationships to one another, and the number of recognized species. In this thesis, in order to try to answer some of these questions, a 896 bp segment of the mitochondrial D-loop region of 120 samples belonging to *N. xanthodon*, *N. leucodon* and *N. Ehrenbergi* were amplified by the PCR method and sequenced. The relationships between species and between chromosomal forms of these species were investigated through various phylogenetic analyses. The results showed that *N. leucodon* and *N. ehrenbergi* were distinct species living in Thrace and Southeast Anatolia, repectively. Moreover, the idea that only *N. xanthodon* was distributed in the rest of Anatolia was not supported. Nine cytotpes were seen to cluster into three main groups, suggesting the presence of three different species in Turkey. *N. labaumei* includes 2n= 52S, 56W, 58 and 60 cytotpes, *N. xanthodon* contains 2n=36, 38, 40, and 52N cytotypes (western populations) and *N. nehringi* has 2n=50E, 54C and 56S cytotypes.

TÜRKİYE'Kİ *NANNOSPALAX* CİNSİNİN EVRİM VE TAKSONOMİSİ ÜZERİNE BİR GENETİK ARAŞTIRMA

Günümüzde Türkiye'de *Nannospalax* cinsinin evrimsel tarihi ve taksonomik sınıflandırılmasının detayları üzerine bir görüş birliği yoktur. Bunlar farklı sitotiplerin coğrafik dağılımını, sitotiplerin birbirleriyle ilişkilerini ve kabul edilen türlerin sayılarını içerir. Bu tez çalışmasında bu sorulardan bazılarına cevap bulmak için *N. xanthodon*, *N, leucodon* ve *N. ehrenbergi* türlerine ait 120 örneğin 896 baz çiflik mitokondrial D-loop bölgeleri PCR metodu ile çoğaltılmış ve dizilenmiştir. Bu türlerin ve türlerin kromozomal formlarının arasındaki ilişki çeşitli filogenetik analizlerle araştırılmıştır. Sonuçta, *N, leucodon* ve *N. ehrenbergi* türlerinin sırasıyla Trakya ve Güneydoğu Anadolu bölgelerinde yaşayan ayrı türler olduğu görülmüştür. Ayrıca, Anadolunun geri kalan kısmında sadece *N. xanthodon* türünün yayılış gösterdiği görüşü desteklenmemiştir. Dokuz sitotip, Türkiye'de üç farklı türün varlığını düşündüren üç ana grup oluşturmuştur. Bunlardan *N. labaumei*, 2n= 52S, 56W, 58 ve 60 sitotiplerini, *N.xanthodon*, 2n=36, 38, 40, ve 52N sitotiplerini ve *N. nehringi*, 2n=50E, 54C ve 56S sitotiplerini içerir.

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LIST OF SYMBOLS/ABBREVIATIONS

Symbol	Explanation
%	Percent
°C	Degree Centigrade
μl	Microliter
π	Nucleotide Diversity

Abbreviation	Explanation
2n	Diploid Number of Chromosomes
A	Adenin
bp	Base Pair
C	Cytosine
cyt *b*	Cytochrome *b*
D-loop	Displacement Loop
DNA	Deoxyribonucleic Acid
DNTP	Deoxyribonucleotide Triphosphate
Et-Br	Ethidium Bromide
Hap	Haplotype
Hp	Haptoglobin gene
Hd	Haplotype Diversity
Kb	Kilo-Base Pair
ML	Maximum Likelihood
mtDNA	Mitochondrial Deoxyribonucleic Acid
mya	Million Years Ago
NCBI	National Center for Biotechnology Information
NF	Number of Chromosomal Arms
NJ	Neighbour Joining
PCR	Polymerase Chain Reaction
RAPD	Random Amplified Polymorphic DNA
RFLP	Restriction Fragment Length Polymorphism
rRNA	Ribosomal Ribonucleic Acid

TAE   Tris-Acetate-EDTA

tRNA   Transfer RNA

TSS   Turkish Straits System

1. INTRODUCTION

Rodentia is the largest group among mammalian orders, including 29 families, 426 genera and more than 2800 species (Nowak, 1991; Wilson and Reeder, 2005). Mole rats were previously considered to be in the family Muridae (Ronald and John, 1983; Corbet and Hill, 1991). Today, however, they are included in the family Spalacidae, which was originally identified by Gray (1821) (Wilson and Reeder, 2005).

Considering the details of their basic biology, mole rats or the East-Mediterranean rodents, are adapted to live in underground habitats. They eat roots, rhizomes and onions. Morphologically, they have cylindrical bodies, short legs and no tail. Body sizes vary depending on the climate, soil structure and nutrient richness of area. Their average weight is about 100-570 grams. They are separated from other rodents because of the absence of eyes and atrophied external ears. Their feet have not been adapted to dig. They dig the soil with powerful front teeth and push it with their heads, which is why their necks are very muscular (Figure 1.1).

Figure 1.1. General appearance of *Nannospalax nehringi* by Mustafa Sözen. (http://www.treknature.com/gallery/photo143119.htm)

Spalacidae family probably emerged in or near Anatolia during the late Oligocene-early Miocene about 20 million years ago and expanded its distribution area up to Balkans,

the Russian Steppes, Central Asia and Northern Africa by showing adaptations to live underground (Savic ve Nevo, 1990; Wilson and Reeder, 2005). Wahrman et al. (1969) asserted that the first ancestral mole rat had appeared in the region of Southeastern Europe or somewhere in Anatolia. The oldest member of Spalacidae; *Heramys eviensis,* thought to have lived in the Miocene Period, was found in Greece (Hofmeijer and De Bruijin, 1985). Yüksel and Gülkaç (1990), on the other hand, stated that European mole rat species originated in Asia. They suggest that mole rats passed into the Balkan Peninsula before early Pleistocene and remained isolated as a result of the formation of the Bosphorus and Dardanelles straits. Today mole rats have a wide Palearctic distribution spanning Southeastern Europe, Anatolia, the Caucasus, Transcaucasia, the Ukraine, Armenia, Syria, Palestine, Israel, Iraq, Jordan and Northern Africa (Nehring; 1898a; 1898b; Miller, 1912; Ognev, 1947; Darlington, 1957; Ondrias, 1966; Peshev and Mitev, 1975; Corbet, 1978; Corbet and Hill, 1991; Pantalayev, 1998; Wilson and Reeder 2005).

1.1. Taxonomy of the Genus *Nannospalax* (Palmer, 1903)

Detailed taxonomic, phylogenetic, zoogeographical and morphometric studies on Spalacidae familia were first undertaken by Mehely (1909). Mehely (1909) identified three subgenera (*Mesospalax, Macrospalax and Microspalax*) under the genus *Spalax*. Ellerman (1940) changed this classification and separated *Spalax* into *Spalax*, *Mesospalax* and *Nannospalax* subgenera. However, Ognev (1947) stated that Spalacidae only comprised the genus *Spalax* with two subgenera *Spalax* and *Microspalax.*

Ellerman and Morrison-Scott (1951), on the other hand, allocated *Spalax* genus into three species *Spalax microphthalmus*, *Spalax leucodon* and *Spalax ehrenbergi.* Also, they pointed out that *Spalax leucodon* and *Spalax ehrenbergi* were found in Turkey. Topachevskii (1969) divided family Spalacidae into two subfamilies: Prospalacinae (Extinct) and Spalacinae and divided Spalacinae into two genera *Microspalax* and *Spalax.* Besides, Topachevskii (1969) introduced three species; *M. nehringi* (Satunin, 1898)*, M. leucodon* (Nordmann, 1840) and *M. ehrenbergi* (Nehring, 1898) in the genus *Microspalax* and reported that *Microspalax nehringi* (in Anatolia), *Micropalax leucodon* (in Thrace) and *Micropalax ehrenbergi* (in Southeastern Anatolia) were found in Turkey. Topachevskii (1969) also synonimized four species (*S. ehrenbergi*, *S. kirgisorum*, S. *intermedius* and *S.*

aegyptiacus) identified by Nehring (1898) into *S. ehrenbergi*. Thus, distribution area of *S. ehrenbergi* was modified to include Egypt, Syria, Lebanon, Jordan and southeast of Turkey. Corbet (1978) stated that there was only one genus (*Spalax*) and three species; *Spalax microphtalmus*, *Spalax giganteus* and *Spalax leucodon*, and only *Spalax leucodon* was found in Turkey, and other names recorded in Turkey were synonyms.

Gromov and Baranova (1981) and Pantalayev (1998) classified two genera (*Spalax* and *Nannospalax*). They included *N. leucodon*, *N. nehringi, N. ehrenbergi* in the genus *Nannospalax,* and *S.arenarius, S. giganteus, S. graecus, S. microphthalmus, S. polonicus* in the genus *Spalax*.

Currently, the majority of researchers working on mole rats accept Topachevski (1969) 's classification. Since Gromov and Baranova (1981) used *Nannospalax* instead of *Microspalax* because of homonym, today Turkey's mole rats are classified under the genus *Nannospalax* (Palmer, 1903). The most comprehensive morphological study on *Nannospalax* genus in Turkey was made by Kıvanç (1988). He collected 1100 samples from different regions of Turkey. After evaluating the individuals morphologically, he indicated that *N. leucodon* and *N. ehrenbergi*, and the subspecies *N. leucodon nehringi*, *N. leucodon armeniacus*, *N. leucodon cilicicus*, *N. leucodon anatolicus*, *N. leucodon turcicus*, *N. ehrenbergi intermedius* and *N. ehrenbergi kirgisorum* belonging to these two species are distributed throughout Turkey (Figure 1.2).
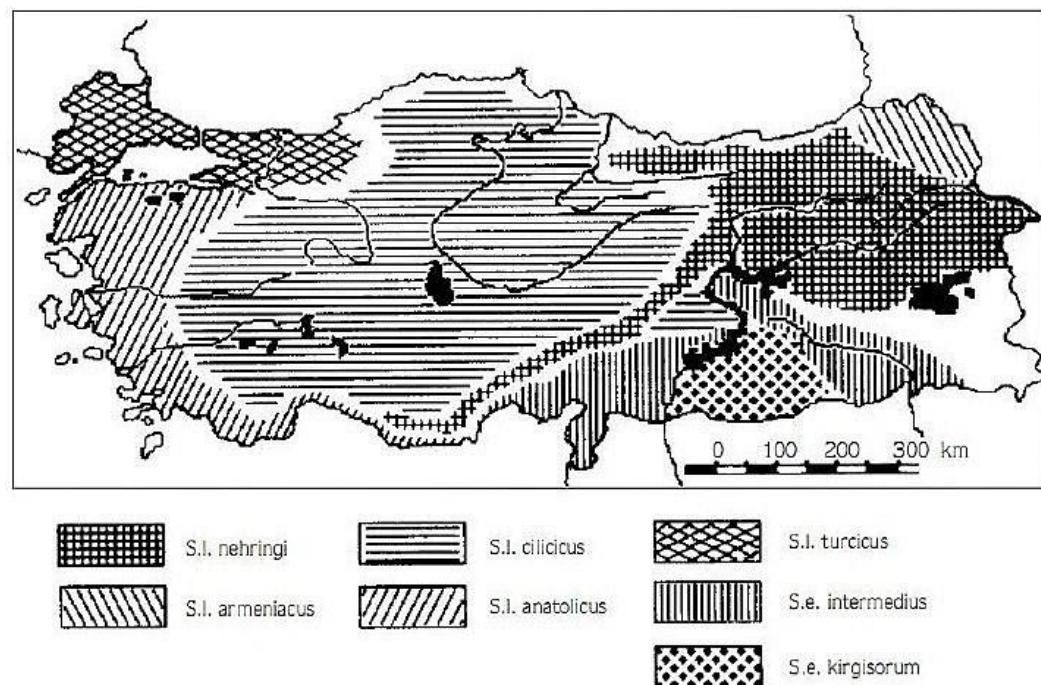
Figure 1.2. Map showing the species and subspecies of *Spalax* in Turkey (Kıvanç, 1988).

To date, it has been accepted by many researchers that there are two species in Turkey; *N. ehrenbergi* in Southeastern Anatolia and *N. leucodon* in the rest of Turkey. However, in other studies three species have been recognized. *N. ehrenbergi, N. leucodon* and *N. nehringi* have existed in Southeastern Anatolia, in Thrace and in other parts of Anatolia, respectively (Wilson and Reeder, 2005). On the other hand, Krystufek and Vohralik (2009) reported that *N. nehringi* (Satunin, 1898) from Kars was the synonym of *N. xanthodon* (Nordmann, 1840) identified in Izmir. Consequently they concluded that only *N. ehrenbergi* and *N. xanthodon* to be present in Anatolia.

The studies above are usually related to morphological characteristics and their results show how difficult taxonomic evaluation of the *Nannospalax* genus is. Karyological studies that have gained momentum in recent years brought a different perspective to the taxonomy of *Nannospalax* in Turkey and directed the attention of taxonomists to differences of populations within subspecies.

1.2. Karyological Studies on *Nannospalax* Genus in Turkey

Karyological and molecular studies on this genus have been steadily increasing in Turkey and other countries in the last decade. In these studies, numerous karyotype forms have been identified with regards to the distribution of the genus. These karyological forms are defined by the number of diploid chromosomes (2n) and the differences in chromosome arm numbers (NF).

Taking into consideration the karyological studies made so far on the *Nannospalax* genus, 11 (2n: 36, 38, 40, 48, 50, 52, 54, 56, 58, 60, 62), five (2n= 48, 52, 54, 56, 58), and one (2n=56) karyotype forms of *N. xanthodon, N. ehrenbergi*, and *N.leucodon*, have been detected in Turkey, respectively. Moreover, the number of chromosome arms of these species ranges from 66 to 90 (Soldatovic and Savic, 1978; Savic and Soldatovic, 1979; Yüksel, 1984; Gülkaç and Yüksel, 1989; Butler et al., 1993; Nevo et al., 1994, 1995; Coşkun, 1996a, 1996b, 1999, 2003; Ivanitskaya et al., 1997; Sözen and Kıvanç, 1998a, 1998b; Sözen et al., 1999, 2000a,b, 2006a,b; Yüksel and Gülkaç, 2001; Tez et al., 2001, 2002; Sözen, 2004). The most widespread one among chromosomal forms of *N. leucodon* is 2n=60 which has eight different NF values (NF: 72, 74, 76, 77, 78, 80, 82, 84) (Kankılıç et al., 2005 and Kankılıç et al., 2009).

Until now, two opinions were put forward about the most ancestral chromosomal forms. Nevo et al. (1994) suggested that 2n=38 karyotype is the ancestral form and other karyotypes have emerged as a result of Robertsonian fissions occuring in metacentric chromosomes. However, the second view accepts that showing wider distribution, the ancestral karyotype might be 2n=60. Other karyotypes have been formed from 2n=60 by chromosomal rearrangements, especially by Robertsonian fusion and pericentric inversion (Ivanitskaya et al., 1997; Ivanitskaya et al., 2008; Matur et al., 2011).

Nevo et al. (1995) emphasized that Anatolia mole rats having different diploid chromosome numbers should qualify them as a separate species because of their different allozyme patterns. If this view is accepted, Turkey would have almost 20 distinct species. However, Krystufek and Vohralik (2009) stated that there were only three species and refute Nevo (1995)'s hypothesis. Kankılıç et al. (2014) also did not support the idea that

each chromosomal form should be regarded as separate biological species. However, they emphasized that some cytotypes (2n = 36, 38, 40, 50, 52) of *N. xanthodon* had genetic and morphological differences large enough to be treated a separate species and Anatolia populations consisting of 2n = 60, 2n = 58 and 2n = 56 chromosomal forms were not different from each other karyologically. They determined five allopatric species as *N. leucodon* in Thrace, *N. ehrenbergi* in Southeastern Anatolia, *N. nehringi* (2n=50) in Eastern Anatolia, *N. xanthodon* (2n=36, 38, 40, 52) in Western Anatolia and *N. labaumei* in Central Anatolia (2n=56, 58, 60).

1.3. Molecular Studies on the Genus *Nannospalax* in Turkey

After the 1950s, with the emergence of phylogenetic systematics methods, molecular characteristics of organisms started to be investigated using allozyme, mitochondrial DNA (mtDNA), Ribosomal ribonucleic acid (rRNA) (12S and 16S), and nuclear DNA, random amplification of polymorphic DNA (RAPD) analyses, besides morphological, karyological, biometric features. The results obtained with the implementation of these methods help support morphological studies and reveal genetic differences between sibling species (Ben-Shlomo et al., 1996; Nevo et al., 1999; Nevo et al., 2003; Reyes et al., 2003).

The initial molecular DNA studies on the genus *Nannospalax* started in Israel in 1989, with DNA-DNA hybridization studies among chromosomal forms of *N. ehrenbergi* species (Catzeflis et al., 1989). These were followed by Haptoglobin gene (Hp) (Nevo et al., 1989) and Aldolase gene (A and B genes) (Nevo et al., 1990) DNA polymorphism studies in Israel. In these two studies, genetic variation was explored by cutting DNA with different restriction enzymes (RFLP) and significant levels of variation were detected. Subsequently, by using the polymerase chain reaction (PCR), restriction fragment length polymorphism (RFLP), RAPD (random amplification of polymorphic DNA) and DNA sequencing analyzes were carried out. (Nevo and Beiles, 1992; Ben-Shlomo et al., 1996; Nevo et al., 1993; Nevo et al., 1999; Reyes et al., 2003). Nevo et al. (2001) evaluated the data obtained by the methods mentioned above as a whole and identified four karyotypic forms of *N. ehrenbergi* in Israel as four different species: karyotypes of *S. galili*, *S. golani*, *S. carmeli* and *S. judaei* were accepted as 2n=52, 54, 58 and 60, respectively. According to these studies, the oldest species was *S. golani*, which branched off approximately 1.6 ±

0.30 mya. *S. golani* and *S. galili* were the first differentiated species in the superspecies category. *S. judaei* and *S. carmeli* splitted approximately 0.2 ± 0.04 mya.

The first allozyme study on *Nannospalax* in Turkey was carried out by Nevo et al. (1994). Researchers collected 14 samples (three chromosomal forms) from four locations where *N. ehrenbergi* was found, and 55 samples (six chromosomal forms) from 20 locations where *N. leucodon* was found. Subsequently, they investigated allozyme diversity of these samples by examining them electrophoretically. The researchers claimed that speciation and adaptation were positively associated with drought stress and climatic changes. It was emphasized that 2n value and heterozygosity tend to increase towards the Central Anatolian plateau which is ecologically harsh and dry, climatically variable and geologically young.

Suzuki et al. (1996) performed another study on genetic differences of mole rats. In the study, three chromosomal forms (2n=38, 54, 62) of superspecies *N. leucodon* and two chromosomal forms (2n=52 and 58) of *N. ehrenbergi* from Turkey, one chromosomal form (2n=54) from Israel, and one chromosomal form (2n=60) from Egypt for *N. ehrenbergi* were examined. Using RFLP analysis sample DNA were cut with 10 different restriction enzymes, and variation of ribosomal DNA and mitochondrial DNA was analyzed. As a result, differences between *N. leucodon* and *N. ehrenbergi* were seen to be quite high. In addition, substantial intra-species differences between different chromosomal forms were observed. The maximum levels of genetic polymorphism were observed in the *N. leucodon* superspecies.

The first study of mtDNA sequence analysis on *Nannospalax* in Turkey was made by Arslan et al. (2010). They used cytochrome b (*cyt b*) gene sequences of 13 mole rats belonging to *N. xanthodon* from Konya province. Three distinct cytotypes (2n=40, 58 and 60) were compared with each other. In the end, it was suggested that mitochondrial differences were very high among cytotypes and they were different allopatric species. Moreover, they concluded that the cytotype having smallest chromosomal number (2n=40) had evolved most recently. As for the 2n=60 cytotype, it was considered to be the ancestral form.

Kandemir et al. (2012) studied three species (*N. xanthodon, N. leucodon and N. ehrenbergi*) from western Turkey. They used *cyt b* sequences, 402 bp long, of nine cytotypes. Based on the phylogenetic analyses, *N. xanthodon* and *N. leucodon* were found as monophyletic species; however, previously defined *N. galili*, *N. golani*, *N. carmeli* and *N. judaei* species in Israel (Nevo et al., 2001), and *N. ehrenbergi* were observed to be paraphyletic. It was found that cytotypes with low chromosome numbers were separated from higher chromosomal forms as a monophyletic group. They suggested that more detailed investigations were required to conclude if cytotypes of *N. xanthodon* and *N. ehrenbergi* belong to different species.

Krystufek et al. (2012) studied the evolutionary history of the genus *Nannospalax* by using *cyt b* sequences from different 34 localities including Turkey, Israel, Egypt and Bosnia and Herzegovina. Although cytotypes of *Nannospalax* which are difficult to distinguish morphologically are known to be allopatric, their taxonomy is not unequivocal and a clear conclusion could not be reached. As a result of the analyses two different groups were specified as subgenera *Nannospalax* and *Mesospalax*. In this study the relationships within *Mesospalax* were unresolved. It was stated that among these three morphological groups the genetic diversity was distributed from highest to lowest in *N. leucodon*, *N. ehrenbergi* and *N. xanthodon*. The researchers also did not support Nevo et al.'s (2001) idea that every chromosomal form of mole rats is a distinct biological species.

In another study, Hadid et al. (2012) studied ~4 kb of mtDNA sequences of 41 samples of family Spalacidae from eastern Mediterranean steppes. They examined the harmony between tectonic history and paleoclimate. They concluded that the formation of the marine barrier between Anatolia and the Balkans, Turkish Straits System (TSS) caused the separation of the branch *Nannospalax* from branch *Spalax*. Furthermore, during formation of the Taurus Mountains, Anatolian high plateaus and mountains got uplifted as a result of tectonic movements and this might have caused split of *N. ehrenbergi* and *N. vasvarii*. It was expressed that *Nannospalax* genus was more dominant than *Spalax* in Turkey, and that *Nannospalax* comprised four species (*N. ehrenbergi*, *N. vasvarii*, *N leucodon* and *N. xanthodon*). rRNA and mtDNA analyses in the study showed that *N. ehrenbergi* was basal to the *N. leucodon* clade, and the split took place in the late Miocene to early-Pliocene era. *N. ehrenbergi* and *N. leucodon* were thought to spread through plains

and plateaus depending on the salinity of the Mediterranean. This study supported the separation of *N. xanthodon* and *N. leucodon* from a common ancestor because of the TSS. Today *N. leucodon* is considered to inhabit Thrace, and *N. xanthodon* Anatolia.

In the most recent study upto date, Kankılıç and Gürpınar (2014) analyzed the levels of genetic polymorphism in chromosomal forms of *N. xanthodon* and *N. ehrenbergi* by using restriction fragment length polymorphism (RFLP) analysis. A significant variety in diploid chromosome numbers was identified for *N. xanthodon.* They claimed that *N. nehringi* was a distinct species and was not the synonym of *N. xanthodon.* They also stated that two additional species (*N. nehringi* and *N. labaumei*) were found in Anatolia apart from *N. xanthodon* and *N. ehrenbergi.*

1.4. Mitochondrial DNA

The marker of choice for this thesis is mtDNA, which in multicellular organisms except some cnidaria is circular. Its average length changes between 14 and 17 kb. The main reason of this difference is the change of lengths of non-coding regions or repetition of some regions of mtDNA (Hwang et al., 1999).

Metazoa mtDNA generally contains 36 or 37 genes; 13 protein coding regions related to oxidative phosphorylation, two ribosomal RNAs (16S rRNA and 12S rRNA), 22 tRNAs and at least one non-coding region (Hwang et al., 1999). These non-coding regions (control region, A+C rich region etc.) contain elements that start and regulate replication and transcription of mtDNA.
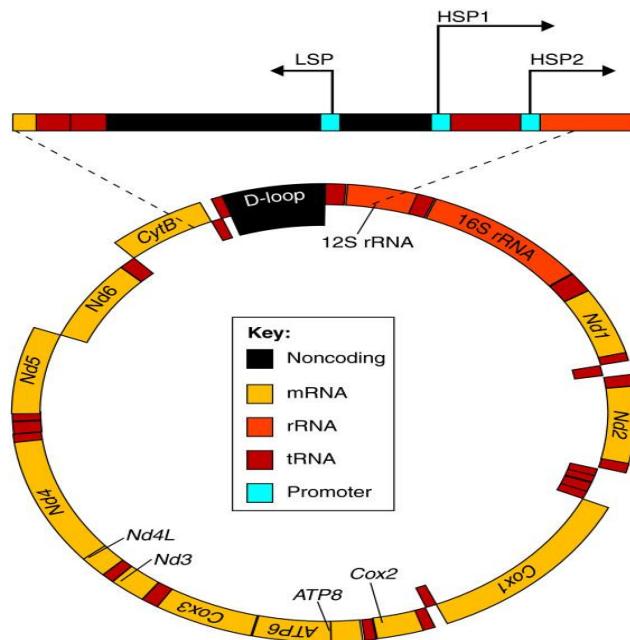
Figure 1.3: Mitochondrial DNA map and D-loop region (Leigh-Brown et al., 2010).

There are various reasons why mtDNA is the preferred marker of choice in phylogenetic studies. It is inherited maternally and it lacks recombination. Also, it evolves approximately 10 times faster than nuclear DNA (Brown et al., 1979). Therefore, genes coding most mitochondrial proteins are used to construct phylogenetic relationships of subcategories such as family, genus and species. The non-coding regions can be used in species, subspecies and population level pylogenetic studies (Table 1.1) (Zhang and Hewitt, 1997).

Displacement loop (D-loop), also known as control region, is the largest non-coding region of mtDNA. It has the highest mutation rate in comparison with the other regions of mtDNA (Saccone et al., 1993). Larizza et al. (2002) stated that although there are very conserved regions within D-loop, the rate of variable regions are generally higher; therefore, it is convenient for phylogenetic studies on rodents.

Table 1.1. Appropriate taxonomic level for each gene region of rDNA and mtDNA.

	Kingdom	Phylum	Class	Order	Family	Genus	Species	Population
Nuclear rDNA								
SSU (16-18S)	━	━	━	━	┄			
LSU (23-28S)			━	━	━	┄		
5.8S	━	━	━	┄				
IGS							━	━
ITS						━	━	━
MtDNA								
rDNA								
12S				━	━	┄		
16S					━	━	┄	
Protein								
Coding genes								
ND1					┄	━	━	┄
ND2					┄	━	━	┄
COI					┄	━	━	┄
COII					┄	━	━	┄
Cytb					┄	━	━	┄
Control region							━	━
Gene arrangement	┄	━	━	━	┄			

1.5. Thesis Objectives

Studies made so far on Anatolian mole rats showed uncertainties at different taxonomic levels. Today, questions like how many species of *Nannosplax* exist in Turkey and what the geographic distributions of these species are, do not have clear answers. Many different species have been proposed to exist so far in Anatolia, such as *N. xanthodon*, *N. nehringi*, *N. vasvari*, *N. leucodon*, *N. ceyhanus*, *N. tuncelicus*, *N. labaumei*, *N. intermedius, N.munzuri*. However, they have not been investigated in detail morphologically, genetically and karyologicaly, in order to evaluate their status as different biological species. Although many species were defined in Anatolia creating taxonomic confusion, accepting only one species for all Anatolian mole rat populations (except Southeastern Anatolia) can be overly simplistic. Therefore, the validity of existing species should be studied with detailed morphological, karyological, zoogeographical and genetical perspectives. (Corbet, 1978; Corbet, 1991; Ellerman ve Morrison-Scott, 1951; Harrison and Bates, 1991; Gromov ve Baranova, 1981; Kıvanç, 1988; Kryštufek ve Vohralik, 2009; Mehely, 1909; Mursaloğlu, 1979; Ognev, 1947; Topachevskii, 1969; Wilson ve Reeder, 2005).

As it can be seen above, even though Turkey has far more species, subspecies and karyotypic forms of *Nannospalax* genus when compared to other neighboring regions,

extensive DNA and molecular studies are still needed. Hence, mtDNA analysis of chromosomal forms should be performed with larger sample sizes to discover the genetic characteristics of each karyotype.

The aims of the thesis are to reveal genetic differences within and among *N. xanthodon*, *N.leucodon* and *N. ehrenbergi* in Turkey, to determine the phylogenetic relationships of these taxa and their chromosomal forms, to understand the degree of evolutionary change between the populations, and to contribute to a better understanding of the taxonomic status of each karyotypic form. To address these questions, sequencing analyses of the highly variable mtDNA D-loop region were used on the largest collection of samples and cytotypes of *Nannosplax* from Turkey, to date.

2. MATERIALS AND METHODS

2.1. Collection of Samples

One hundred and twenty individuals of three species (*N. xanthodon*, *N. leucodon* and *N. ehrenbergi*) were collected from 30 provinces (62 locations) in Turkey. Locations of samples are shown in Table 2.1 and Figure 2.1. The collection and morphologically identification of samples were done by Teoman Kankılıç (Nigde University, Department of Zoology). Also, Kankılıç determined diploid chromosome numbers of specimens. 105 samples of nine different cytotypes (2n=36, 38, 40, 50, 52, 54, 56, 58, 60) for *N. xanthodon*, three samples of one cytotype (2n=56) for *N. leucodon*, and 12 samples of one cytotype (2n=56) for *N. ehrenbergi* were evaluated.

Figure 2.1. Sampling locations of *Nannospalax xanthodon*, *Nannospalax leucodon* and *Nannospalax ehrenbergi*.

Table 2.1. List of sampling locations, species, number of samples collected, and diploid number of chromosomes.

Sampling Location	Name of Sampling Location	Species	Number of Samples	2n
1	Aydın- Ortaklar	*N.xanthodon*	2	36
2	Aydın-Koçarlı	*N.xanthodon*	4	36
3	Balıkesir-Çömlekçi	*N.xanthodon*	2	38
4	İzmir- Foça	*N.xanthodon*	2	38
5	Manisa- Akhisar	*N.xanthodon*	2	38
6	Isparta- Yenişarbademli	*N.xanthodon*	4	40
7	Konya- Beyşehir-Yeşildağ	*N.xanthodon*	4	40
8	Ardahan- 10 km W	*N.xanthodon*	1	50
9	Ardahan- Göle	*N.xanthodon*	1	50
10	Ardahan-Merkez	*N.xanthodon*	1	50
11	Bayburt- Demirözü	*N.xanthodon*	2	50
12	Giresun- Eğribel geçidi	*N.xanthodon*	1	50
13	Kars-Susuz	*N.xanthodon*	2	50
14	Manisa- Pamukören	*N.xanthodon*	2	50
15	Rize- Ovid dağ	*N.xanthodon*	2	50
16	Bolu- Merkez	*N.xanthodon*	2	52
17	Bolu- Mudurnu	*N.xanthodon*	1	52
18	Bolu- Seben	*N.xanthodon*	2	52
19	Bolu-Abant	*N.xanthodon*	1	52
20	Bolu-Mengen	*N.xanthodon*	2	52
21	Mersin- Çamlıyayla	*N.xanthodon*	2	52
22	Kırıkkale- Keskin	*N.xanthodon*	3	54
23	Kırıkkale-10 km E	*N.xanthodon*	2	54
24	Kırıkkale-5 km E	*N.xanthodon*	2	54
25	Kırşehir- Seyfe Gölü	*N.xanthodon*	2	54
26	Manisa- Kula	*N.xanthodon*	3	56
27	Mersin- Tarsus-Gülek	*N.xanthodon*	9	56
28	Uşak- Organize sanayi sitesi	*N.xanthodon*	1	56
29	Adana -Pozantı- Alpu	*N.xanthodon*	2	58
30	Niğde- Ulukışla	*N.xanthodon*	4	58
31	Afyon- Eber göl	*N.xanthodon*	1	60
32	Aksaray- Şereflikoçhisar	*N.xanthodon*	1	60
33	Ankara- Çeltikli	*N.xanthodon*	1	60
34	Ankara- Gölbaşı-Ahırboz	*N.xanthodon*	1	60
35	Ankara- Haymana	*N.xanthodon*	1	60
36	Ankara- Kalecik	*N.xanthodon*	1	60
37	Ankara- Kızılcahamam	*N.xanthodon*	1	60
38	Ankara- Sarayköy	*N.xanthodon*	1	60
39	Antalya- Akseki - Salamut Y.	*N.xanthodon*	1	60
40	Bilecik-Söğüt	*N.xanthodon*	1	60
41	Bolu- Ayman Yaylası	*N.xanthodon*	2	60

Table 2.1. List of sampling locations, species, number of samples collected, and diploid number of chromosomes (cont.).

Sampling Location	Name of Sampling Location	Species	Number of Samples	2n
42	Burdur- Yeşilova-Harmanlı K.	*N.xanthodon*	1	60
43	Burdur-5 km S-Göl kenarı	*N.xanthodon*	1	60
44	Erzincan- Tercan-Yollarüstü K.	*N.xanthodon*	1	60
45	Eskişehir- Günyüzü-Sivrihisar	*N.xanthodon*	2	60
46	Isparta- Atabey	*N.xanthodon*	1	60
47	Isparta- Gönen	*N.xanthodon*	1	60
48	Isparta- Madenli-Gelendost	*N.xanthodon*	2	60
49	Isparta- Yalvaç	*N.xanthodon*	1	60
50	Konya- Akşehir	*N.xanthodon*	1	60
51	Konya- Beyşehir	*N.xanthodon*	2	60
52	Konya- Cihanbeyli	*N.xanthodon*	1	60
53	Konya- Kulu	*N.xanthodon*	1	60
54	Konya- Yunak	*N.xanthodon*	1	60
55	Kütahya- Emet	*N.xanthodon*	3	60
56	Kütahya- Hava Tugayı	*N.xanthodon*	2	60
57	Manisa- Selendi	*N.xanthodon*	1	60
58	Sivas- İmranlı	*N.xanthodon*	1	60
59	Kırklareli- Pınarhisar-Evciler	*N.leucodon*	2	56
60	Tekirdağ- Marmara Ereğlisi	*N.leucodon*	1	56
61	Adana- Şeyhmurat Köyü	*N.ehrenbergi*	2	56
62	Mersin- Tarsus	*N.ehrenbergi*	10	56

2.2. DNA Extraction

Total DNA was extracted from liver tissues of the samples using Roche High Pure PCR Template Preparation Kit (Mannheim, Germany). The isolated DNA samples were eluted in 100 μl of elution buffer. After the extraction, DNA samples were stored at -20°C until further processing. In order to evaluate presence of DNA 1% agarose gels were prepared. 0.40 grams of agarose was dissolved in 40 ml of 1X TAE buffer by using a microwave oven. 1% agarose gel was stained with 2 μl of Ethidium Bromide for visualization. A mixture of 3 μl of DNA and 3 μl of loading dye were loaded in wells of the gels and 1 kb ladder was used for approximate quantification. The gel was run at 100 V for 25 minutes. The images of gels were taken using Quantity One software (Figure 2.2).
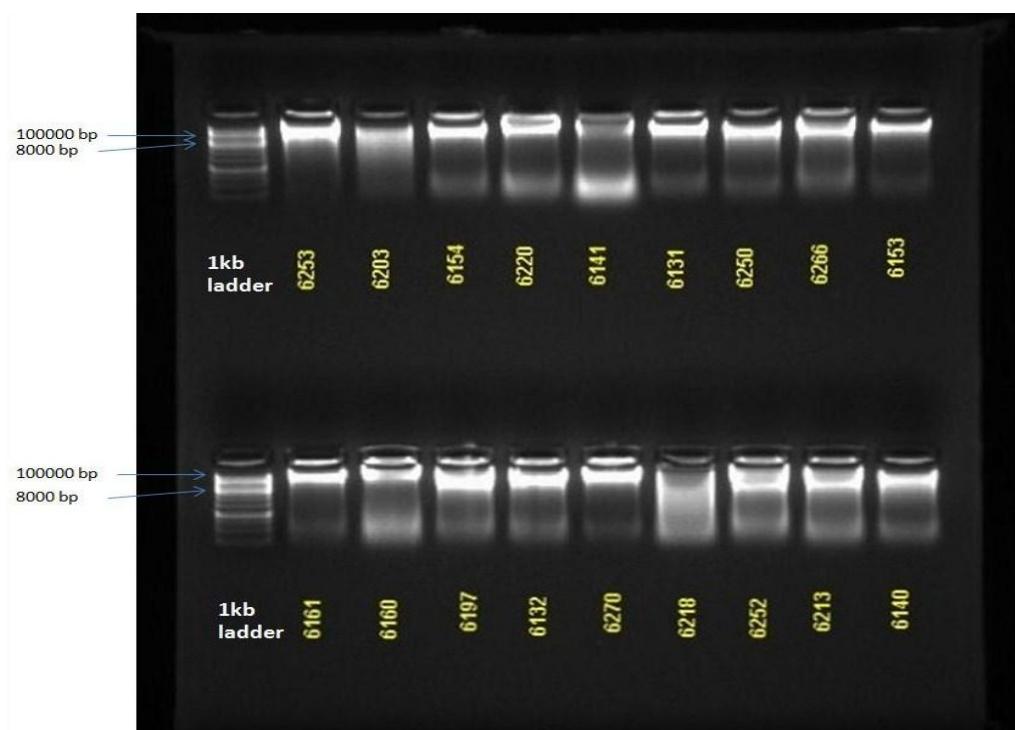
Figure 2.2. An agarose gel image showing extracted DNA.

2.3. PCR Amplification

Forward and reverse primers, 1FR (5'-TAATTACCCTGGTCTTGTAA- 3') and 4RV (5'-CTAATAATAAGGCCAGGACC-3'), were used in order to amplify the D-loop fragment of mtDNA (Reyes et al., 2003). PCR amplification was performed in a 50 μl reaction volume composed of 1 μl mt DNA, 3 μl of 25mM MgCl$_2$, 5 μl of 10X buffer, 1.25 μl of DNTP, 1.25 μl of each primer, 1.25U Taq DNA polymerase (Thermo Scientific) and double distilled water. PCR cycling conditions contained an initial denaturation step at 95°C for 10 minutes, followed by 30 cycles of 45 seconds at 95°C, 45 seconds at 46°C and 1 minute and a half at 72°C, and a final extension step at 72°C for 7 minutes. PCR samples were run in a 1% agarose gel at 100 V for 25 minutes and visualized.

Double bands were seen in some PCR results (Figure 2.3). To get rid of the PCR bands of the incorrect sizes, the E-Gel-Agarose Gel Electrophoresis System (Invitrogen, USA) was used. Before sending PCR products to sequencing, their concentration was measured using Picodrop Microliter UV/Vis Spectrophotometer (Picodrop, UK).
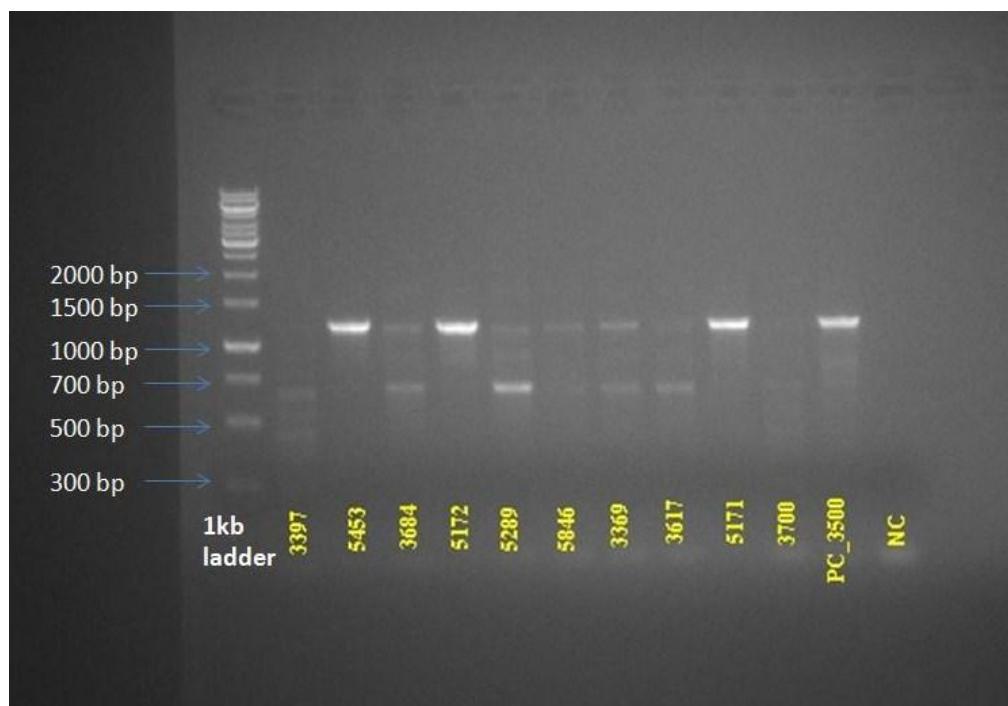
Figure 2.3. An agarose gel image showing showing double bands after PCR.

2.4. Data Analyses

Amplified DNA products were sequenced commercially (Macrogen, Korea). Sequences were edited and aligned with the Sequencer 4.8 program (Gene Codes Corp.). After alignment of the sequences, they were trimmed and 896 bp region of each sample was analysed. For comparison, 10 mtDNA control region sequences of *N. ehrenbergi carmeli* were used from GenBank, NCBI (National Center for Biotechnology Information) with the accession numbers AJ440439, AJ440440, AJ440441, AJ440443, AJ440444, AJ440445, AJ440446, AJ440447, AJ440448 and AJ440450.

In order to reveal the relationship of species Maximum Likelihood (ML) and Neighbor-Joining (NJ) trees were constructed with the software Mega v.5 (Tamura et al., 2011). Test of phylogeny was done with the bootstrap method and 1000 replications for all trees. The Jukes-Cantor model was used in building maximum likelihood tree and Maximum composite likelihood model was for the neighbor-joining tree. Mega v.5 was also used to show divergence between and within species by computing genetic distances using corrected and uncorrected p-distance. Statistics of haplotype diversity (Hd), nucleotide diversity (π), number of haplotypes, number of polymorphic sites, total number

of mutations and average number of nucleotide differences were computed with DnaSP v.5 (Rozas et al., 2003). Additionally, NETWORK Version 4.6.1.1 (Bandelt et al., 1999) was used to build a haplotype network, using the median joining method.

3. RESULTS

3.1. PCR Results

Primers 1FR and 4RV were used to amplify mitochondrial DNA D-loop region. With the PCR an approximately 1200 bp long fragment was amplified for each sample. The obtained DNA was transferred to an agarose gel electrophoresis device and run in 1% agarose gel. Gel image of the DNA samples stained with Et-Br and the size of mtDNA studies are shown in Figure 3.1.
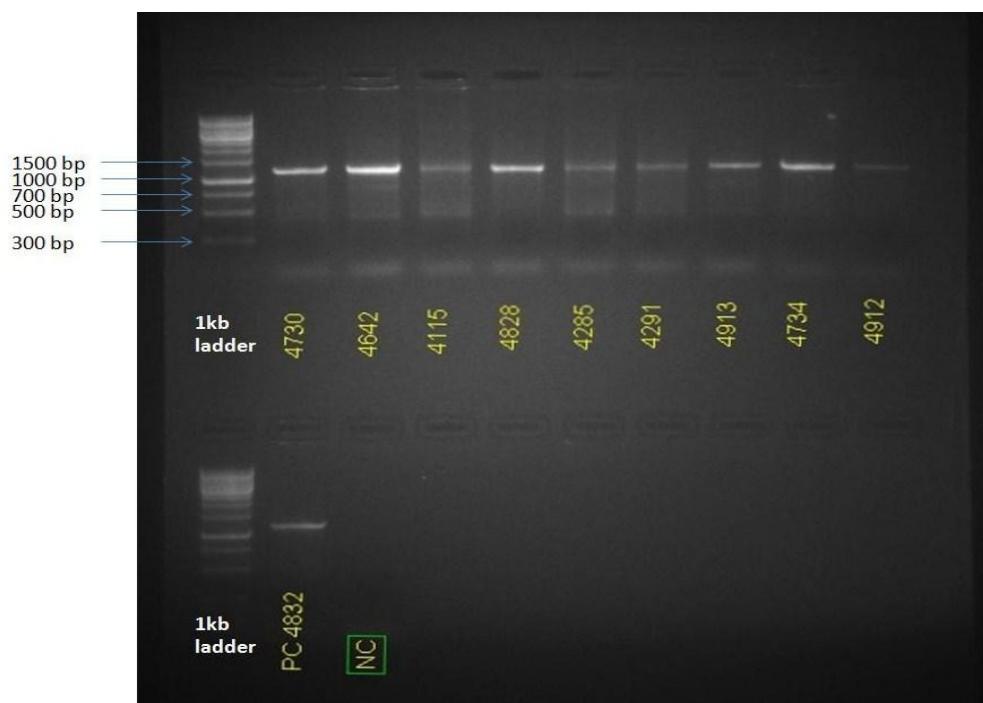
Figure 3.1. An agarose gel image showing the PCR products.

3.2. Phylogenetic Analysis Results

In this thesis, 896 bp-long mtDNA control region fragments of 130 specimens were used for phylogenetic analyses. 105 specimens were *N. xanthodon*, 12 specimens were *N. ehrenbergi* and three specimens were *N. leucodon*. In addition, mtDNA control regions of 10 specimens of *N. carmeli* from GenBank were used for comparison. 95 haplotypes were

found in the 130 specimens analyzed. Number of haplotypes and haplotype distribution on the basis of chromosomal forms and species are given in table 3.1 and figure 3.2.

Table 3.1. Haplotype distribution with respect to species and chromosomal forms.

Species	Population	Number of Haplotypes	Haplotype
N xanthodon	2n=36	3	Hap_63, Hap_64, Hap_66
N. xanthodon	2n=38	4	Hap_56, Hap_61, Hap_62, Hap_67
N. xanthodon	2n=40	5	Hap_59, Hap_65, Hap_77, Hap_78, Hap_79
N. xanthodon	2n=50	7	Hap_22, Hap_28, Hap_29, Hap_35, Hap_57, Hap_58, Hap_80
N. xanthodon	2n=52	7	Hap_17, Hap_18, Hap_19, Hap_36, Hap_41, Hap_68, Hap_69
N. xanthodon	2n=54	6	Hap_20, Hap_21, Hap_23, Hap_73, Hap_74, Hap_75
N. xanthodon	2n=56	7	Hap_14, Hap_30, Hap_31, Hap_33, Hap_34, Hap_38, Hap_60
N. xanthodon	2n=58	4	Hap_5, Hap_8, Hap_9, Hap_15
N. xanthodon	2n=60	34	Hap_1, Hap_2, Hap_3, Hap_4, Hap_6, Hap_7, Hap_10, Hap_11, Hap_12, Hap_13, Hap_16, Hap_24, Hap_25, Hap_26, Hap_27, Hap_32, Hap_37, Hap_39, Hap_40, Hap_42, Hap_43, Hap_44, Hap_45, Hap_46, Hap_47, Hap_48, Hap_49, Hap_50, Hap_51, Hap_52, Hap_53, Hap_54, Hap_55, Hap_71
N. leucodon	2n=56	3	Hap_70, Hap_72, Hap_76
N. ehrenbergi	2n=56	6	Hap_90, Hap_91, Hap_92, Hap_93, Hap_94, Hap_95
N. carmeli	2n=58	9	Hap_81, Hap_82, Hap_83, Hap_84, Hap_85, Hap_86, Hap_87, Hap_88, Hap_89
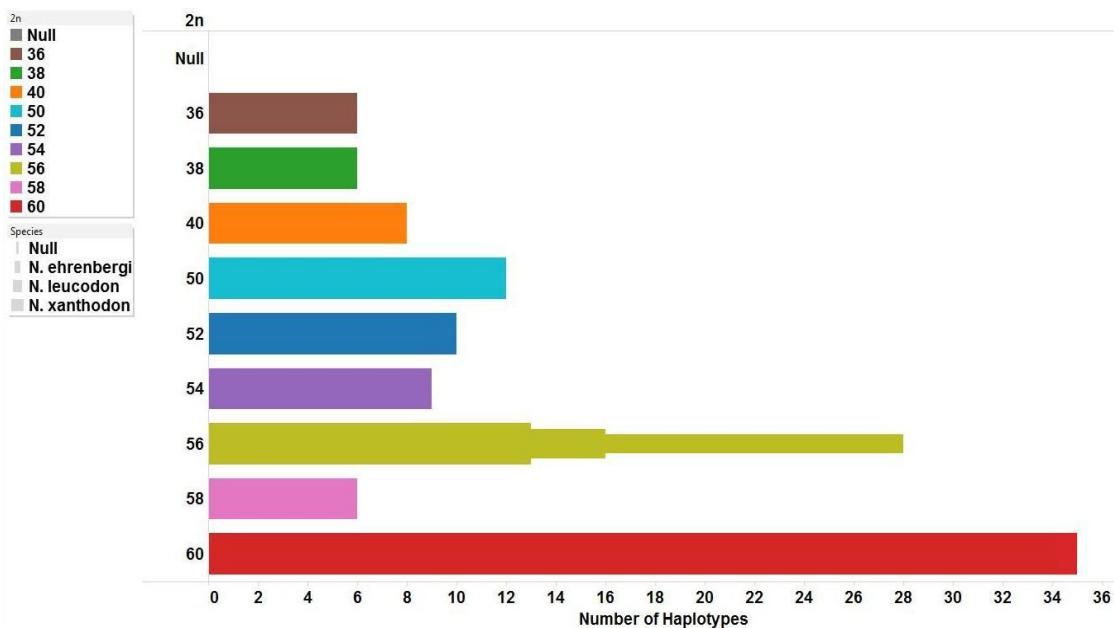
Figure 3.2. Chromosomal distribution of species including number of haplotypes.

The trees showed two main clades, which corresponded to the subgenera *Nannospalax* and *Mesospalax* of Krystufek et al. (2012). Among the species investigated, *N. ehrenbergi* was seen under subgenus *Nannospalax*, while subgenus *Mesospalax* contained *N. leucodon* and *N. xanthodon.*

When the trees were examined on the basis of species, southeastern populations (*N. ehrenbergi*) were clustered in a group of their own, similar to the Thracian populations (*N. leucodon*). On the other hand, *N. xanthodon* has been considered to exist, except for the southeastern parts, in the entire Anatolian peninsula. However, this species showed quite a polymorphic structure in the trees. Some populations of *N. xanthodon* were observed to be separated from each other by diploid chromosome numbers and/or geographical location. While chromosomal forms 2n = 52S, 56W, 58 and 60 were clustered on one branch, Western Anatolian chromosomal forms (2n = 36, 38, 40) were clustered on separate branches (Figure 3.3, Figure 3.5).

The results of the NJ analysis shows that *N. ehrenbergi* was separated from other species and chromosomal forms with a bootstrap value of 100. Haplotypes of *N. leucodon* were also clustered in a distinct branch with very high bootstrap support. Central Anatolian chromosomal forms of *N. xanthodon,* having mostly high number of chromosomes

(2n=52S, 56W, 58, 60), were grouped together and formed a distinct clade. Each chromosomal lineage of 2n = 36, 38, 40, 52N, 54, 56S classified within *N. xanthodon* was clustered on separate branches. While three haplotypes of 2n=50 cytotype were grouped together with 100% bootstrap support, other haplotypes were grouped based on other cytotypes. Cytotypes with the same number of chromosomes 2n=52 and 2n=56 were found in the northern and southern populations, and western and southern populations of the cytotypes, respectively (Figure 3.3). These are referred to as 2n=52N, 2n=52S, 2n=56W and 2n=56S from this point forward.
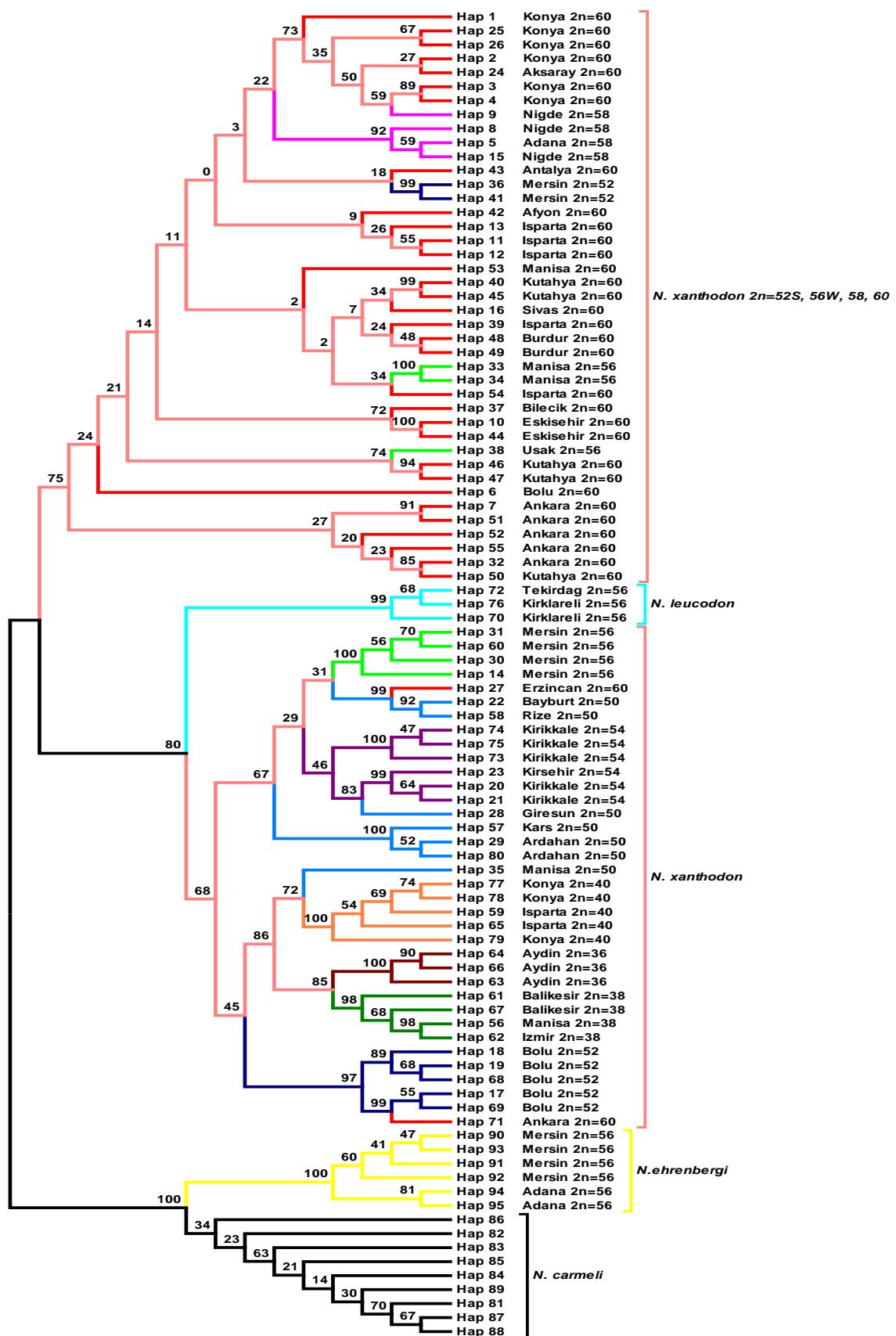
Figure 3.3. Neighbour-joining tree constructed with maximum composite likelihood distances.
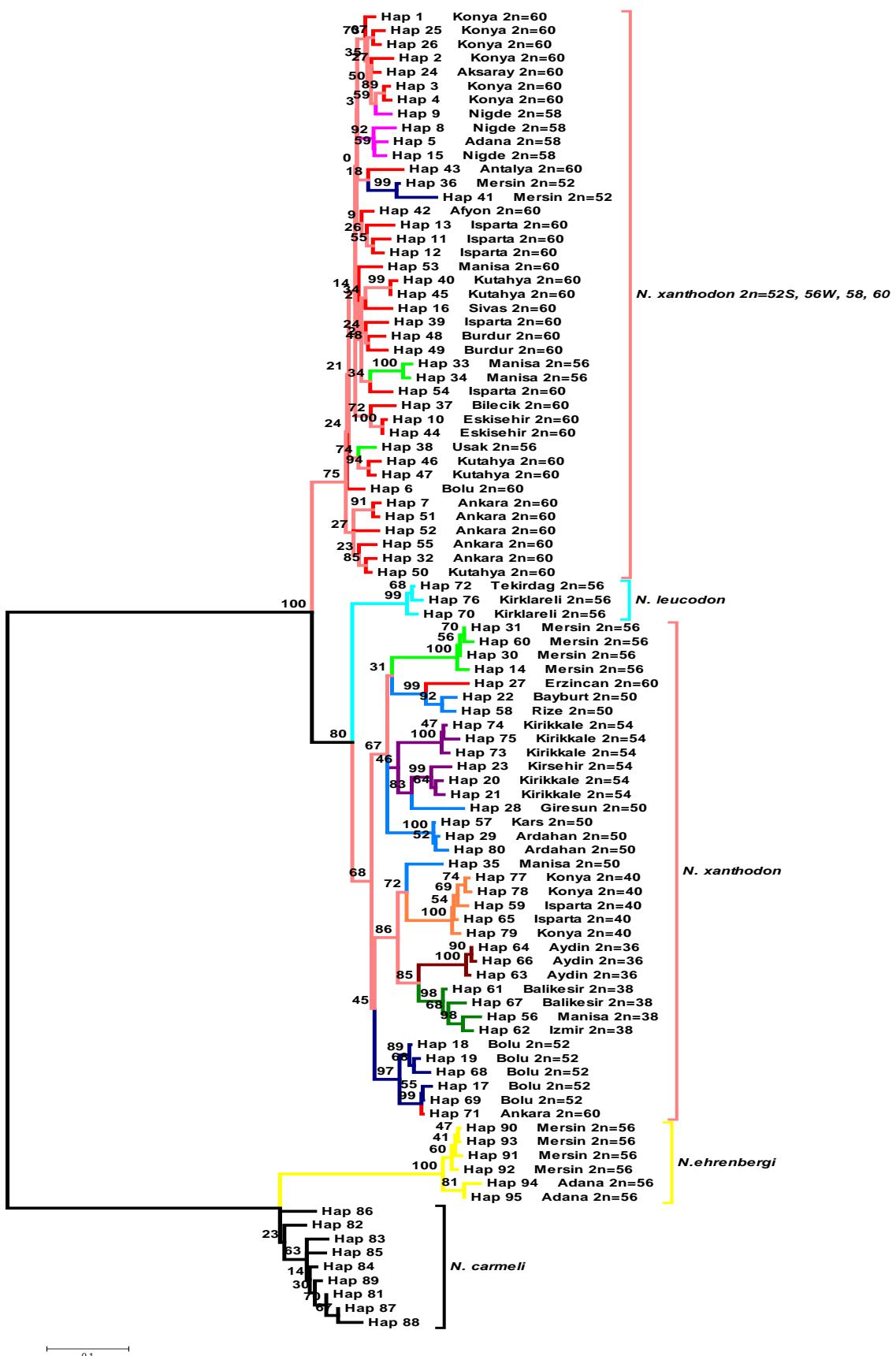
Figure 3.4. The neighbor-joining phylograms.

Maximum Likelihood trees were constructed using Jukes-Cantor model (Figure 3.5 and Figure 3.6). The maximum likelihood tree showed a similar topology to the NJ tree. *N. ehrenbergi* and all other populations were separated from each other by bootstrap values of 100, and *N. leucodon* was a sister species to *N. xanthodon* as seen in the NJ tree. For *N. xanthodon* species, haplotypes belonging to each chromosomal form were grouped together. However, differently from the NJ analysis, haplotypes of four chromosomal forms (2n = 52, 2n = 56W, 2n = 58 and 2n = 60) formed a mixed group.

Median-joining network constructed from sequences of 130 specimens also supported the clustering patterns and relationships observed in the NJ and ML trees. As in other phylogenetic trees, *N. ehrenbergi* and *N. leucodon* were clustered in different sections of the network from chromosomal forms of *N. xanthodon*. Haplotypes having the number of chromosomes with 2n=52S, 56W, 58, and 60 created a group, which was clearly separated from other populations of *N. xanthodon*. However, haplotypes belonging 2n=36, 38, 40, 52N, 54, 56S chromosomal forms were clustered in their own groups (Figure 3.7).
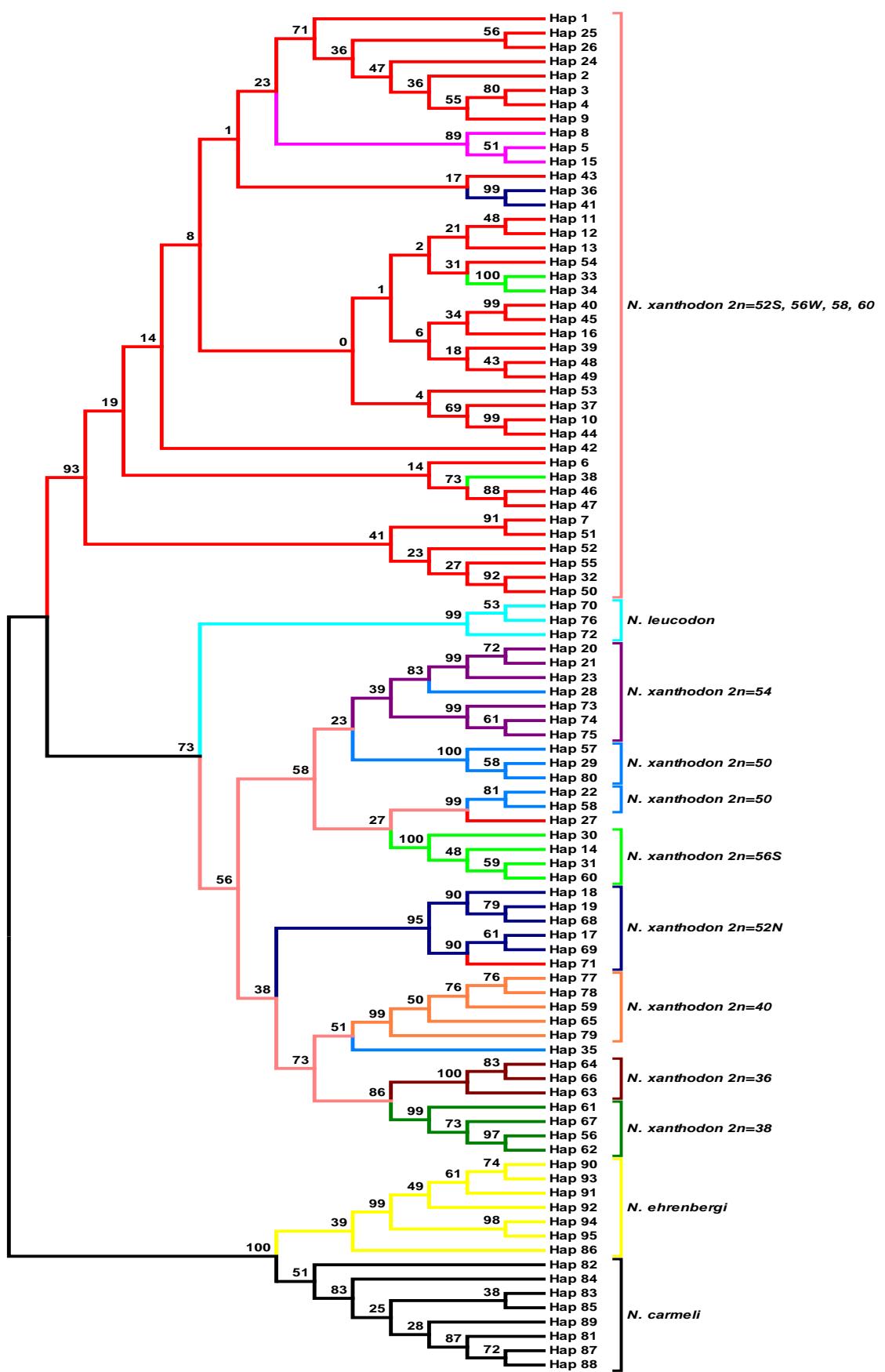
Figure 3.5. Maximum likelihood tree based on Jukes-Cantor model.
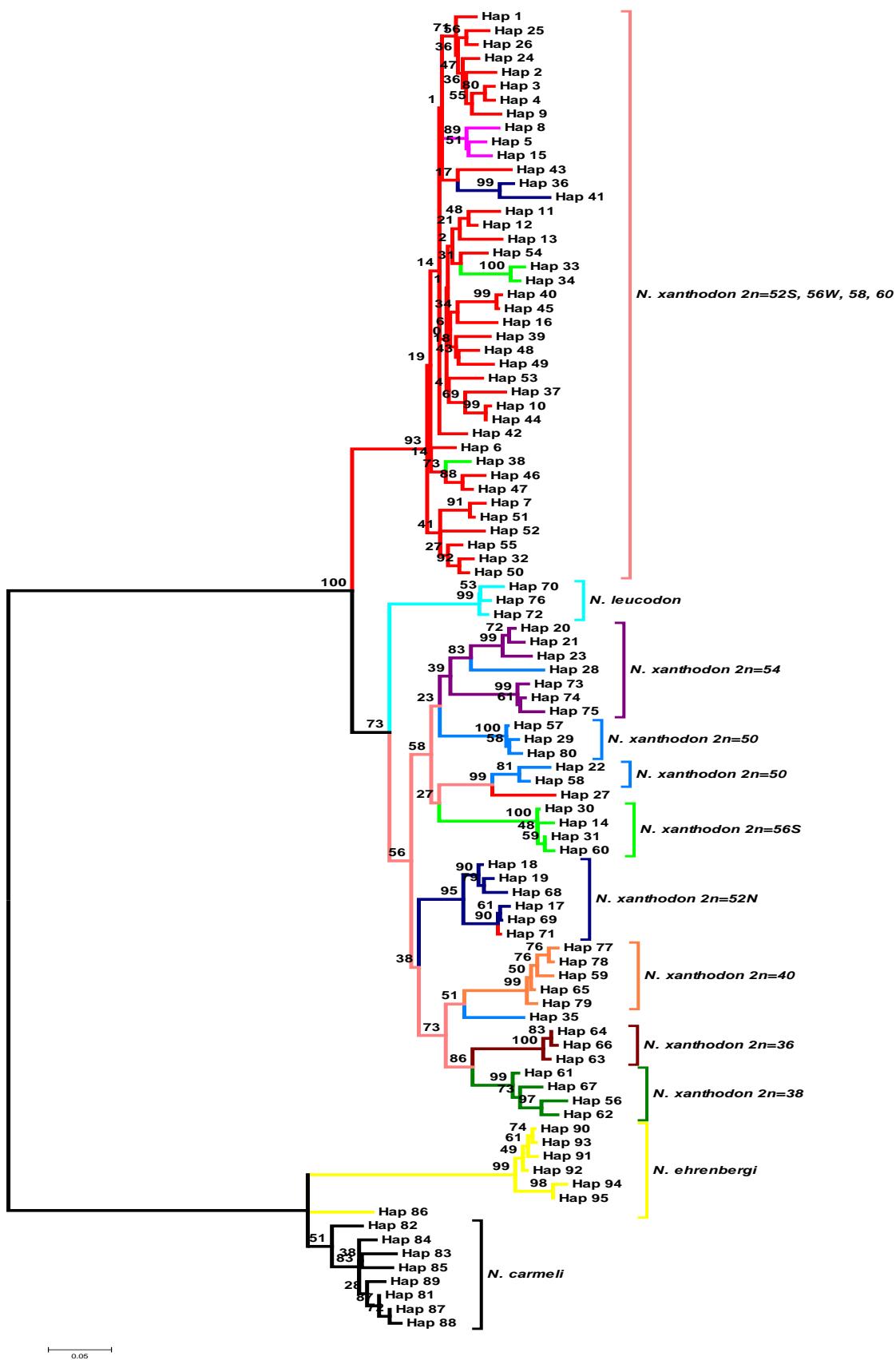
Figure 3.6. The maximum phylogram, with branch lengths measured in terms of the number of substitutions *per* site.
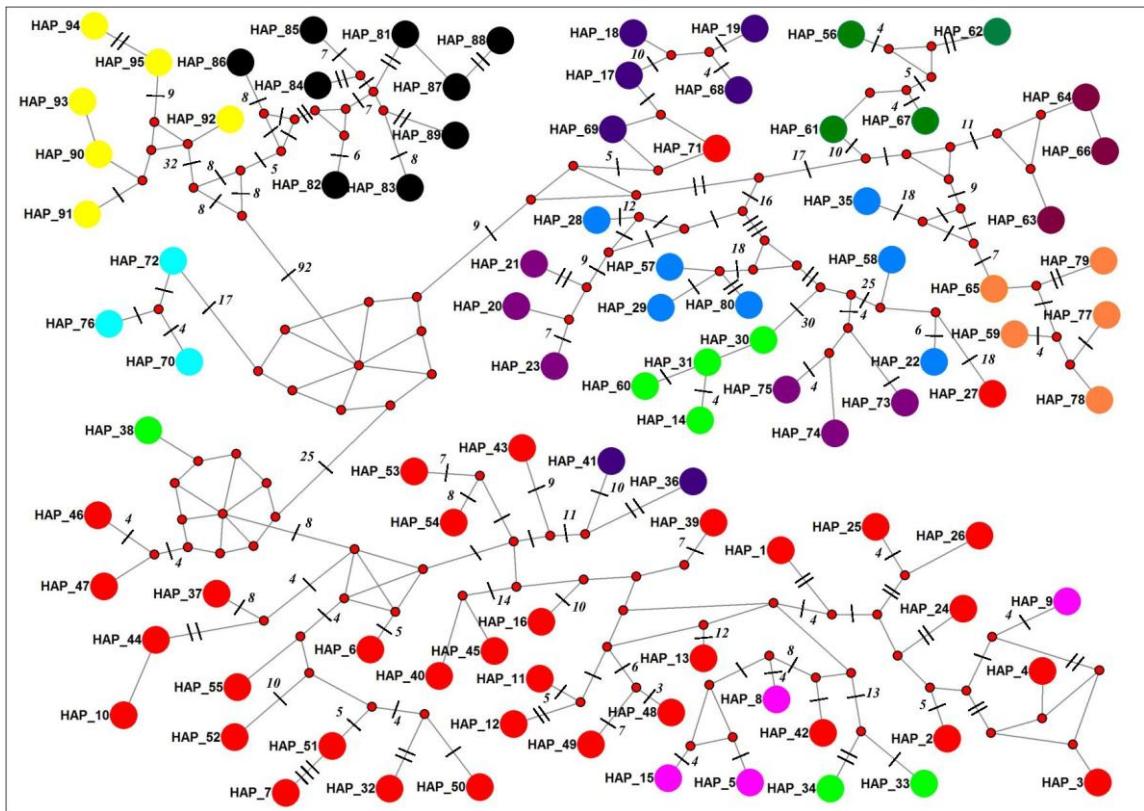
Figure 3.7. Median Network of Turkish mole rat haplotypes including 10 GenBank sequences. Haplogroups are colored as follows; Red= 2n=60, Pink= 2n=58, Light green= 2n=56, Dark purple= 2n=54, Dark blue= 2n=52, Light blue= 2n=50, Orange= 2n=40, Dark green= 2n=38, Dark red= 2n=36, Turquoise= *N. leucodon*, Yellow= *N. ehrenbergi* and Black= *N. carmeli.*

In summary, four major clades were found under the *Mesosplax* subgenus. The clade including 2n=52S, 56W, 58 and 60 cytotypes was named as *N. labaumei.* Other cytotypes were divided into two main clades referred to as *N. nehringi* (Clade 1), and as *N. xanthodon* (Clade 2). Additionally, *N. leucodon* was seen sister species of these clades, and *N. labaumei* as basal to all. Also the *Nannospalax* subgenus contained one clade of *N. ehrenbergi* (Figure 3.8).
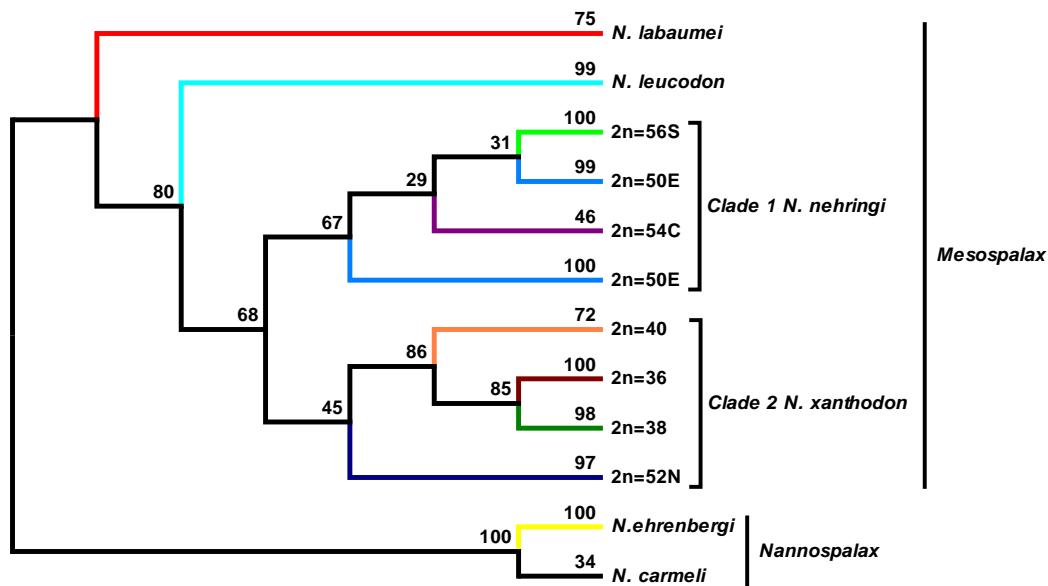
Figure 3.8. Summary of the NJ tree including all valid species and cytotypes.

3.3. Genetic Diversity Analyses

Considering descriptive statistics of genetic diversity, as mentioned previously 95 haplotypes were retrieved from 130 samples. *N. xanthodon* had the greatest number of haplotypes among species. However, the highest haplotype diversity (Hd) was observed in *N. leucodon*. Since each sample of this species had a different haplotype, Hd value was 1.000. The lowest haplotype diversity was seen in *N. ehrenbergi*. Aditionally, the highest nucleotide diversity (π) was found in *N. xanthodon* while *N. leucodon* had the lowest π value.

As among the chromosomal forms of *N. xanthodon*, 2n=60 had the highest Hd value (0.998) while 2n=36 chromosomal form had the lowest value (Hd=0.600). In addition, 2n=50 (π=0.04567) and 2n=56 (π=0.04436) chromosomal forms had the two highest π values, and the lowest nucleotide diversity was observed in 2n=36 chromosomal form (π=0.00227).

The 130 sequences, comprising 896 bp had 288 polymorphic sites with 22 singleton variable sites and 266 parsimony informative sites. The total number of mutations was 370 (Table 3.2).

Table 3.2. Population diversity parameters.

Population Name	Number of Sequences	Nucleotide Diversity π	Haplotype Diversity Hd	Number of Haplotypes (h)	Number of Polymorphic Sites	Total Number of Mutation	Average Number of Nucleotide Differences
N.xanthodon 2n:36	6	0.00227	0.600	3	4	4	1.933
N.xanthodon 2n:38	6	0.01280	0.867	4	22	23	10.867
N.xanthodon 2n:40	8	0.00808	0.786	5	17	17	6.857
N.xanthodon 2n:50	12	0.04567	0.924	7	99	107	38.636
N.xanthodon 2n:52	10	0.03820	0.933	7	86	90	32.089
N.xanthodon 2n:54	9	0.02988	0.917	6	54	54	25.278
N.xanthodon 2n:56	13	0.04436	0.872	7	91	93	37.436
N.xanthodon 2n:58	6	0.01620	0.867	4	31	32	13.800
N.xanthodon 2n:60	35	0.03386	0.998	34	159	185	28.440
N.xanthodon **Total**	**105**	**0.06093**	**0.993**	**77**	**210**	**255**	**50.081**
N.leucodon 2n:56	**3**	**0.00782**	**1.000**	**3**	**10**	**10**	**6.667**
N.ehrenbergi 2n:56	**12**	**0.01071**	**0.864**	**6**	**27**	**28**	**8.985**
N.carmeli 2n:58	**10**	**0.02069**	**0.978**	**9**	**58**	**62**	**17.422**
TOTAL	**130**	**0.09407**	**0.994**	**95**	**288**	**370**	**73.089**

Pairwise corrected (upper diagonal) and uncorrected (lower diagonal) p-distances were calculated between all chromosomal forms of *N. xanthodon* and other three species (Table 3.3). The greatest genetic distance was observed between 2n=36 and 2n=58 (0.077) by using corrected p-distance, although using the uncorrected p-distance method the highest value (0.087) was seen between 2n=36 and 2n=60, between 2n=36 and 2n=58, and between 2n=38 and 2n=58. The lowest value was calculated between 2n=58 and 2n=60 among chromosomal forms of *N. xanthodon* by both (corrected and uncorrected) p-distance methods.

Table 3.3. Between group genetic distances by using corrected (upper diagonal) and uncorrected (lower diagonal) p-distance.

	1	2	3	4	5	6	7	8	9	10	11	12
1. *N. xanthodon* 2n:36	-	0.036	0.047	0.046	0.041	0.053	0.053	0.077	0.069	0.070	0.222	0.192
2. *N. xanthodon* 2n:38	0.044	-	0.050	0.033	0.045	0.046	0.056	0.071	0.063	0.068	0.214	0.183
3. *N. xanthodon* 2n:40	0.052	0.061	-	0.036	0.042	0.056	0.051	0.072	0.064	0.067	0.221	0.189
4. *N. xanthodon* 2n:50	0.068	0.062	0.062	-	0.025	0.014	0.023	0.052	0.042	0.041	0.198	0.166
5. *N. xanthodon* 2n:52	0.061	0.071	0.064	0.066	-	0.030	0.029	0.040	0.032	0.036	0.196	0.164
6. *N. xanthodon* 2n:54	0.069	0.067	0.074	0.051	0.064	-	0.031	0.060	0.050	0.044	0.205	0.174
7. *N. xanthodon* 2n:56	0.076	0.085	0.076	0.067	0.070	0.067	-	0.040	0.032	0.044	0.194	0.172
8. *N. xanthodon* 2n:58	0.087	0.087	0.085	0.082	0.067	0.083	0.071	-	0.007	0.062	0.205	0.175
9. *N. xanthodon* 2n:60	0.087	0.086	0.084	0.080	0.067	0.080	0.070	0.031	-	0.051	0.193	0.165
10. *N. leucodon* 2n:56	0.076	0.078	0.075	0.066	0.059	0.062	0.070	0.074	0.071	-	0.213	0.179
11. *N.ehrenbergi* 2n:56	0.228	0.225	0.229	0.224	0.219	0.223	0.220	0.217	0.214	0.221	-	0.067
12. *N.carmeli* 2n:58	0.203	0.200	0.203	0.198	0.193	198	0.204	0.193	0.191	0.193	0.081	-

Between species, *N. leucodon* and *N. ehrenbergi* were the most different from each other, whereas the smallest genetic distance was seen between *N. leucodon* and *N. xanthodon* species (Table 3.4). The pairwise distances within studied populations and species were also calculated. Among chromosomal forms of *N. xanthodon,* the greatest value (0.044) was found within cytotypes of 2n=50 and 2n=56, while 2n=36 and 2n=40 had the smallest genetic distance values within. In terms of species, the highest value (0.065) was observed within *N. xanthodon,* and the lowest genetic distance (0.008) was observed within both *N. leucodon* and *N. ehrenbergi* (Table 3.5).

Table 3.4. Corrected (Bold) and uncorrected (Italic) P-distance values between Species.

	N. xanthodon	*N. leucodon*	*N.ehrenbergi*	*N.carmeli*
N. xanthodon	-	**0.033**	**0.183**	**0.154**
N. leucodon	*0.070*	-	**0.213**	**0.179**
N.ehrenbergi	*0.220*	*0.221*	-	**0.067**
N.carmeli	*0.197*	*0.193*	*0.081*	-

Table 3.5. Genetic distance within populations

Population	d
N. xanthodon **2n:36**	0.002
N. xanthodon **2n:38**	0.013
N. xanthodon **2n:40**	0.008
N. xanthodon **2n:50**	0.044
N. xanthodon **2n:52**	0.038
N. xanthodon **2n:54**	0.029
N. xanthodon **2n:56**	0.044
N. xanthodon **2n:58**	0.017
N. xanthodon **2n:60**	0.032
N. xanthodon **Total**	**0.065**
N. leucodon **2n:56**	**0.008**
N.ehrenbergi **2n:56**	**0.008**
N.carmeli **2n:58**	**0.020**

4. DISCUSSION

Comprehensive revisions made previously (Corbet et al., 1991; Gromov and Baranova,1981; Wilson and Reeder, 2005) indicated that three *Nannospalax* species were found in Turkey and among these species *N. nehringi* was distributed throughout Turkey except Imbros, Tenedos and Southeastern Anatolia, *N. leucodon* was found only in Thrace, and *N. ehrenbergi* was present only in Southeastern Anatolia. However, a more recent revision made by Kryštufek and Vohralík (2009) on mammals of Turkey and Cyprus, suggested that *N. nehringi* was not found in Anatolia, but it was a synonym of *N. xanthodon* defined in Izmir by Nordmann (1840). These authors accepted that *N. xanthodon* was distributed in Anatolia, except Thrace and Southeastern Anatolia.

Considering molecular genetics studies on *Nannospalax* and their findings, different studies showed different number of species, and geographic distributions for these species. Kandemir et al. (2012) studied the chromosomal forms of these species of Turkey by using cytochrome b region sequences. Their phylogenetic analyzes showed that western chromosomal forms formed a monophyletic group and were separated from other chromosomal forms. Moreover, the authors claimed that new species should be defined in the regions since studied chromosomal lineages had relatively high genetic diversity. Another study by Arslan et al. (2010) indicated that three cytotypes studied (2n=40, 58 and 60) should comprise three separate species.

Investigating nine cytotypes of *N. xanthodon*, Kankılıç and Gürpınar (2014) found high genetic diversity between chromosomal forms of Western, Eastern and Central Anatolia populations. They proposed three species (*N. xanthodon, N. nehringi* and *N. labaumei*) instead of the single *N. xanthodon* name for Anatolia.

Krystufek et al. (2012) found two main lineages referring to subgenera *Nannospalax* and *Mesospalax. Nannospalax* included *N. ehrenbergi*, while *Mesospalax* consisted of *N. leucodon* and *N. xanthodon*. Hadid et al. (2012) determined four major clades corresponding to *N. ehrenbergi*, *N. vasvarii*, *N leucodon* and *N. xanthodon* by using mtDNA sequences.

Studies conducted until now agree that *N. ehrenbergi* is accepted as a valid species in Southeastern Anatolia. Another consensus is that considering *N. xanthodon* and *N. leucodon*, the Turkish Straits System between Anatolia and the Balkans has caused the differentiation of these two species. Data obtained in this study supported that *N. ehrenbergi* and *N. leucodon* are valid species in Southeastern Anatolia and in Thrace, respectively. However, the idea suggesting that only one species (*N. xanthodon*) is dominant throughout the rest of Anatolia was not supported.

Nannospalax xanthodon was considered by many researchers as the dominant species of Anatolia. Furthermore, previously defined *N. nehringi*, *N. labaumei* and *N. vasvarii* have been considered as synonyms of *N. xanthodon* (Krystufek and Vohralik, 2009; Hadid et al., 2012) (Table 4.1). Based on karyological studies on samples from type locality for each *Nannospalax* species, *N. labaumei* and *N. vasvarii* had the same diploid chromosome number (2n=60) (Coşkun et al., 2010; Ivanitskaya et al., 1997; Kankılıç et al., 2009; Kryštufek and Vohralik, 2009, Kryštufek et al., 2012; Matur and Sözen, 2005; Nevo et al., 1995; Nevo et al., 1994; Savic and Soldatovic, 1979; Yüksel, 1984; Gülkaç and Yüksel, 1989). Hadid et al. (2012) accepted *N. vasvarii* as a valid species in Central Anatolia and the Taurus. However, Kankılıç and Gürpınar (2014) accepted the name of *N. labaumei* for the central populations of Anatolia, as it was the oldest species previously defined.

Table 4.1. *Nannospalax* species considered to be found in Anatolia.

Species	Type Locality	2n	Author	Year
N. xanthodon	İzmir	2n = 38	Nordman	1840
N. nehringi	Kars (Kazkoparan)	2n = 48	Satunin	1898
N. labaumei	Eskişehir (Porsuk Nehri	2n = 60	Metschie	1919
N. vasvarii	Malatya	2n = 60	Szunyoghy	1941

As a result of the analyses of this thesis, *N. xanthodon* was observed to be paraphyletic. Populations belonging to cytotypes especially in Western Anatolia were found to be quite different from populations of cytotypes living in Central Anatolia.

In Central Anatolia 2n= 52S, 56W, 58 and 60 chromosomal forms formed a monophyletic group. These cytotypes did not contain differences at the level of separate species or subspecies. Therefore, the 2n=60 cytotype and derivatives that evolved from this cytotype should be collected under a separate species. Based on this study *N. labaumei* is accepted as a valid species in Central Anatolia comprising 2n=52S, 56W, 58 and 60 cytotypes.

Geographical polarization among animals having limited movement ability like mole rats is seen even in populations which are very close to each other (Warhman et al., 1969; Nevo, 1979; Nevo, 1982). In this study, cytotypes that were geographically close to each other showed relatively smaller genetic distances, while cytotypes living in distant areas had higher distance values. Limited mobility of mole rats seems to work as a geographic isolation mechanism, causing cytotypes living in close regions to differentiate.

Each cytotype living in a specific region did not have differences at the level of species, although there were obvious differences between some specific cytotypes. To illustrate, the 2n=36 cytotype was restricted to the city of Aydın, the 2n=38 cytotype to Izmir, the 2n=40 cytotype to Konya-Beysehir, the 2n=52N cytotype to Bolu, the 2n=54 cytotype to the Kızılırmak Basin in Central Anatolia, and the 2n=56S cytotype to Southern Anatolia.

Kankılıç and Gürpınar (2014) accepted *N. xanthodon* as a distinct species, and since type locality of this species is Izmir, they proposed that it was found in Izmir, Manisa, Balikesir, and the vicinity thereof. The authors suggested that *N. xanthodon* included the 2n=36 and 2n=38 chromosomal forms and was distributed in Western Anatolia. This suggestion was also supported by our results.

Sözen (2004) suggested that the northern and southern populations of the 2n=52 cytotype were different from each other. Moreover, Matur and Sözen (2005) proposed that Sakarya river formed a barrier between the 2n=52 (from east of Sakarya river) and 2n=60 (western populations). Also, Köroğlu and Ilgaz mountains could have caused differentiation of central population from northern populations (Gülkaç and Yüksel, 1999). In our study the northern 2n=52 population formed a clade, which did not cluster with the

central 2n=60 clades in the trees. Therefore, Sakarya river and Köroğlu and Ilgaz mountains may indeed have played a role in the differentiation of the northern 2n=52 cytotype.

In our study, *N. xanthodon* is accepted as a valid species and all of these western cytotypes (2n=36, 38, 40 and 52N) were grouped within species *N. xanthodon.* On the other hand, among these cytotypes the 2n=40 and 2n=52 may be subspecies of *N. xanthodon,* since they were isolated in certain areas geographically.

Kankılıç and Gürpınar (2014) also suggested that as type locality of *N. nehringi* species was Kars, it should not be considered as a synonym of *N. xanthodon*, and *N. nehringi* should be accepted as a valid species in Eastern Anatolia where the 2n=50 chromosomal form was widespread. Our results do not support Kankılıç and Gürpınar (2014) in these regards. Although, six haplotypes out of seven were close to each other geographically, these haplotypes of the 2n=50 cytotype did not form a monophyletic group. Additionally, Matur et al. (2011) examined G- and C-banded karyotypes of the 2n=50 cytotype from north, south, west and east of Turkey and found them to be different from each other. This result was supported by results of phylogenetic analyses of this study since western, northern and eastern populations were separated from each other. Hence, it can be concluded that the 2n=50 cytotype has not been differentiated enough to be considered as a separate species. The suggestion made by Kryštufek and Vohralík (2009) that *N. nehringi* was a synonym of *N. xanthodon* was also not supported by this thesis. Instead, forming a clade sister to *N. xanthodon, N. nehringi* is proposed as a different species including the 2n=50E, 54C and 56S cytotypes, and not only for the 2n=50 cytotype as Kankılıç and Gürpınar (2014) suggested.

Considering some other cytotypes, although the 2n=40 cytotype was distributed in the same region (Konya and Isparta) with the 2n=60 cytotype, it was found to be considerably different. Besides, the clade containing the 2n=40 cytotype was close to western 2n=36 and 2n=38 chromosomal forms (*N. xanthodon*). Also the 2n=54 chromosomal form in Central Anatolia and the 2n=56 cytotype from Southern Anatolia were differentiated from other chromosomal groups. However, as sample location of each cytotype is only one province,

there is not enough evidence to consider them as separate species or subspecies in this study.

Some researchers also tried to address the question of the most ancestral chromosomal forms. Nevo et al. (1994) claimed the 2n=38 cytotype as ancestral form, while Ivanitskaya (1997, 2008) and Matur (2011) proposed the 2n=60 cytotype. Additionally, Kankılıç and Gürpınar (2014) suggested the ancestral form to be the 2n=38 cytotype for the western populations (2n=36, 40 and 52N) and the 2n=60 cytotype for the southern populations (2n=52S, 56, 58 and 52), by considering Zima (2000)'s hypothesis that chromosomal forms having widespread distribution are ancestral. Along with this reasoning, based on our results, it can be concluded that the 2n=60 chromosomal form is ancestral for *N. labaumei*. However, our data do not support the 2n=38 cytotype being ancestral for *N. xanthodon*.

Previous to this thesis, the molecular study with the greatest number of samples and cytotypes of *N. xanthodon* and *N. ehrenbergi* was conducted by Kankılıç and Gürpınar (2014). In that study, they had used RFLP analysis of the D-loop and *cyt b* regions. In their results, *N. ehrenbergi* was shown to cluster with the 2n=54 cytotype of *N. xanthodon*. In our investigation, *N. ehrenbergi* was in a basal clade to *N. xanthodon* and *N. leucodon*, which is in concordance with the literature. This suggests that the higher resolution achieved through sequencing gives more accurate results when compared to the RFLP method applied by by Kankılıç and Gürpınar (2014).

5. CONCLUSION

The findings of this study are summarized as individual points as follows:

1. *N. ehrenbergi* is a valid species in Southeastern Anatolia.

2. *N. leucodon* is accepted as a separate species in Thrace.

3. Previously defined species *N. labaumei* Metschie (1919) (Eskişehir) and *N. nehringi* Satunin (1898) (Kars) are not synonyms of *N. xanthodon*. They correspond to two different species represented as two reciprocally monophyletic clades.

4. Central populations of 2n=52S, 56W, 58 and 60 cytotypes cluster together, and *N. labaumei* is accepted as the species containing these cytotypes. Moreover, the 2n=60 may be the ancestral form for this species.

5. The designation of *N. xanthodon* is supported for western populations including 2n=36, 38, 40 and 52N. Among these cytotypes 2n=40 and the 2n=52N may be subspecies under *N. xanthodon*.

6. The suggestion of Kankılıç and Gürpınar (2014) that *N. nehringi* consists exclusively of the eastern 2n=50 cytotype is not supported. We proposed *N. nehringi* to include 2n=50E, 54C and 56S cytotypes.

7. The results do not support the Nevo (1994)'s hypothesis that every cytotype is a separate species.

As follow-up steps to this study, and in order to make firmer conclusions, especially with regards to if the different cytotypes are separate species, and to give them proper species names, more molecular (especially nuclear), karyological and morphological studies should be performed with larger sample sizes, and also considering the potential geographical barriers between different cytotypes and species.

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APPENDIX A : 896 BP LONG mtDNA D-LOOP SEQUENCES
OF 120 *Nannospalax* INDIVIDUALS

N. xanthodon

AU-4787

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AU-4271

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AU-4541

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AU-4938

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AU-4201

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AU-4849

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AU-4840

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AU-4912

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AU-4913

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AU-4668

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AU-4571

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AU-4917

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NU-184

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AU-4307

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AU-4306

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AU-4662

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AU-4642

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AU-4572

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AU-5313

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NU-138

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NU-139

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NU-134

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AU-4505

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NU-151

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AU-4933

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AU-6135

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AU-6141
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AU-6117

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NU-111

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NU-121

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NU-110

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AU-6136

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AU-6224

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AU-6208

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AU-5846

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NU-122

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AU-5563

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NU-195

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AU-5938

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AU-5848

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AU-3700

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AU-3684

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AU-2516

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AU-6205

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NU-137

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AU-5847

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AU-4269

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AU-4287

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AU-6143

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AU-6252

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AU-4290

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AU-6153

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AU-3321

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AU-4670

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AU-6266

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AU-6255

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AU-6254

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NU-150

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AU-6154

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AU-6138

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AU-6140

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AU-6131

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AU-6250

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AU-6197

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AU-6256

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AU-6225

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AU-6251

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AU-6134

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AU-4203

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AU-4937

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NU-152

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NU-151

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AU-3988

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AU-3986

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AU-4828

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AU-5172

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AU-5170

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AU-5453

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AU-5452

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AU-4671

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AU-3323

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AU-6218

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AU-4731

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AU-4730

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AU-6232

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AU-4734

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AU-6269

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AU-3322

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AU-3369

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AU-4669

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N. leucodon

NU-209
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NU-211

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NU-214

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N. ehrenbergi

NU-223

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NU-225

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NU-224

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NU-219

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NU-220

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AU-2137

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CACCCCAGGTGATGGGCCTTATCTTAAAATTTGCCAAACCCCAAAAACAAAAT
TAAGTAAGACTTAAAACCCTCAATTATTTTCTTTCTATAAGTTGCCA

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ACATTCAACTATATATCGCATCAACAATTAAGCAAGTACGAACACACAATTCC
CACACAACCACACCTATGTATATAGTACATTAAATTATTTACCACTAGCATATA
AGCAAGTACAATATATTATTAATATTACATAATACATATAATTATCAACGTACA
TAACACTATTATCCACATGAATATTCATGTATACATAATATTAATGTTCTACTG
ACATATCTGCGTTATCAGGCATACACCATCTTAGTCAAATCATTTCTCTACCAC
ATGACTATCCACTCCCAACGTTGGTCTCTTTATCTACCATCCTCCGTGAAACCA
GCAACCCGCCCACTAGTACCTCTCTTCTCGCTCCGGGCCCATTTAACTTGGGGG
TAGCTAACAATGCACTTTATCAGACATCTGGTTCTTACTTCAGGGCCATTGAAT
GCTTTATCGTCCATACGTTCCCCTTAAATAAGACATCTCGATGGATTAATGTCT
AATCAGCCCATGCCTAACATAACTGTGGTGTCATACATTTGGTATTTTTATTTT
TGGGGATGCTGTGACTCAGCATAGCCGTCAAGGCATGAAGGATCCAACCTCAG
TCTAGCTGGACTTGTATATATTATTTACTCCACACATCTCCAACAAGTGGCTAT
TTAATTAATGCTTGTAGGACATATTAATAATTAATACTAAATTTCAATTCAACA
ACGCACGCACCACGCAGTATTATTTTTTTACTGCAAACCCCCCTTACCCCCCA
TCACCCCAGGTGATGGGCCTTATCTTAAAATTTGCCAAACCCCAAAAACAAAA
TTAAGTAAGACTTAAAACCCTCAATTATTTTCTTTCTATAAGTTGCCA

NU-222

ACATTCAACTATATATCGCATCAACAATTAAGCAAGTACGAACACACAATTCC
CACACAACCACACCTATGTATATAGTACATTAAATTATTTACCACTAGCATATA
AGCAAGTACAATATATTATTAATATTACATAATACATATAATTATCAACGTACA
TAACACTATTATCCACATGAATATTCATGTATACATAATATTAATGTTCTACTG
ACATATCTGCGTTATCAGGCATACACCATCTTAGTCAAATCATTTCTCTACCAC
ATGACTATCCACTCCCAACGTTGGTCTCTTTATCTACCATCCTCCGTGAAACCA
GCAACCCGCCCACTAGTACCTCTCTTCTCGCTCCGGGCCCATTTAACTTGGGGG
TAGCTAACAATGCACTTTATCAGACATCTGGTTCTTACTTCAGGGCCATTGAAT
GCTTTATCGTCCATACGTTCCCCTTAAATAAGACATCTCGATGGATTAATGTCT
AATCAGCCCATGCCTAACATAACTGTGGTGTCATACATTTGGTATTTTTATTTT
TGGGGATGCTGTGACTCAGCATAGCCGTCAAGGCATGAAGGATCCAACCTCAG
TCTAGCTGGACTTGTATATATTATTTACTCCACACATCTCCAACAAGTGGCTAT
TTAATTAATGCTTGTAGGACATATTAATAATTAATACTAAATTTCAATTCAACA
ACGCACGCACCACGCAGTATTATTTTTTTTACTGCAAACCCCCCTTACCCCCCA
TCACCCCAGGTGATGGGCCTTATCTTAAAATTTGCCAAACCCCAAAAACAAAA
TTAAGTAAGACTTAAAACCCTCAATTATTTTCTTTCTATAAGTTGCCA

NU-218

ACATTCAACTATATATCGCATCAACAATTAAGCAAGTACGAACACACAATTCC
CACACAACCATACCTATGTATATAGTACATTAAATTATTTACCACTAGCATATA
AGCAAGTACAATATATTATTAATATTACATAATACATACAGTTATTAACGTACA
TAACACTATTATCCACATGAATATTCATGCATACATAATATTAATGCTCTACTG
ACATATCTGCGTTATCAGGCATACACCATCTTAGTCAAATCATTTCTCTACCAC
ATGACTATCCACTCCCAACGTTGGTCTCTTTATCTACCATCCTCCGTGAAACCA
GCAACCCGCCCACTAGTACCTCTCTTCTCGCTCCGGGCCCATTTAACTTGGGGG
TAGCTAACAATGCACTTTATCAGACATCTGGTTCTTACTTCAGGGCCATTGAAT
GCTTTATCGTCCATACGTTCCCCTTAAATAAGACATCTCGATGGATTAATGTCT
AATCAGCCCATGCCTAACATAACTGTGGTGTCATACATTTGGTATTTTTATTTT
TGGGGATGCTGTGACTCAGCATAGCCGTCAAGGCATGAAGGATCCAACCTTAG
TCTAGCTGGACTTGTATATATTATTTACTCCACACATCTCCAACAAGTGGCTAT
TCAGTTAATGCTTGTAGGACATATTAATAATTAATACTAAATTTCAATTCAACA
ACACACGCACCACACAGTATTATTTTTTTTACTGCAAACCCCCCTTACCCCCCA

TCACCCCAGGTGATGGGCCTTATCTTAAAATTTGCCAAACCCCAAAAACAAAA
TTAAGTAAGACTTAAAACCCTCAATTATTTTCTTTCTATAAGTTGCCA

NU-227

ACATTCAACTATATATCGCATCAACAATTAAGCAAGTACGAACACACAATTCC
CACACAACCATACCTATGTATATAGTACATTAAATTATTTACCACTAGCATATA
AGCAAGTACAATATATTATTAATATTACATAATACATACAGTTATTAACGTACA
TAACACTATTATCCACATGAATATTCATGCATACATAATATTAATGCTCTACTG
ACATATCTGCGTTATCAGGCATACACCATCTTAGTCAAATCATTTCTCTACCAC
ATGACTATCCACTCCCAACGTTGGTCTCTTTATCTACCATCCTCCGTGAAACCA
GCAACCCGCCCACTAGTACCTCTCTTCTCGCTCCGGGCCCATTTAACTTGGGGG
TAGCTAACAATGCACTTTATCAGACATCTGGTTCTTACTTCAGGGCCATTGAAT
GCTTTATCGTCCATACGTTCCCCTTAAATAAGACATCTCGATGGATTAATGTCT
AATCAGCCCATGCCTAACATAACTGTGGTGTCATACATTTGGTATTTTTTATTTT
TGGGGATGCTGTGACTCAGCATAGCCGTCAAGGCATGAAGGATCCAACCTTAG
TCTAGCTGGACTTGTATATATTATTTACTCCACACATCTCCAACAAGTGGCTAT
TCAGTTAATGCTTGTAGGACATATTAATAATTAATACTAAATTTCAATTCAACA
ACACACGCACCACACAGTATTATTTTTTTTACTGCAAACCCCCCTTACCCCCCCA
TCACCCCAGGTGATGGGCCTTATCTTAAAATTTGCCAAACCCCAAAAACAAAA
TTAAGTAAGACTTAAAACCCTCAATTATTTTCTTTCTATAAGTTGCCA

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ACATTCAACTATATATCGCATCAGCAATTAAGCAAGTACAAACACACAATTCC
CACCACACAATATACTTATGTATATAGTGCATTAAATTATTTACCACTAGCATA
TAAGCAGTACAATATATTATTAATATTACATAATACATACAGTTATTAACGTAC
ATAACACTATTATCCACATGAATATTCATGTATACATAATATTAATGTTCTACT
GACATATCTGCGTTATCAGGCATACACCATCTTAGTCAAATCATTTCTTTACCA
CATGACTATCCACTCCCAACGTTGGTCTCTTTATCTACCATCCTCCGTGAAACC
AGCAACCCGCCCACTAGTACCTCTCTTCTCGCTCCGGGCTCATTAAACTTGGGG
GTAGCTAACAATGCACTTTATCAGACATCTGGTTCTTACTTCAGGGCCATTGAA
TGCTTTATCGTCCATACGTTCCCCTTAAATAAGACATCTCGATGGATTAATGTC
TAATCAGCCCATGCCTAACATAACTGTGGTGTCATACATTTGGTATTTTTTATTT
TTGGGGATGCTGTGACTCAGCATAGCCGTCAAGGCATGAAGGATCCAACCTTA

GTCTAGCTGGACTTGTATATATTATTTACTCCACACATCTCCAACAAGTGGCTA
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AACGTACACACCACACAGTATTATTTTTTTTACTGCAAACCCCCCTTACCCCCC
ACCACCCCAGGTGGTGGGCCTTATCTTAAAATTTGCCAAACCCCAAAAACAAA
ATTAAGTAAGACTTAAAACCCTCAATTATTTTCTTTCTATAAGTTGCCA

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ACATTCAACTATATATCGCATCAGCAATTAAGCAAGTACAAACACACAATTCC
CACACAACCATACCTATGTATATAGTGCATTAAATTATTTACCACTAGCATATA
AGCAAGTACAATATATTATTAATATTACATAATACATACAATTATTAACGTACA
TAACACTATTATCCACATGAATATTCATGTATACATAATATTAATGTTCTACTG
ACATATCTGCGTTATCAGGCATACACCATCTTAGTCAAATCATTTCTTTACCAC
ATGACTATCCACTCCCAACGTTGGTCTCTTTATCTACCATCCTCCGTGAAACCA
GCAACCCGCCCACTAGTACCTCTCTTCTCGCTCCGGGCCCATTAAACTTGGGGG
TAGCTAACAATGCACTTTATCAGACATCTGGTTCTTACTTCAGGGCCATTGAAT
GCTTTATCGTCCATACGTTCCCCTTAAATAAGACATCTCGATGGATTAATGTCT
AATCAGCCCATGCCTAACATAACTGTGGTGTCATACATTTGGTATTTTTTATTTT
TGGGGATGCTGTGACTCAGCATAGCCGTCAAGGCATGAAGGATCCAACCTTAG
TCTAGCTGGACTTGTATATATTATTTACTCCACACATCTCCAACAAGTGGCTAT
TTAATTAATGCTTGTAGGACATATTAATAATTAATACTAAATTTCAATTCAACA
ACGTACACACCACACAGTATTATTTTTTTTACTGCAAACCCCCCTTACCCCCCA
CCACCCCAGGTGGTGGGCCTTATCTTAAAATTTGCCAAACCCCAAAAACAAAA
TTAAGTAAGACTTAAAACCCTCAATTATTTTCTTTCTATAAGTTGCCA