Boris KRYŠTUFEK and Vladimír VOHRALÍK

## Mammals of Turkey and Cyprus

Rodentia II: Cricetinae, Muridae, Spalacidae, Calomyscidae,
Capromyidae, Hystricidae, Castoridae

Boris KRYŠTUFEK<br>VLADIMíR VOHRALÍK

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CRICETINAE, MURIDAE, SPALACIDAE, CALOMYSCIDAE, CAPROMYIDAE, HYSTRICIDAE, CASTORIDAE

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## Foreword by Friederike Spitzenberger

Turkey is situated in a unique spot on the globe, at the junction of three continents. It is a meeting point of different biogeographic regions, and enjoys a wide range of climates and landscapes, thus providing the conditions for an extraordinarily diverse mammal fauna. My interest in Turkish mammals goes back to the 1960s, when I joined a small group of students from the University of Vienna, collecting small mammals in the Pontus mountains. On the very first trip I fell in love with the beautiful country and its people, their friendliness and overwhelming hospitality. Up until 1985, I went back to Turkey frequently, in 1969 even as the "foreign expert" of the Ege University/Izmir, invited by the unforgettable Professor Muhtar Başoğlu.

In the 1980s, I began to focus my work on the mammal fauna of my own country. As it turned out later, this was not only a time of a radical change in the faunistic and taxonomic study of mammals in general and Turkish mammals in particular, but also of the geopolitical situation in Europe. Corbet's review of Palaearctic mammals published in 1978 marked the end of the traditional morphology-based taxonomy. In Turkey, Professor Bahtiye Mursaloğlu of Ankara University, having studied mammalogy in the USA, had compiled a huge collection of small mammals. She published contributions to the knowledge of the Turkish mammal fauna in Turkish between 1963 and 1981. Kumerloeve's compilation of all available information on Turkish mammals appeared in 1975 in German.

In the 1980s, the Iron Curtain lifted and this allowed Eastern European mammalogists to study the unique Turkish fauna personally. A Czech -Slovenian cooperation started in 1993 with frequent collecting trips to Turkey. At the same time, a group of young and keen Turkish mammalogists emerged. They had accession to the B. Mursaloğlu's collection and, dispersed all over the country, collected new material in order to apply new techniques.

In the 1990s, a new age of taxonomic research began in Turkey. Partly performed with the cooperation of the two teams, chromosomal and molecular analyses did not only unravel taxonomical problems already envisaged by former students of Turkish mammals, but also revealed a completely unexpected diversity of species. The first result of this new period was a Turkish mammal fauna (editor: A. Demirsoy) published in 1996 in Turkish. It was followed by a review on distribution and taxonomy of bats in Turkey by Benda and Horáček in 1998 in English.

In 2001 the first part (Introduction, Checklist, Insectivora) of the "Mammals of Turkey and Cyprus" by Kryštufek and Vohralík appeared, followed by the second (Sciuridae, Dipodidae, Gliridae and Arvicolinae) in 2005 and third volume (Cricetinae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae and Castoridae) in 2009. This compilation is the result of 16 years of intensive and unremitting scientific work by the authors. It is based on 2327 small mammals collected by the authors and on Turkish specimens housed in 16 museum and private collections in Turkey, Western and Central Europe and USA. The large amount of data collected have been analysed in great detail, enabling an exact picture to be drawn up of the species' distribution, but also contributing substantially to taxonomic questions. With their single-minded persistence, obdurate determination and unremitting perseverance, the authors have crammed in-depth studies of Turkish mammals into the last 16 years. They have discovered two species new to science. The photographs and illustrations are of the highest professional standards, drawings of a discriminating character are most helpful for identifying species. Many authors will benefit from this work and it will further enhance the interest in Turkish mammals and encourage future research.

Dr. Friederike Spitzenberger<br>Naturhistorisches Museum Wien

## Preface and Acknowledgements

With the $3^{\text {rd }}$ volume of the "Mammals of Turkey and Cyprus" we are finishing the series of our compilations on the mammals of the region. Insectivores (Soricomorpha and Erinaceomorpha sensu Wilson \& Reeder, 2005) have already been elaborated upon (Kryštufek \& Vohralík, 2001), and together with the $2^{\text {nd }}$ volume (Kryštufek \& Vohralík, 2005), the rodents are now complete. Bats were reviewed by Benda \& Horáček (1998) and Benda et al. (2007). Various limitations prevent us to continue this series with Lagomorpha, Artiodactyla, Carnivora and Cetacea, and to complete it. This work remains a challenge for other mammalogists, who would perhaps find themselves in a more advantageous position to execute the task.

Since 2001, when the $1^{\text {st }}$ volume was published, knowledge about the mammals of Turkey and Cyprus has increased tremendously. This has induced us to provide a revised checklist in this volume. Comparing with 141 species listed in 2001, 154 species are currently recognized, i.e. an increase of nearly $10 \%$ in less than a decade. That number is certainly still not the final one and we are just at the beginning of exciting discoveries. Molecular studies in the region are at the very start and majority of taxonomic groups were not subjected to comprehensive multidisciplinary taxonomic revisions. At this stage, we can only guess what new discoveries the future will bring.

Our compilation of rodents from 2005 was reviewed by P. Benda (2005; Lynx, n.s., 36: 132) and G. R. Rácz (2007; J. Mammalogy, 88: 262-263). Both reviewers did appreciate its contribution to mammalogy of the Near East. Both volumes are quoted by mammalogists working in the region, and were utilised during the IUCN Global Mammal Assessment workshop devoted to south-western Asia. All of this gives us great satisfaction. Volume 1 of Rodents is now available also through the web: http:// www2.pms-lj.si/pdf/Mammals_of_Turkey_and_Cyprus.pdf.

Two important works were published in the interim period. The $3^{\text {rd }}$ edition of the "Mammal Species of the Wold" (Wilson \& Reeder, 2005), which was long expected, provides firm taxonomic and nomenclatural standards for future work. Both, taxonomy and nomenclature has changed in comparison to
those we adopted in 2001. This gave us a further reason for providing a revised list of the mammals found in Turkey and Cyprus. Another noteworthy contribution is a review of the Turkish rodent fauna by Yiğit et al. (2006c). Already in 2001 we acknowledged the fact that the period when mammalogists from abroad did the bulk of research on Turkish mammals is over, and that the initiative is firmly in hands of scientists from Turkey. Compilation by Yiğit et al. (2006c) is just one in a line of facts confirming this view. Such a progress is most welcome since it allows more meticulous studies of various problems on the one hand, and also ensures proper conservation measures to be undertaken on the other.

Similarly as was the case with our previous volumes, we owe gratitude to many people and institutions, who supported us during various phases of our work. Again, our first and deepest thanks go to all those who accompanied us during our field work or provided specimens collected on their independent trips to the study area (in alphabetical order): Dr. Michal Andreas (Prague), Dr. Petr Benda (Prague), Dr. Ebru Buruldağ (Edirne), Dr. Jovana Čiháková (Prague), Professor Dr. Daniel Frynta (Prague), Professor Dr. Ivan Horáček (Prague), Dr. Bogdan Horvat (Ljubljana), Mr. František Hubínek (Hřebeč), MSc. Eduard Kletečki (Zagreb), Ing. Alenka Kryštufek (Ljubljana), Professor Dr. Miloš Macholán (Brno), Professor Dr. Beytullah Özkan (Edirne), Dr. Antonín Reiter (Znojmo), Dr. Petr Vořišek (Prague), and Professor Dr. Jan Zima (Brno).

Our work would not have been possible without the efforts of numerous other collectors who provided voucher specimens to various museums around the world, as well as curators who preserved them and made them available to us (in alphabetical order of collections; see Material and methods section for the acronyms of collections): Dr. Paula Jenkins (BMNH), Dr. William Stanley (FMNH), Dr. Georges Lenglet (IRSNB), Dr. Petr Benda and Dr. Miloš Anděra (NM), Dr. Linda Gordon (NMNH), Dr. Friederike Spitzenberger, Dr. Barbara Herzig, Dr. Kurt Bauer, and Simon Engelberger (NMW), Dr. Gerhard Storch and Dr. Dieter Kock (SMF), Professor Dr. Cengiz Kurtonur and Professor Dr. Beytullah Özkan (TUE), Dr. Rainer Hutterer (ZFMK), Dr. Vladimir
S. Lebedev and Dr. Igor Ya. Pavlinov (ZMMU), and Mrs. Saskia Jancke (ZMB).

Our field trips to Turkey and Cyprus were sponsored by the grants from the Ministry of Science and Technology, Republic of Slovenia (B.K.) and by the Grant Agency of the Czech Republic (V.V.); the final work was partly sponsored by the MŠMT ČR, grant 0021620828 (to V.V.) and by the research programme "Biodiversity" by the Agency for Research of the Republic of Slovenia (to B.K.). The SYS-RESOURCE grant enabled B.K. to stay for almost two months in 2002 at the Natural History Museum London. Grants to earlier visits to collections were provided (to B.K.) by the Slovenian Science Foundation (visits to FMNH and NMNH) and the Ministry of Science and Technology of the Republic of Slovenia (the remaining trips). Charles University, Prague, supported four visits by B.K., of about one month each in 2006, 2008 and 2009, which allowed us to concentrate on text and drawings.

Many people supported our work in various ways. B.K. wishes to express his gratitude to the late Dr. Gordon L. Kirkland and Mrs. Carol Kirkland (Shippensburg, USA) who helped him in his travels to visit the USA collections in 1998. Dr. Drago Žepič (Praše) provided accommodation and hospitality during his visit to ZMMU in 2007. Professor Dr. Darko Darovec, the Director of the Science and Research Centre Koper, University of Primorska (Koper), and Dr. Breda Činč Juhant, the Director of the Slovenian Museum of Natural History (Ljubljana) provided continuous support.

In Turkey, both of us enjoyed the hospitality, friendship and support by Professor Dr. Cengiz Kurtonur and Professor Dr. Beytullah Özkan (Trakya University, Edirne), and of Professor Dr. Haluk Kefelioğlu (Ondokuz Mayıs University, Samsun). V.V. wishes to express his particular thanks to the staff of
the Faculty of Science and Literature, Çukurova University in Adana, for their hospitality during his stay in 1993.

Our colleagues and friends with whom we worked in the field during the 1993-1995 expeditions to Turkey shared with us their experience and knowledge, and provided their unpublished results, which significantly strengthened our conclusions. We are particularly grateful to Professor Dr. Jan Zima, Professor Dr. Ivan Horáček, Professor Dr. Miloš Macholán, Professor Dr. Daniel Frynta, and Dr. Petr Benda. Professor Dr. Michael Stubbe (Martin-Luther University, Halle, Germany) allowed us to quote his unpublished results from a field survey for the beaver in Anatolia.

Dr. Jan Hošek (Prague) prepared black-and-white drawings for each genus and Dr. Petr Benda provided blank digital map of the region. The remaining drawings are by B.K. Wherever the illustrations, measurements, or conclusions are based on material not under our surveillance, full credit is given to the respective collection.

Mr. Ciril Mlinar (Ljubljana) photographed the majority of skins for colour plates. We express our gratitude to Dr. Vladimir S. Lebedev and Dr. Igor Ya. Pavlinov (ZMMU) for the loan of Meriones dahli skin, and Dr. Georges Lenglet (IRSNB) for loan of M. vinogradovi collected in Syria by X. Misonne. Photographs on habitats and animals were provided by Dr. Adwan Shehab (Damascus), Dr. Ivan Horáček (Prague), Ing. Tomáš Peš and Mr. Jaroslav Vogeltanz (Zoo Plzeň), Dr. Petra Nová (Prague), Dr. Christian Kern (Berlin), Dr. Eckhard Grimmberger (Berlin), Dr. Beytullah Özkan (Edirne), and Ing. Alenka Kryštufek (Ljubljana).

Many people made most helpful comments and suggestions, thought as usual the views and mistakes remain our own responsibility.

## Introduction

The Mammals of Turkey and Cyprus (Rodents: Cricetinae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae, Castoridae) is closing our compilation on the current knowledge of the rodent fauna in the diverse northeastern corner of the Mediterranean realm: Turkey and the Island of Cyprus.

Similarly as with our previous reviews, the work contains information on the taxonomy, distribution, variation and life history of thirty-two species of hamsters, mice, rats, spiny mice, gerbils, jirds and dipodils, mole rats, calomyscus, crested porcupine, nutria, and beaver.

Each species account contains the following categories of information:

Species names. The valid scientific name (in bold) is followed by the name as it first appeared, together with the name of the authority and the year of publication. We should like to remind the reader that the author's name and the year are in parentheses if the generic name when first used differs from the current one (for the proper use of complete scientific names see Annotated Checklist below). Given are also the junior synonyms originating from Turkey and Cyprus. In exceptional cases we also listed names and type localities from outside this geographic region. In the captions to species accounts, the scientific name is given together with the English vernacular name; here we largely relied on Wilson \& Reeder (2005). Turkish vernacular names are available in Yiğit et al. (2006c).

Taxonomy. This category is added for species or species groups with unstable taxonomy, and includes historical facts and reasons for the actual status. Comparisons with closely related and/or morphologically similar taxa are also provided where appropriate.

Description. Data on the external characters (col-
our, size, body proportions, nipple count, genitals) are followed by cranial and dental descriptions and the chromosomal complement. In some cases we were able to report molecular data derived from recent studies. A table of standard external and selected cranial measurements completes the "Description". Data in the table are given as summarised statistics: sample size ( N ), arithmetic average (mean) and the observed range (min - max).

Variation. While this category is mainly devoted to describe patterns of geographic (i.e. interlocal) variation, cases of individual (i.e. intrapopulation) variation are also given where appropriate. In general, geographic variation is poorly understood in Turkish mammals, even at the level of conventional morphological data sets. Particularly evident is the lack of comprehensive statistical elaborations based on representative samples from large geographic areas. Conventional subspecies are considered although we frequently lacked proof of discontinuity for the majority of the trinomials.

Distribution. The species range in Turkey follows a description of the general distribution. It is accompanied by a dot distribution map with individual records and the approximate range (shaded). Fossil evidence is also provided.

Habitat. This category gives information on the habitat selection of a particular species, i.e. of the plant communities inhabited, the altitudinal range populated, the co-existing small mammals, and the population densities.

Biology. The available information on the various aspects of life of Turkish rodents is sufficient to allow the inclusion of a chapter on biology. Covered are the activity, shelters, reproduction, diet, and predation.

## Annotated Checklist of the Mammals of Turkey and Cyprus

The aim of this list is to update our previous compilation (Kryštufek \& Vohralík, 2001) which is already out of date in many respects. Namely, taxonomy changed on all levels, form the infraspecific level (which benefited tremendously from advances in molecular phylogeography), to classification of mammalian orders. Besides, distributional ranges have become better known and several species, known earlier from adjacent territories, are now documented also for the region under study. And finally, a number of new papers contributed noteworthy information on various biological aspects.

The information from 2001 is repeated when appropriate. We therefore list all the synonyms and provide brief comments relevant for the region, except for species which are reviewed in this volume. Species new to the region, either due to taxonomic advance, or improved knowledge on their distributions, are elaborated upon in greater detail, but not in a monographic fashion.

Classification and taxonomic nomenclature follow Wilson \& Reeder (2005). In several cases we deviate from this source; e.g. we report Myotis aurascens (although it is not recognized by Wilson \& Reeder, 2005), do not distinguish between Myotis blythii and M. oxygnathus, and prefer Plecotus macrobullaris instead of $P$. alpinus.

In total we list 154 species, but presence of three species (Gazella dorcas, Sicista caucasica, Meri-


Figure 1. Division of Turkey and Cyprus into ten geographic regions. Modified from Cook (1997). I - Thrace; II - Marmara; III - Aegean; IV - Taurus; V - central Anatolia; VI - western Black Sea Mts.; VII - eastern Black Sea Mts.; VIII - eastern Anatolia; IX - south-eastern Anatolia; X - Cyprus.
ones libycus) is dubious and requires further verification. Three species from our list are already extinct (Panthera tigris, Ochotona rufescens, Castor fiber), however the number of mammals extirpated in Turkey before modern times is longer: Acinonyx jubatus, Panthera leo, Equus onager, Elephas maximus, and Bos primigenius (Kryštufek \& Vohralík, 2001). At least two species were introduced to Turkey by man (Myocastor coypus, Oryctolagus cuniculus); this list is longer for Cyprus, where only two nonvolant mammals are the survivors from the Pleistocene period; they are both endemic to the island and recognized as such in the last few years (Crocidura cypria and Mus cypriacus). Two species new for science were named since 2005 (Spermophilus taurensis and Mus cypriacus). Further three species result from taxonomic splitting: Erinaceus roumanicus (formerly part of E. concolor), Eptesicus anatolicus (formerly in E. bottae), and Microtus hartingi (formerly in M. guentheri). New evidence puts a further seven species onto the list: Plecotus macrobullaris, Plecotus kolombatovici, Pipistrellus pygmaeus, Microtus schidlovskii, Microtus irani, Nesokia indica, and Calomyscus bailwardi. Some of them were already reported from Turkey in earlier studies, but the evidence was not convincing. On the other hand, we suggest that spiny mice from Cyprus and the vicinity of Silifke are conspecific with Acomys cahirinus from Egypt, rather than representing independent small range endemics.

| Order | Thrace Anatolia |  | Turkish <br> Total | Cyprus | Area <br> Total |
| :--- | ---: | ---: | ---: | ---: | ---: |
| Erinaceomorpha | 1 | 3 | 3 | 1 | 3 |
| Soricomorpha | 7 | 12 | 15 | 2 | 16 |
| Chiroptera | 24 | 36 | 37 | 19 | 37 |
| Carnivora $^{1}$ | 10 | 18 | 19 | 1 | 19 |
| Artiodactyla | 4 | 8 | 8 | 3 | 8 |
| Lagomorpha | 2 | 2 | 2 | 1 | 2 |
| Rodentia | 21 | 59 | 64 | 5 | 65 |
| Total | 69 | 138 | 148 | 32 | 150 |

${ }^{1}$ Not including Monachus monachus
Table 1. Taxonomic breakdown of the mammals of Turkey and Cyprus, by orders (number of species).

Anatolia has twice as many mammal species as Thrace, and about four-times as many as Cyprus. More than half of the mammals on Cyprus are bats. The single most abundant mammalian group in the region are rodents ( $43 \%$ of species), followed by bats (25\%), carnivores (13\%), and soricomorphs (11\%). Five species are endemic for Turkey (Crocidura arispa, Spermophilus taurensis, Dryomys laniger, Microtus anatolicus, Microtus dogramacii), and ranges of further three species are largely within the borders of the country (Spermophilus xanthoprymnus, Myomimus roachi, Spalax xanthodon). As already mentioned, two small mammals are endemic to Cyprus. Therefore, the level of endemism is high.

## Order: Erinaceomorpha Gregory, 1910

Comments: Reviewed by Kryštufek \& Vohralík (2001).

Family: Erinaceidae G. Fischer, 1814
Subfamily: Erinaceinae G. Fischer, 1814
Genus: Erinaceus Linnaeus, 1758
Comments: Hutterer (2005) recognized E. roumanicus to be specifically distinct from E. concolor. This step is supported by molecular (Santucci et al., 1998), morphological (Kryštufek, 2002a) and karyological evidence (Arslan et al., 2008b).

1. Erinaceus concolor Martin, 1838

Erinaceus concolor Martin, 1838. Type loc.: near Trebizon (= Trabzon), Turkey.
Distribution: Anatolia.
2. Erinaceus roumanicus Barrett-Hamilton, 1900

Erinaceus roumanicus Barrett-Hamilton, 1900. Type loc.: Gageni, Prahova, Romania. Distribution: Thrace; possibly also north-eastern Anatolia (Filippucci \& Simson, 1996; Kryštufek, 2002a).

## Genus: Hemiechinus Fitzinger, 1866

3. Hemiechinus auritus (Gmelin, 1770):

Erinaceus auritus Gmelin, 1770. Type loc.: Astrakhan Region, Russia.
Erinaceus calligoni Satunin, 1901. Type loc.: Aralık, Kars, Turkey.

Hemiechinus auritus dorotheae Spitzenberger, 1978. Type loc.: River Pouzis, 14 km east of Mazotos, Larnaca, Cyprus.
Distribution: South-eastern and (marginally) eastern Anatolia; Cyprus.
Comments: Our earlier map (Kryštufek \& Vohralík, 2001) requires correction in Syria and Iraq (Kryštufek \& Vohralík, 2005: 233). Arslan et al. (2009) report C-stained karyotype and NORs on material from Turkey.

Order: Soricomorpha Gregory, 1910
Comments. Reviewed by Kryštufek \& Vohralík (2001).

Family Soricidae G. Fischer, 1814<br>Subfamily Soricinae G. Fischer, 1814<br>Genus: Sorex Linnaeus, 1758

4. Sorex minutus Linnaeus, 1766

Sorex minutus Linnaeus, 1766. Type loc.: Krasno-
yarsk, western Siberia, Russia.
Distribution: Thrace.
5. Sorex volnuchini Ognev, 1922

Sorex minutus volnuchini Ognev, 1922. Type loc.: Kisha River, Adygejskaja Autonomous Region, north-western Caucasus, Russia.
Distribution: Black Sea Mts.; an isolate in East Anatolia.
6. Sorex araneus Linnaeus, 1758

Sorex araneus Linnaeus, 1758. Type loc.: Uppsala, Sweden.
Sorex caucasicus sultanae Şimşek, 1986. Type loc.: Velika Bridge (= ca 5 km south-east to Velika köy), Demirköy, Thrace, Turkey.
Distribution: Thrace.
7. Sorex satunini Ognev, 1921

Sorex araneus satunini Ognev, 1921. Type loc.: Goele, (=Göle), Kars region, Turkey.
Distribution: Black Sea Mts. and adjacent East Anatolia; Marmara.
Comments: Chromosomal and allozyme characterization provided by Macholán (1996a).
8. Sorex raddei Satunin, 1895

Sorex raddei Satunin, 1895. Type loc.: neighbourhood of Kutais, Georgia.
Sorex batis Thomas, 1913. Type loc.: Sumela (= Meryemana), Trabzon, Turkey.
Distribution: eastern Black Sea Mts.

## Genus: Neomys Kaup, 1829

9. Neomys anomalus Cabrera, 1907

Neomys anomalus Cabrera, 1907: Type loc.: San Martin de la Vega, Jarama River, Madrid Province, Spain.
Distribution: Thrace and Anatolia, except much of Black Sea Mts.
10. Neomys teres Miller, 1908

Neomys teres Miller, 1908: Type loc.: 25 miles north of Erzurum, Turkey.
Distribution: Black Sea Mts.; vicinity of Van in East Anatolia.

Subfamily: Crocidurinae Milne-Edwards, 1872
Genus: Crocidura Wagler, 1832
11. Crocidura leucodon (Hermann, 1780)

Sorex leucodon Hermann, 1780. Type loc.: Vicinity of Strasbourg, Bas Rhin, France.
Crocidura leucodon lasius Thomas, 1906. Type loc.: Scalita (= Altindere), Trabzon, Turkey.
Distribution: widespread in Turkey except for south-eastern Anatolia.
Comments: This shrew is in two phylogeographic lineages, separated by the Marmara straits (Dubey et al., 2007a).
12. Crocidura suaveolens (Pallas, 1811)

Sorex suaveolens Pallas, 1811. Type loc.: Khersones, near Sevastopol, Crimea, Russia. Crocidura russula monacha Thomas, 1906. Type loc.: Scalita (= Altindere), Trabzon, Turkey.
Crocidura russula aralychensis Satunin, 1914. Type loc.: marshy shores of River Karasu, near Aralyk (= Aralık), Turkey.
Distribution: widespread in Turkey.
Comments: At least two allopatric phylogeographic lineages occur in Turkey; C. s. guldenstaedtii (Pallas, 1811) (type loc.: near Dusheti,

Georgia) is the subspecies in Anatolia (Dubey et al., 2007b).
13. Crocidura cypria Bate, 1904

Crocidura russula cypria Bate, 1904. Type loc.: Cyprus.
Crocidura suaveolens praecypra Reumer \& Oberli, 1988. Type loc.: Kouklia, Cyprus.
Distribution: Endemic to Cyprus.
Comments. Previously mainly considered as a subspecies of C. suaveolens. Spitzenberger (1978a) ranked it as a species, a view confirmed in a recent phylogenetic study; possibly diverged from the ancestral stock about 1.54 million years ago (Dubey et al., 2007b).
14. Crocidura arispa Spitzenberger, 1971

Crocidura pergrisea arispa Spitzenberger, 1971. Type loc.: 20 km east-south-east of Ulukişla, Niğde.
Distribution: Known from two localities in the Taurus Mts.

Genus: Suncus Ehrenberg, 1832
15. Suncus etruscus (Savi, 1822)

Sorex etruscus Savi, 1822. Type loc.: Pisa, Italy.
Distribution: Scattered across Anatolia; Cyprus; probably Thrace. For updates to our 2001 map cf. Kryštufek \& Vohralík (2005: 233).

Family: Talpidae G. Fischer, 1814
Subfamily: Talpinae G. Fischer, 1814
Genus: Talpa Linnaeus, 1758
16. Talpa europaea Linnaeus, 1758

Talpa europaea Linnaeus, 1758. Type loc.: Engelholm, Kristianstad, Sweden.
Distribution: Thrace.
17. Talpa caucasica Satunin, 1908

Talpa caucasica Satunin, 1908. Type loc.: Stavropol, Russia.
Distribution: Eastern Black Sea Mts.
18. Talpa levantis Thomas, 1906

Talpa caeca levantis Thomas, 1906. Type loc.: Scalita (= Altindere), Trabzon, Turkey.

Distribution: Thrace, Marmara, Black Sea Mts., Bitlis.
19. Talpa davidiana (Milne-Edwards, 1884)

Scaptochirus davidianus Milne-Edwards, 1884. Type loc.: Meydanekbes, SW of Gaziantep, Turkey.
Distribution: Eastern Anatolia (Hakkari, Van); a single historical record from south-eastern Anatolia.

## Order Chiroptera Blumenbach, 1779

Comments. Reviewed by Benda \& Horáček (1998) and Benda et al. (2007).

Family: Pteropodidae Gray, 1821
Genus: Rousettus Gray, 1821
20. Rousettus egyptiacus (E. Geoffroy, 1810)

Pteropus egyptiacus E. Geoffroy, 1810. Type loc.: Giza, Egypt.
Distribution: Coastal slopes of the Taurus Mts.; Cyprus.
Comments: For a review see Albayrak et al. (2008a).

Family: Emballonuridae Gervais, 1855
Genus: Taphozous E. Geoffroy, 1818
21. Taphozous nudiventris Cretzschmar, 1830

Taphozous nudiventris Cretzschmar, 1830. Type loc.: Giza, Egypt.
Distribution: South-eastern Anatolia.

Family: Rhinolophidae Gray, 1825
Genus: Rhinolophus Lacépède, 1799
22. Rhinolophus ferrumequinum (Schreber, 1774)

Vespertilio ferrum-equinum Schreber, 1774. Type loc.: France.
Distribution: Widespread in Turkey; Cyprus.
23. Rhinolophus hipposideros (Bechstein, 1800)

Vespertilio hipposideros Bechstein, 1800. Type loc.: France.
Distribution: Possibly widespread in Turkey; Cyprus.
24. Rhinolophus euryale Blasius, 1853

Rhinolophus euryale Blasius, 1853. Type loc.: Milan, Italy.
Distribution: Possibly widespread in Turkey, except for central Anatolia; occurrence in Cyprus requires confirmation.
25. Rhinolophus mehelyi Matschie, 1901

Rhinolophus mehelyi Matschie, 1901. Type loc.: Bucharest, Rumania.
Distribution: Turkey and Cyprus.
26. Rhinolophus blasil Peters, 1867

Rhinolophus blasii Peters, 1867: Type loc.: Trieste, Italy.
Distribution: Possibly widespread in Turkey, except for central Anatolia; Cyprus.

Family: Vespertilionidae Gray, 1821
Subfamily: Vespertilioninae Gray, 1821
Genus: Vespertilio Linnaeus, 1758
27. Vespertilio murinus Linnaeus, 1758

Vespertilio murinus Linnaeus, 1758. Type loc.: Sweden.
Distribution: Few records available from western Black Sea Mts. and eastern Anatolia.

Genus: Eptesicus Rafinesque, 1820
28. Eptesicus serotinus (Schreber, 1774)

Vespertilio serotinus Schreber, 1774. Type loc.: France.
Distribution: Possibly widespread in Turkey; Cyprus.
29. Eptesicus anatolicus Felten, 1971

Eptesicus anatolicus Felten, 1971. Type loc.: Alanya, Antalya, Turkey.
Distribution: Aegean, the Taurus Mts, Euphrates valley; Cyprus.
Comments: Formerly a subspecies of E. bottae
(Peters, 1869). Specific status confirmed by Benda et al. (2006) and Mayer et al. (2007).

## Genus: Nyctalus Bowdich, 1825

30. Nyctalus leisleri (Kuhl, 1817)

Vespertilio leisleri Kuhl, 1817. Type loc.: Hanau, Hessen-Nassau, Germany.
Distribution: Thrace, Black Sea Mts; Cyprus.
31. Nyctalus noctula (Schreber, 1774)

Vespertilio noctula Schreber, 1774. Type loc.: France.
Distribution: Thrace; rare in Anatolia (Taurus Mts., Euphrates valley); possibly also Cyprus.
32. Nyctalus lasiopterus (Schreber, 1780)

Vespertilio lasiopterus Schreber, 1780. Type loc.: northern Italy.
Distribution: Three records are available from coastal Anatolia (Yiğit et al., 2008b); Cyprus.

Genus: Pipistrellus Kaup, 1829
33. PIPISTRELLUS PIPISTRELLUS (Schreber, 1774)

Vespertilio pipistrellus Schreber, 1774. Type loc.: France.
Distribution: Turkey and Cyprus.
34. Pipistrellus pygmaeus (Leach, 1825)

Vespertilio pygmaeus Leach, 1825. Type loc.: Dartmoor, Devonshire, England.
Pipistrellus pygmaeus cyprius Benda, 2007 (In: Benda et al., 2007). Type loc.: Kryos River near the upper end of the Kalidonia Trail., ca. 2 km south-west of Troodos, Troodos Mts, district of Lemassol, Cyprus.
Distribution: Turkey and Cyprus.
Comments: Endemic subspecies (P. p. cyprius) occurs on Cyprus.
35. Pipistrellus nathusii (Keyserling \& Blasius, 1839)

Vespertilio nathusii Keyserling \& Blasius, 1839. Type loc.: Berlin, Germany.
Distribution: Thrace, Marmara, central Anatolia, Lake Van.
36. Pipistrellus kuhlit (Kuhl, 1817)

Vespertilio kuhlii Kuhl, 1817. Type loc.: Trieste, Italy.
Distribution: Turkey and Cyprus.

## Genus: Hypsugo Kolenati, 1856

37. Hypsugo Savii (Bonaparte, 1837)

Vespertilio savii Bonaparte, 1837. Type loc.: Italy, Pisa.
Distribution: Anatolia and Cyprus.
Genus: Plecotus E. Geoffroy Saint-Hilaire, 1818
Comments: Revised by Benda et al. (2004) and Spitzenberger et al. (2006).
38. PLECotus auritus (Linnaeus, 1758)

Vespertilio auritus Linnaeus, 1758. Type loc.: Sweden.
Distribution: Thrace and Anatolia.
39. Plecotus austriacus (J. Fischer, 1829)

Vespertilio auritus austriacus J. Fischer, 1829. Type loc.: Vienna, Austria.
Distribution: Thrace.
Comments: Localities recently published for Anatolia (Karataş et al., 2003) probably relate to $P$. macrobullaris.
40. Plecotus macrobullaris Kuzyakin, 1965

Plecotus macrobullaris Kuzyakin, 1965. Type loc.: Ordzonikidze (= Vladikavkaz), North Ossetia, Russia.
Distribution: Anatolia.
41. Plecotus kolombatovici Đulić, 1980

Plecotus austriacus kolombatovici Đulić, 1980.
Type loc.: Island of Korčula, Dalmatia, Croatia. Distribution: Southern Anatolia and Cyprus.

## Genus: Barbastella Gray, 1821

42. Barbastella barbastellus (Schreber, 1774)

Vespertilio barbastellus Schreber, 1774. Type loc.: Burgundy, France.
Distribution: Thrace, eastern Black Sea Mts., central Anatolia and the Euphrates Valley.

## Genus: Отолүстeris Peters, 1859

43. Оtonycteris hemprichi Peters, 1859

Otonycteris hemprichi Peters, 1859. Type loc.: Nile Valley south of Aswan, Egypt.
Distribution: A single record from south-eastern Anatolia.

Subfamily: Myotinae Tate, 1942
Genus: Myoтis Kaup, 1829
44. Myotis mystacinus (Kuhl, 1817)

Vespertilio mystacinus Kuhl, 1817. Type loc.: Germany.
Distribution: Eastern Anatolia.
45. Myotis aurascens Kuzjakin, 1935

Myotis mystacinus aurascens Kuzjakin, 1935.
Type loc.: Kurkužin village, near Vladikavkaz, the Caucasus Mts, Russia.
Distribution: Widespread in Turkey.
46. Myotis nipalensis (Dobson, 1871)

Vespertilio nipalensis Dobson, 1871. Type loc.: Katmandu, Nepal.
Distribution: Eastern Anatolia.
47. Myotis brandtiI (Eversmann, 1845)

Vespertilio brandtii Eversmann, 1845. Type loc.: Spasskoe, Bolšoj Ik River, southern Ural Mts, Russia.
Distribution: Eastern Black Sea Mts.
48. Myotis emarginatus (E. Geoffroy, 1806)

Vespertilio emarginatus E. Geoffroy, 1806. Type loc.: Charlemont, Ardennes, France.
Distribution: Turkey and Cyprus.
49. Myotis nattereri (Kuhl, 1817)

Vespertilio nattereri Kuhl, 1817. Type loc.: Hanau, Hessen, Germany.
Distribution: Turkey and Cyprus.
50. Myotis bechsteini (Kuhl, 1817)

Vespertilio bechsteini Kuhl, 1817. Type loc.: Hanau, Hessen, Germany.
Distribution: Thrace, eastern Black Sea Mts., Taurus.
51. Муотіs муотіs (Borkhausen, 1897)

Vespertilio myotis Borkhausen, 1897. Type loc.:
Thuringia, Germany.
Distribution: Widespread in Turkey.
52. Myotis blythil (Tomes, 1857)

Vespertilio blythii Tomes, 1857. Type loc.: Nasirabad, Rajasthan, India.
Distribution: Turkey and Cyprus.
53. Myotis daubentonii (Kuhl, 1817)

Vespertilio daubentonii Kuhl, 1817. Type loc.: Hessen, Germany.
Distribution: Thrace, Marmara, eastern Black Sea Mts.
54. Myotis capacciniI (Bonaparte, 1837)

Vespertilio capaccinii Bonaparte, 1837. Type loc.: Sicily, Italy.
Distribution: Turkey and possibly Cyprus.
Subfamily: Miniopterinae Dobson, 1875
Genus: Miniopterus Bonaparte, 1837
55. Miniopterus schreibersil (Kuhl, 1817)

Vespertilio schreibersii Kuhl, 1817. Type loc.:
Kolumbacs cave, near Coronini, Rumania.
Distribution: Turkey and Cyprus.
Comments: Molecular evidence suggests presence of two subspecies in Turkey (Bilgin et al., 2006).

Family: Molossidae Gervais, 1856
Genus: Tadarida Rafinesque, 1814
56. Tadarida teniotis (Rafinesque, 1814)

Cephalotes teniotis Rafinesque, 1814. Type loc.: Giza, Egypt.
Distribution: Anatolia and Cyprus.

## Order: Carnivora Bowdich, 1821

Comments: No comprehensive recent review available.

Family: Canidae G. Fischer, 1817
Genus: Canis Linnaeus, 1758
57. Canis lupus Linnaeus, 1758

Canis lupus Linnaeus, 1758. Type loc.: Sweden. Distribution: Thrace and Anatolia.
58. Canis aureus Linnaeus, 1758

Canis aureus Linnaeus, 1758. Type loc.: Benna Mountains, Laristan, Iran.
Distribution: Thrace and Anatolia (coastal regions and south-east).

Genus: Vulpes Frisch, 1775
59. Vulpes vulpes (Linnaeus, 1758)

Canis vulpes Linnaeus, 1758. Type loc.: Upsala, Sweden.
Vulpes kurdistanica Satunin, 1906. Type loc.: Gelsk valley, Kars, Turkey.
Vulpes indutus Miller, 1907. Type loc.: Cape Pyla, Cyprus.
Vulpes vulpes anatolica Thomas, 1920. Type loc.: Smyrna (=İzmir), Turkey.
Distribution: Widespread in Turkey and Cyprus.

## Family: Ursidae G. Fischer, 1817 <br> Genus: URSUS Linnaeus, 1758

60. Ursus arctos Linnaeus, 1758

Ursus arctos Linnaeus, 1758. Type loc.: Northern Sweden.
Distribution: Marmara, Black Sea Mts., Taurus Mts., eastern Anatolia.

Family: Mustelidae G. Fischer, 1817
Subfamily: Mustelinae G. Fischer, 1817
Genus: Martes Pinel, 1792
61. Martes martes (Linnaeus, 1758)

Mustela martes Linnaeus, 1758. Type loc.: Upsala, Sweden.
Distribution: Marmara, Black Sea Mts., Aegean, Taurus Mts., eastern Anatolia.
62. Martes foina (Erxleben, 1777)

Mustela foina Erxleben, 1777. Type loc.: Germany.
Distribution: Widespread in Turkey (for Anatolia see Albayrak et al., 2008b).

Genus: Mustela Linnaeus, 1758
63. Mustela nivalis Linnaeus, 1766

Mustela nivalis Linnaeus, 1766. Type loc.: Sweden.
Distribution: Thrace and Anatolia; subfossil evidence also from Cyprus.
64. Mustela putorius Linnaeus, 1758

Mustela putorius Linnaeus, 1758. Type loc.: Sweden.
Distribution: Thrace.

## Genus: Vormela Blasius, 1884

65. Vormela peregusna (Güldenstaedt, 1770)

Mustela peregusna Güldenstaedt, 1770. Type loc.: steppes at lower Don River, Rostov region, Russia.
Distribution: Thrace and Anatolia (except southeast).

Genus: Meles Brisson, 1762
66. Meles meles (Linnaeus, 1758)

Ursus meles Linnaeus, 1758. Type loc.: Upsala, Sweden.
Distribution: Widespread in Turkey.
Subfamily: Lutrinae, Bonaparte, 1838
Genus: Lutra Brisson, 1762
67. Lutra lutra (Linnaeus, 1758)

Mustela lutra Linnaeus, 1758. Type loc.: Upsala, Sweden.
Distribution: Widespread in Turkey.
Family: Herpestidae Bonaparte, 1845
Genus: Herpestes Illiger, 1811
68. Herpestes ichneumon (Linnaeus, 1758)

Viverra ichneumon Linnaeus, 1758. Type loc.: Egypt.
Distribution: Aegean, eastern Taurus Mts. and south-eastern Anatolia.

Family: Hyaenidae Gray, 1821
Genus: Hyaena Brisson, 1762
69. Hyaena hyaena (Linnaeus, 1758)

Canis hyaena Linnaeus, 1758. Type loc.: Benna Mountains, Laristan, Iran.
Distribution: Marmara (marginally), Aegean, Taurus Mts. and south-eastern Anatolia.

Family: Felidae G. Fischer, 1817
Subfamily: Felinae G. Fischer, 1817
Genus: Felis Linnaeus, 1758
70. Felis silvestris Schreber, 1777

Felis (Catus) silvestris Schreber, 1777. Type loc.: Germany.
Felis silvestris trapezia Blackler, 1916. Type loc.: Khotz (= Çosandere), Trabzon, Turkey. Distribution: Widespread in Turkey.
71. FeLIS Chaus Schreber, 1777

Felis chaus Schreber, 1777: Type locality: Terek River, Northern Caucasus, Dagestan.
Distribution: scattered in the Aegean, central Anatolia, eastern Taurus Mts., south-eastern Anatolia, Black Sea Mts.

Genus: Lynx Kerr, 1792
72. LyNX LYNX (Linnaeus, 1758)

Felis lynx Linnaeus, 1758. Type loc.: Wennersborg, Sweden.
Distribution: Possibly present throughout Anatolia, except for south-east.

## Genus: Caracal Gray, 1843

73. Caracal caracal (Schreber, 1776)

Felis caracal Schreber, 1776. Type loc.: Table Mountain near Cape Town, South Africa.
Distribution: Extremely rare, recorded in the Aegean and in eastern Anatolia.

Subfamily: Pantherinae Pocock, 1917
Genus: Panthera Oken, 1816
74. Panthera pardus (Linnaeus, 1758)

Felis pardus Linnaeus, 1758. Type loc.: Egypt.

Felis tulliana Valenciennes, 1856. Type loc.: Ninfi, 40 km east of İzmir, Turkey.
Distribution: Perhaps survived only in south-eastern and eastern Anatolia, and in eastern Black Sea Mts.
75. Panthera tigris (Linnaeus, 1758)

Felis tigris Linnaeus, 1758. Type loc.: India.
Distribution: Survived into $20^{\text {th }}$ century in eastern Anatolia where extirpated before 1950.

Family: Phocidae Gray, 1821
Genus: Monachus Fleming, 1822
76. Monachus monachus (Hermann, 1779)

Phoca monachus Hermann, 1779. Type loc.: Dalmatia, Croatia.
Distribution: Between 1994-1998 still present along all coasts of Turkey. Populations were estimated at $2-3$ individuals in the Black Sea, $\geq 1$ in the Sea of Marmara, $\geq 63$ in the Aegean Sea, and $\geq 37$ in the Mediterranean Sea (Güçlüsoy et al., 2004).

## Order: Artiodactyla Owen, 1848

Comments. No comprehensive recent review available.

Family: Suidae Gray, 1821
Genus: Sus Linnaeus, 1758
77. Sus scrofa Linnaeus, 1758

Sus scrofa Linnaeus, 1758. Type loc.: Germany. Distribution: Widespread in Turkey; in 1990s introduced to Cyprus (Hadjisterkotis, 2000).

Family: Cervidae Goldfuss, 1820
Genus: Cervus Linnaeus, 1758
78. Cervus elaphus Linnaeus, 1758

Cervus elaphus Linnaeus, 1758: Type locality: southern Sweden.
Distribution: Fenced populations scattered across Turkey (Thrace, Marmara, Black Sea Mts., Taurus Mts.).

Genus: Dama Frisch, 1775
79. Dama dama (Linnaeus, 1758)

Cervus dama Linnaeus, 1758. Type locality: Sweden.
Distribution: Turkey and Cyprus.
Genus: Capreolus Gray, 1821
80. Capreolus capreolus (Linnaeus, 1758)

Cervus capreolus Linnaeus, 1758. Type loc.: Sweden.
Capreolus capreolus armenius Blackler, 1916. Type loc.: Sumela (= Meryemana), Trabzon, Turkey.
Capreolus capreolus whittalli Barclay, 1936. Type loc.: near Alemdagh, 15 miles from Moda, İstanbul, Turkey.
Distribution: Thrace, Marmara, Black Sea Mts., Taurus Mts., scattered in eastern Anatolia.

## Family: Bovidae Gray, 1821

Subfamily: Antilopinae Gray, 1821
Genus: Gazella de Blainville, 1816
Comments: Reviewed by Ölçer (2001); see also our earlier comments (Kryštufek \& Vohralík, 2005: 236).
81. Gazella subgutturosa (Güldenstaedt, 1780)

Antilope subgutturosa (Güldenstaedt, 1780): Type locality: steppes of east Transcaucasica, Azerbaijan.
Distribution: Information on the original range contradictory, but possibly restricted to southeastern Anatolia.
82. Gazella dorcas (Linnaeus, 1758)

Capra dorcas Linnaeus, 1758. Type loc.: Lower Egypt.
Comments: Presence in Turkey is under question.
Subfamily: Caprinae Gray, 1821
Genus: Rupicapra de Blanville, 1816
83. RUPICAPRA RUPICAPRA (Linnaeus, 1758)

Capra rupicapra Linnaeus, 1758. Type loc.: Switzerland.
Rupicapra rupicapra asiatica Lydekker, 1908.

Type loc.: Trabzon, Turkey.
Distribution: Eastern Black Sea Mts., eastern Anatolia.

Genus: Capra Linnaeus, 1758
84. Capra aegagrus Erxleben, 1777

Capra aegagrus Erxleben, 1777. Type loc.: Daghestan District of the Caucasus, southern Russia. Capra florstedti Matschie, 1907. Type loc.: Bulghar (= Bolkar) Dağları, Turkey.
Capra cilicica Matschie, 1907. Type loc.: Bulghar (= Bolkar) Dağları, Turkey.
Distribution: Taurus Mts, central Anatolia (marginal), eastern Anatolia, eastern Black Sea Mts.

Genus: Ovis Linnaeus, 1758
85. Ovis orientalis Gmelin, 1774

Ovis orientalis Gmelin, 1774: Type locality: Eastern Alborz (Elburz) Mountains, Iran.
Ovis gmelinii Blyth, 1841. Type loc.: Erzurum, Turkey (probably erroneous).
Ovis anatolica Valenciennes, 1856. Type loc.: Bulghar (= Bolkar) Dağ, Cilician Taurus, Turkey. Ovis ophion armeniana Nasonov, 1919. Type loc.: Ağrı Dağı, near Doğubayazıt, Turkey.
Distribution: Central Anatolia, Taurus Mts., eastern Anatolia; Cyprus.

## Order: Lagomorpha Brandt, 1855

Comments. No comprehensive recent review available.

Family: Оснотоnidae Thomas, 1897
Genus: Оснотола Link, 1795
86. Оснотолa RUFESCENS (Gray, 1842)

Lagomys rufescens Gray, 1842. Type loc.: Baber’s (?) Tomb, Kabul, Afghanistan.
Comments: Čermák et al. (2006) uncovered a mandibular fragment in Ishak Paşa Sarayi (Ağrı Province) at $1,950 \mathrm{~m}$ of elevation. The fragment matches recent $O$. rufescens from Iran but also differs by a more robust mandibular corpus. This record proves an earlier wider range of $O$. rufescens, which is no longer a member of Turkish mammal fauna.

Family: Leporidae Fischer, 1817
Genus: Lepus Linnaeus, 1758
87. Lepus europeus Pallas, 1778

Lepus europeus Pallas, 1778. Type loc.: southwestern Poland.
Lepus cyprius Barrett-Hamilton, 1903. Type loc.: Cyprus.
Distribution: Widespread in Turkey; Cyprus.
Genus: Oryctolagus Lilljeborg, 1873
88. Oryctolagus cuniculus (Linnaeus, 1758)

Lepus cuniculus Linnaeus, 1758. Type loc.: Germany.
Distribution: Feral on some islands offshore Turkey.

## Order: Rodentia Bowdich, 1821

Comments: Reviewed in Yiğit et al. (2006c), and Kryštufek \& Vohralík (2005, this volume).

## Family: Sciuridae G. Fischer, 1817

Subfamily: Sciurinae G. Fischer, 1817
Genus: Sciurus Linnaeus, 1758
89. Sciurus vulgaris Linnaeus, 1758

Sciurus vulgaris Linnaeus, 1758. Type loc.: Upsala, Sweden.
Distribution: Thrace; introduced to the easternmost Black Sea Mts.
90. Sciurus anomalus Gmelin, 1778

Sciurus anomalus Gmelin, 1778. Type loc.: Sabeka, 25 km south-west of Kutais, Georgia.
Distribution: Anatolia and the Island of Gökçeada; introduced to Belgrad Forest near İstanbul.
Comments: With Gmelin, 1778 (instead of Gueldenstaedt, 1785) as the authority, we follow Thorington \& Hoffmann (2005). Tez et al. (2006) reported on interpopulation variability in a position of autosomal centromers; Albayrak \& Arslan (2006) provide morphological and karyological information; they also call for immediate conservation action. Oshida et al. (2009) sequenced a complete cytochrome $b$ gene in three individuals from Anatolia.

Subfamily: Xerinae Osborn, 1910
Genus: Spermophilus F. Cuvier, 1825
Comments: Reviewed by Gündüz et al. (2007a) and Özkurt et al. (2007).
91. Spermophilus citellus (Linnaeus, 1766)

Mus citellus Linnaeus, 1766. Type loc.: Wagram, Austria.
Citellus citellus thracius Mursaloğlu, 1964. Type
loc.: south-eastern slope of Murattepe near Yenibedir, Lüleburgaz, Turkey.
Distribution: Thrace.
Comments: Sousliks from Turkish Thrace belong to the Southern phylogeographic group of S. citellus, which holds basal position in phylogenetic tree (Kryštufek et al., 2009a). For new biological information see Özkurt et al. (2005).
92. SPERMOPHILUS XANTXOPRYMNUS (Bennett, 1835)

Citillus xanthoprymnus Bennett, 1835. Type loc.: Erzurum Turkey.
Citellus schmidti Satunin, 1908. Type loc.: Diğor, Kars, Turkey.
Citellus citellus gelengius Mursaloğlu, 1965. Type loc.: 5 km east of Koçaş, Aksaray, Turkey.
Distribution: Anatolia. Özkurt et al. (2007) confirmed our earlier presumptions on the presence of S. xanthoprymnus in the Adana region and in western Iran. Despite of strong arguments against the occurrence of the Anatolian ground squirrel to the south of Anatolia (summarised in Kryštufek \& Vohralík, 2005), Thorington \& Hoffmann (2005) continue to report this species for Syria and Israel. Range was evidently more extensive during Early Holocene and encompassed also Mesopotamia; ground squirrel (reported as Spermophilus citellus) is part of a pre-pottery Neolithic faunal assemblage of Göbekli Tepe near Şanliurfa, dated about 9,500 years before present (Peters \& Schmidt, 2004).
Comments. Phylogeographic study uncovered five allopatric or parapatric lineages (Gündüz et al., 2007a), consequently invalidate an earlier division into two subspecies. For new biological information see Gür \& Gür (2005), Özkurt et al. (2005), and Gür \& Barlas (2006).
93. Spermophilus taurensis Gündüz, Jaarola, Tez, Yeniyurt, Polly \& Searle, 2007
Spermophilus taurensis Gündüz, Jaarola, Yeniyurt, Polly \& Searle, 2007a. Type loc.: Yarpuz, Akseki, 111 km east of Antalya, Turkey.
Spermophilus torosensis Özkurt, Sözen, Yiğit, Kandemir, Çolak, Gharkheloo \& Çolak, 2007. Type loc.: Çatılıçukur village, Eşekçukuru area of Salamut Plateau, district Antalya, Taurus Mts., Turkey.
Comments: We pointed on the taxonomic inconsistencies regarding ground squirrels from the Taurus Mts. (Kryštufek \& Vohralík, 2005), and a new species was named from this area in 2007; taurensis holds priority over torosensis (Gündüz et al., 2007b). A multigenic study place it as a sister species to S. citellus and the divergence time between the two is estimated to be about 2,5 million years (Gündüz et al., 2007a). Diploid number of chromosomes in S. taurensis is $2 \mathrm{n}=40$. The new species differs from S. xanthoprymnus in external morphology (tail is wider and longer, with a black tip) but in skull morphology resembles more closely $S$. xanthoprymnus than $S$. citellus (Gündüz et al., 2007a). Dorsum is light reddish brown, more reddish than in S. citellus and $S$. xanthoprymnus, speckled; underside is gray to white. Dimensions of type specimens of taurensis and torosensis (both females) are (in mm ; except body mass, in g): length of head and body 201/194; length of tail 64/62; length of hind foot $43 / 39$; length of ear $6 / 7$; body mass 200.7/260; condylobasal length of skull 44.5/41.5; zygomatic breadth 29.3/28.5; length of maxillary tooth-row 9.3/9.9. Number of alveoli is same as in S. citellus (Özkurt et al., 2007).
Spermophilus taurensis has a small allopatric range in the Taurus Mts., from Erenkaya (Meram) in the north, to Morca Yaylası (Çukurköy, Akseki) in the south, and from the Salamut Plateau in the west, to Mut (Mersin) in the east; cf. also Fig. 24 in Kryštufek \& Vohralík, 2005: 48) where tentative range is indicated by triangles (pts. 2325). The species inhabits rocky areas with sparse vegetation (Marrubium globosum, Phlomis armeniaca, Astragalus creticus, Euphorbia kotschyana, Daphne oleoides, Bromus tomentollus Festuca valesiaca) above $1,500 \mathrm{~m}$ of elevation; the
habitat is also occupied by Dryomys laniger, Apodemus mystacinus, Chionomys nivalis, and Spalax xanthodon (Özkurt et al., 2007).

Family: Dipodidae G. Fischer, 1817<br>Subfamily: Allactaginae Vinogradov, 1925<br>Genus: Allactaga F. Cuvier, 1837

94. Allactaga elater (Lichtenstein, 1828)

Dipus elater Lichtenstein, 1828. Type loc.: Inderskij Region, Gur' ev District, Western Kazakhstan. Distribution: Aralık in eastern Anatolia.
95. Allactaga euphratica Thomas, 1881

Allactaga euphratica Thomas, 1881. Type loc.: Iraq.
Allactaga euphratica kivanci Çolak \& Yiğit, 1998. Type loc.: Çaylıkköyü, Urfa, Turkey.

Distribution: South-east Anatolia.
95. Allactaga williamsi Thomas, 1897

Allactaga williamsi Thomas, 1897: Type loc.: near Van Lake, Turkey.
Allactaga williamsi laticeps Nehring, 1903. Type
loc.: Gökçekısık-Eskişehir, Konya, Turkey.
Distribution: Central and eastern Anatolia.

Subfamily: Sicistinae Allen, 1901
Genus: Sicista Gray, 1827
96. Sicista caucasica Vinogradov, 1925

Sicista caucasica Vinogradov, 1925. Type loc.: Majkop, Krasnodar Region, Caucasus, Russia.
Comments: Our earlier inclusion of Sicista caucasica into the list of Turkish mammals (Kryštufek \& Vohralík, 2005) followed Yiğit et al. (2003) who reported this species from "Kars and Ardahan". In their review of Turkish rodents Yiğit et al. (2006c) stated for the birch mouse "to be most likely distributed in birch forests around Posof province". The only reliable evidence is therefore a subfossil mandibular fragment from the Marmara region, which does not allow specific identification (Kryštufek \& Vohralík, 2005).

Family: Gliridae Muirhead, 1819
Subfamily: Glirinae Muirhead, 1819
Genus: Glis Brisson, 1762
97. Glis glis (Linnaeus, 1766)

Sciurus glis Linnaeus, 1766. Type loc.: Slovenia. Myoxus glis orientalis Nehring, 1903. Type loc.: near Scutari (=Üsküdar), Alan Dağ (= Alem Dağı), İstanbul, Turkey.
Glis glis spoliatus Thomas, 1906. Type loc.: Khotz (= Çosandere), Trabzon, Turkey.
Distribution: Thrace, Marmara, Black Sea Mts.
Subfamily: Leithiinae Lydekker, 1896
Genus: Muscardinus Kaup, 1829
98. Muscardinus avellanarius (Linnaeus, 1758)

Mus avellanarius Linnaeus, 1758. Type loc.: Sweden.
Muscardinus trapezius Miller, 1908. Type loc.: Khotz (= Çosandere), Trabzon, Turkey.
Muscardinus avellanarius abanticus Kıvanç, 1983. Type loc.: Abant Gölü, Bolu, Turkey. Distribution: Marmara, Black Sea Mts.

Genus: Dryomys Thomas, 1906
99. Dryomys nitedula (Pallas, 1778)

Mus nitedula Pallas, 1778. Type Loc.: lower Volga River, Russia.
Dryomys nitedula phrygius Thomas, 1907. Type loc.: Uşak, Murat Dağı, Turkey.
Distribution: Thrace and Anatolia (except for the south-east).
Comments: Yiğit et al. (2006c) list D. pictus as a separate species with a range in Hakkari Province.
100. Dryomys laniger Felten \& Storch, 1968 Dryomys laniger Felten \& Storch, 1968. Type loc.: Çığlıkara, Bey Mts., Antalya, Turkey.
Distribution: Taurus and eastern Anatolia.

Genus: Myomimus Ognev, 1924
101. Myomimus roachi (Bate, 1937)

Philistomys roachi Bate, 1937. Type loc.: Tabun Cave, Mt. Carmel, Israel (Pleistocene).

Distribution: Thrace, Marmara, Aegean Anatolia; subfossil record also from the Taurus Mts.
102. Myomimus setzeri Rossolimo, 1976.

Myomimus setzeri Rossolimo, 1976. Type loc.: 4 km west of Bane, Kordestan Prov., Iran. Distribution: Eastern Anatolia.

## Genus: Eliomys Wagner, 1840

## 103. Eliomys melanurus Wagner, 1840

Eliomys (Myoxus) melanurus Wagner, 1840. Type loc.: Mt. Sinai, Sinai.
Distribution: Yiğit et al. (2006c) consider report for Şanlı Urfa Province to be reliable.

Family: Cricetidae G. Fischer, 1817
Subfamily: Arvicolinae Gray, 1821
Comments: Shenbrot \& Krasnov (2005) mapped distribution in great details; Buzan et al. (2008) provided a novel view on evolutionary relationships.

## Genus: Ellobius G. Fischer, 1814

104. Ellobius lutescens Thomas, 1897

Ellobius lutescens Thomas, 1897. Type loc.: Van, Kurdistan, Turkey.
Distribution: Eastern Anatolia.

## Genus: Prometheomys Satunin, 1901

105. Prometheomys schaposchnikowi Satunin, 1901

Prometheomys schaposchnikowi Satunin, 1901. Type loc.: Gudaur, south of Krestovyj Pass, Dušeti District, Georgia.
Distribution: Extreme north-eastern Black Sea Mts.

Genus: Myodes Pallas, 1811
Comments. Known earlier as Clethrionomys.
106. Myodes glareolus (Schreber, 1780)

Mus glareolus Schreber, 1780. Type loc.: Island of Lolland, Denmark.
Evotomys ponticus Thomas, 1906. Type loc.: Sumela (= Meryemana), Trabzon, Turkey.
Distribution: Marmara and Black Sea Mts.

## Genus: Arvicola Lacépède, 1799

107. Arvicola amphibius (Linnaeus, 1758)

Mus amphibius Linnaeus, 1758. Type loc.: England.
Distribution: Thrace, Anatolia (except Aegean, majority of Taurus Mts. and south-east).
Comments: A. amphibius has priority over A. terrestris (Musser \& Carleton, 2005), but see comments in Corbet (1978).

## Genus: Microtus Schrank, 1798

108. Microtus subterraneus (de Sélys Longchamps, 1836)

Arvicola subterraneus de Sélys Longchamps, 1836. Type loc.: Waremme, Liége, Belgium.

Pitymys majori fingeri Neuhäuser, 1936. Type loc.: Karadere, Bolu, Turkey.
Distribution: Thrace, Aegean, Taurus Mts., northern Anatolia.
109. Microtus majori Thomas, 1906

Microtus (Pitymys) majori Thomas, 1906. Type loc.: Sumela (= Meryemana), Trabzon, Turkey. Microtus (Arbusticola) rubelianus Schidlovsky, 1919. Type loc.: near Trabzon, Turkey.

Distribution: Eastern Black Sea Mts., eastern Anatolia.
110. Microtus daghestanicus Schidlovsky, 1919

Microtus (Arbusticola) rubelianus daghestanicus Schidlovsky, 1919. Type loc.: Karda, Gunibskij Region, Daghestan, Caucasus.
Distribution: North-eastern Anatolia.
111. Microtus arvalis (Pallas, 1778)

Mus arvalis Pallas, 1778. Type loc.: Puskhin town, Leningrad Region, Russia.
Distribution: eastern Anatolia.
Comments: We reported this species as M. obscurus (Kryštufek \& Vohralík, 2005) which is genetically very close to M. arvalis, and now considered to be part of it (Musser \& Carleton, 2005).
112. Microtus levis Miller, 1908

Microtus levis Miller, 1908: Type Locality: Gage-
ni, Prahova, Romania.
Distribution: Widespread in Thrace and Anatolia (except south-east).
Comments: We reported this species as M. rossiaemeridionalis and argued against levis (Kryštufek \& Vohralík, 2005).
113. Microtus socialis (Pallas, 1773)

Mus socialis Pallas, 1773. Type Locality:
probably Inderskij Region, Gur'ev District, between Volga and Ural rivers, Kazakhstan.
Distribution: Central, eastern, and south-eastern Anatolia.
114. Microtus irani Thomas, 1921

Microtus irani Thomas, 1921: Type Locality: Bagh-i- Rezi, Fars Province, Shiraz, Iran.
Comments: Material from Balkusan, which we described but not identified to the species level (Kryštufek \& Vohralík, 2005: 187-8) is genetically very close to $M$. irani from Shiraz (Kryštufek et al., 2009b). Note that Yiğit et al. (2006c) use irani in a different content.
115. Microtus anatolicus Kryštufek \& Kefelioğlu, 2001
Microtus anatolicus Kryštufek \& Kefelioğlu, 2001. Type loc.: Yapalı köyü, Cihanbeyli, Konya, Turkey.
Distribution: Still known only from the type locality.
Comments: This species is genetically close to $M$. socialis and M. irani (Kryštufek et al., 2009b).
116. Microtus schidlovskir Argyropulo, 1933

Microtus (Sumeriomys) colchicus schidlovskii Argyropulo, 1933. Type loc.: Leninakan District, north-western Armenia; restricted to "vicinity of Nalband railway station, 35 km east from Leninakan" by Golenishchev et al. (2002).
Distribution: known from two localities (Özalp and Yüksekova) in eastern Anatolia.
Comments: Schidlovsky's vole is one among several sibling species from $M$. socialis group. Achverdjan et al. (1991a,b) were the first to demonstrate its specific distinctiveness. Although still considered conspecific with M. socialis by Musser \& Carleton (1993), it was recognised as a full
species by most recent Russian authors (e.g. Gromov \& Erbajeva, 1995; Golenishchev et al., 2000, 2002) and recently also by Musser \& Carleton (2005).
In comparison to M. socialis, Schidlovsky's vole has smaller bullae, develops supraorbital ridges (Achverdjan et al., 1991a) and shows a very long medial process of a distal baculum (Argyropulo, 1933a; Golenishchev et al., 2002). Previously known only from western Armenia and Georgia (Achverdjan et al. 1991a), but range limits not resolved (Musser \& Carleton, 2005; see also Shenbrot \& Krasnov, 2005).
Our earlier prediction on the presence of $M$. schidlovskii in Turkey (Kryštufek \& Vohralík, 2005) was recently confirmed by Yiğit et al. (2006a). Records in eastern Anatolia (Özalp and Yüksekova) considerably extend range border southwards and suggest possible presence also in Iran. The karyotype of Turkish material ( $2 \mathrm{~N}=60$, $\mathrm{NF}_{\mathrm{a}}=58$ ) is identical to the one reported from Georgia (Yiğit et al., 2006a).
117. Microtus guentheri (Danford \& Alston, 1880)

Arvicola guentheri Danford \& Alston, 1880. Type Locality: Maraş (= Kahramanmaraş), Turkey. Microtus (Sumeriomys) güntheri shevketi Neuhäuser, 1936. Type loc.: Tarsus, Mersin, Turkey. Distribution: south-eastern Anatolia and the eastern Mediterranean coast further south, but borders still need to be resolved.
Comments: Our molecular results (Kryštufek et al., 2009b) confirmed an earlier view on cryptic diversity in M. guentheri (Yiğit \& Çolak, 2002). Therefore we recognize two species, as advocated by Yiğit \& Çolak (2002) and Yiğit et al. (2006c), albeit our nomenclature differs (for arguments see Kryštufek \& Vohralík, 2005): M. guentheri and M. hartingi. Synonymy is based on the examination of the following types: guentheri, phillistinus (extralimital; see Kryštufek \& Vohralík, 2005, p. 16) and shevketi (see below under Voucher specimens).
118. Microtus hartingi Barret-Hamilton, 1903

Microtus (Microtus) hartingi Barret-Hamilton, 1903. Type loc.: Larissa, Thessaly, Greece. Microtus lydius Blackler, 1916. Type loc.: İzmir,

Turkey.
Microtus lydius ankaraensis Yiğit \& Çolak, 2002. Type loc.: Sarayköy, 15 km north of Ankara, Turkey.
Distribution: Thrace and the western portion of Anatolia; eastern borders unresolved.
Comments: A sister species to M. guentheri - M. dogramacii lineage (Kryštufek et al., 2009b). Yiğit \& Çolak (2002) and Yiğit et al. (2006c) reported this vole as M. lydius. Synonymy for hartingi and lydius is based on the examination of type material (see Kryštufek \& Vohralík, 2005, p. 16).
119. Microtus dogramacii Kefelioğlu \& Kryštufek, 1999
Microtus dogramacii Kefelioğlu \& Kryštufek, 1999. Type loc.: Boyali köyü, Sulova, Amasya, Turkey.
Distribution: Still known from only three localities in central Anatolia.

## Genus: Сhionomys Miller, 1908

120. Chionomys nivaLis (Martins, 1842)

Arvicola nivalis Martins, 1842. Type Locality: Faulhorn, Berner Oberland, Switzerland.
Microtus pontius Miller, 1908. Type loc.: 25 miles north of Bayburt, Turkey.
Microtus (Chionomys) nivalis olympius Neuhäuser, 1936. Type loc.: Mt. Uludağ, Bursa, Turkey.
Microtus (Chionomys) nivalis cedrorum Spitzenberger, 1973. Type loc.: Kohu Dağ, Antalya, Turkey.
Chionomys nivalis spitzenbergerae Nadachowski, 1990. Type loc.: south of Maden Köy, Middle Taurus Mts., Turkey.
Distribution: Scattered across Anatolia.
121. Chionomys gud (Satunin, 1909)

Microtus gud Satunin, 1909. Type loc.: Gudaur, near Krestovskii Pass, Caucasus, Georgia.
Microtus (Chionomys) gud lasistanius Neuhäuser, 1936. Type loc.: Varsambeg Dağ, Rize, Turkey.

Distribution: eastern Black Sea Mts.
122. Chionomys roberti (Thomas, 1906)

Microtus roberti Thomas, 1906. Type loc.: Sume-
la (= Meryemana), Trabzon, Turkey.
Distribution: eastern Black Sea Mts.

Subfamily: Cricetinae: G. Fischer, 1817
Comments: Reviewed in this volume.

Genus: Cricetulus Milne-Edwards, 1867
123. Cricetulus migratorius (Pallas, 1773)

Genus: Mesocricetus Nehring, 1898
124. Mesocricetus auratus (Waterhouse, 1839)
125. Mesocricetus brandti (Nehring, 1898)

Family: Muridae Illiger, 1811
Comment. Reviewed in this volume.
Subfamily: MurinaE Illiger, 1811
Genus: Micromys Dehne, 1841
126. Micromys minutus (Pallas, 1771)

Genus: Apodemus Kaup, 1829
127. Apodemus sylvaticus (Linnaeus, 1758)
128. Apodemus flavicollis (Melchior, 1834)
129. Apodemus witherbyi (Thomas, 1902)
130. Apodemus uralensis (Pallas, 1811)
131. Apodemus mystacinus (Danford and Alston, 1877)
132. Apodemus agrarius (Pallas, 1771)

Genus: Rattus Fischer, 1803
133. Rattus rattus (Linnaeus, 1758)
134. Rattus norvegicus (Berkenhout, 1769)

Genus: Nesokia Gray, 1842
135. Nesokia indica (Gray, 1830)

Genus: Mus Linnaeus, 1758
136. Mus domesticus Schwarz \& Schwarz, 1943
137. Mus macedonicus Petrov \& Ružić, 1983
138. Mus cypriacus Cucchi, Orth, Auffray, Renaud, Fabre, Catalan, Hadjisterkotis, Bonhomme \& Vigne, 2006

Subfamily: Deomyinae Thomas, 1888
Genus: Асомуs I. Geoffroy, 1838
Comments: Reviewed in this volume.
139. Acomys cahirinus (É. Geoffroy, 1803)

Subfamily: Gerbillinae Gray, 1825
Comments: Reviewed in this volume.
Genus: Tatera Lataste, 1882
140. Tatera indica (Hardwicke, 1807)

Genus: Meriones Illiger, 1811
141. Meriones tristrami Thomas, 1892
142. Meriones vinogradovi Heptner, 1931
143. Meriones crassus Sundevall, 1842
144. Meriones libycus Lichtenstein, 1823
145. Meriones dahli Shidlovsky, 1962
146. Meriones persicus (Blanford, 1875)

Genus: Dipodillus Lataste, 1881
147. Dipodillus dasyurus (Wagner, 1842)

Family: Spalacidae Gray, 1821
Genus: Spalax Güldenstaedt, 1770
Comments: Reviewed in this volume.
148. Spalax leucodon Nordmann, 1840
149. Spalax xanthodon Nordmann, 1840
150. Spalax ehrenbergi Nehring, 1898

Family: Calomyscidae Vorontsov \& Potapova, 1979
Genus: Calomyscus Thomas, 1905
Comments: Reviewed in this volume.
151. Calomyscus bailwardi Thomas, 1905

Family: Hystricidae G. Fischer, 1817
Genus: Hystrix Linnaeus, 1758
Comments: Reviewed in this volume.
152. Hystrix indica Kerr, 1792

Family: Myocastoridae Ameghino, 1904
Genus: Myocastor Kerr, 1792
Comment: Reviewed in this volume.
153. Myocastor coypus (Molina, 1782)

Family: Castoridae Hemprich, 1820
Genus: Castor Linnaeus, 1758
Comments: Reviewed in this volume.
154. Castor fiber Linnaeus, 1758

## Material and Methods

The present review covers 32 rodent species, out of total 66 for the region. Similarly as with our previous compilations (Kryštufek \& Vohralík, 2001, 2005), we relied on three main sources of information: (i) published data, (ii) voucher specimens in museum collections, and (iii) our own material and data collected in the field.

Published data. The data published on the mammals of Turkey are widely scattered in various journals, books, and reports. Although every attempt was made to include all the papers available on rodents, we are well aware of the fact that our reference list is far from being complete. The most complete bibliographic list of the mammals of Turkey and its neighbouring countries is by Kumerloeve $(1975,1986)$ who already stated that "the number of authors and publications [related to the region] multiplied to such an extent, that a critical appraisal seems to become more and more necessary."

Wherever possible, we checked the published information by examining voucher specimens.

The following general works deal with rodents from the regions adjacent to Turkey and Cyprus:

Europe. Niethammer \& Krapp $(1978,1982)$ : Comprehensive review of all European rodents with detailed descriptions, measurements and drawings of skulls and dentition; distributional maps; biological data; out of date in some respects (in German). Mitchell-Jones et al. (1999): Distributional atlas with species accounts and drawings of animals (in English).

Russia. Gromov \& Erbajeva (1995): Comprehensive review of all rodents living in Russia, with descriptions and determination keys; drawings, photographs and distribution maps for some species; biological data (in Russian).

Greece. Ondrias (1966): Comprehensive review with descriptions, determination keys, measurements and maps; out of date in some respects (in English); Greek Thrace is updated in Vohralík \& Sofianidou (1992a).

Bulgaria. Popov \& Sedevčev (2003): Popular guide covering all Bulgarian mammals; descriptions, drawings of skulls; colour plates; tentative distributional maps; biological data (in Bulgarian). Peshev
et al. (2004): Standard faunal work covering all Bulgarian mammals; descriptions, drawings of skulls; measurements; biological data; no maps (in Bulgarian). Popov et al. (2007): Fifteen rodent species of conservation concern; comprehensive accounts on various aspects of biology; distributional maps and colour photographs (in Bulgarian).

The Caucasus. Šidlovskij (1976): Review of all rodents of the Caucasus region, with descriptions, determination keys, detailed maps and biological information; out of date in many respects (in Russian).

Georgia. Bukhnikashvili \& Kandaurov (1998): Rare and threatened species of Georgia, with descriptions, biological data and distributional maps (in English). Bukhnikashvili (2004): Distributional review of small mammals, with detailed distributional maps and list of localities (in English).

Iran. Lay (1967): Report on the Street Expedition of 1962-63; descriptions, distributional and biological data (in English). Etemad (1978): descriptions, drawings of skulls and photographs of animals and habitats; distributional maps (in Farsi). Karami et al. (2009): Annotated checklist (in English).

Arabia. Harrison \& Bates (1991): Detailed and comprehensive work dealing with all the mammals of the Arabian Peninsula and also covering parts of Turkey; keys, descriptions, photographs and drawings of animals, skulls, dentition, and habitats; biological information; maps (in English). Amr (2000): Standard faunal compilation covering all mammals of Jordan; keys, descriptions, colour photographs of animals and drawings of skulls; biological information; maps (in English); updated by Amr et al. (2004).

Eastern Mediterranean Region: Attalah (1977, 1978): Descriptions, biological and distributional data; measurements. The area covers the Mediterranean coast just south of Turkey and to the north of Sinai (in English). Lewis et al. (1967): a review of the hares and rodents of Lebanon. Qumsiyeh (1996): Detailed and comprehensive treatment of all the mammals of the "Holy Land" (i.e. Israel and Jordan with adjacent parts of Syria and Saudi Arabia), with descriptions; photographs of animals; information on biology, local status and genetics; distributional maps (in English). Mendelssohn \& Yom-

Tov (1999): Detailed and comprehensive work dealing with all the mammals of Israel; keys, descriptions, photographs of skulls; biological information; maps (in English).

Voucher specimens. Voucher specimens were examined by B.K in mammal collections in Europe, Russia, Turkey and the United States of America. The institutions and corresponding abbreviations are as follows:
BMNH Natural History Museum London (formerly British Museum of Natural History), London, UK.
FMNH Field Museum of Natural History, Chicago, USA.
IRSNB Institut Royal des Sciences Naturelles de Belgique, Bruxelles.
NM Department of Zoology, National Museum, Prague, Czech Republic.
NMNH United States National Museum of Natural History, Washington D.C., USA.
NMW Naturhistorisches Museum Wien, Vienna, Austria.
SMF Forschungsinstitut und Natur-Museum Senckenberg, Frankfurt a. M., Germany.
TUE Biology Department, Trakya University, Edirne, Turkey.
ZFMK Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany.
ZMB Zoologisches Museum, Humboldt Universität, Berlin, Germany.
ZMMU Zoological Museum, Moscow University, Moscow, Russia.

In most cases, the examined specimens were standard museum skins and/or skulls; the rest of the material was preserved either in alcohol or in a $4 \%$ solution of formaldehyde. We also considered owl pellets and subfossil material. External measurements were recorded from specimen tags and cranial parameters were scored by a vernier calliper (see below). Drawings of skulls and/or dentition were made using a camera lucida, or scored by the Pixera Visual Communication Suite (Version 2.0). Linear measurements were scored (to the nearest 0.1 mm ) for skulls to roughly describe these structures by numerical means, thus allowing comparisons. Dental measurements were taken on a stereomicroscope fitted with
an eyepiece scale; for definitions see Kryštufek \& Vohralík (2005).

Types of teeth in the heterodont mammalian set are designated by letters. Capitals are used to indicate the maxillary teeth and small letters the mandibular teeth; the position in the tooth-row (anterior $\rightarrow$ posterior) is indicated by the relevant number. E.g.: M1 and m 3 denote the $1^{\text {st }}$ upper and the $3^{\text {rd }}$ lower molar, respectively. Note that rodents lack canines. Abbreviations are as follows:

I/i upper/lower incisors
P/p upper/lower premolars
M/m upper/lower molars
Of the type material, we examined 52 specimens ( 36 holotypes, five paratypes, and 11 syntypes), representing 19 nominal species. Sixteen types were from Turkey. The remaining specimens originated from adjacent regions but were of value in understanding the taxonomic position of rodents in Turkey. The type material is kept in BMNH (32 specimens), ZMB and NMW (ten specimens each). The type material is listed by the name under which it was originally published and reported. Small capital letters denote the valid species names. The collection acronyms and numbers are given as labelled on each specimen; preserved material is given in parentheses.

## Cricetulus migratorius

## Cricetulus migratorius vernula

Holotype: BMNH 6.5.1.83 (skin and skull).

## Mesocricetus auratus

## Cricetus auratus

Holotype: BMNH 55.12.24.120 (skin and damaged skull).

## Mesocricetus brandti

## Mesocricetus koenigi

Syntype: ZMB 85096 (skull).
Presumably a syntype obtained from Satunin.

## Microtus guentheri

## Microtus (Sumeriomys) güntheri shevketi

Holotype: ZMB 47988 (skin and skull without mandible).

## Apodemus flavicollis

Mus arianus
Holotype: BMNH 74.11.21.22 (skull).

## Apodemus witherbyi

Mus witherbyi
Holotype: BMNH 2.10.1.4 (skin and skull).

## Mus sylvaticus tauricus

Holotype: BMNH 77.8.13.9 (skull).
Apodemus mystacinus
Mus mystacinus
Holotype: BMNH 7.7.8.13.6 (alcohol specimen with extracted skull).
Paratype: BMNH 8.1.8.4.1 (skin).

## Mus mystacinus smyrnensis

Holotype: BMNH 3.6.1.3 (skin and skull).
Nesokia indica
Meriones myosurus
Holotype: NMW B1287 (skin and broken skull).
Mus domesticus
Mus bactrianus
Holotype: BMNH 56.2.29.4 (skin and skull).
Mus: not assigned
Mus abbotti
Holotype: BMNH 55.12.26.345 (spirit specimen with skull extracted).

Acomys cahirinus
Acomys cilicicus
Holotype: NMW 13196 (skin and skull).
Paratypes (4): NMW 13267, 13268, 13269, 13270 (skulls).

## Acomys nesiotes

Holotype: BMNH 3.12.4.37 (skin and skull).
Acomys dimidiatus minous
Holotype: BMNH 5.12.2.33 (skin and skull).

## Acomys hunteri

Holotype: BMNH 3.12.8.54 (skull).

## Acomys viator

Holotype: BMNH 2.11.4.72 (skin and skull).

## Acomys sabryi

Holotype: BMNH 22.3.15.8 (skin and skull).
Acomys dimidiatus
Acomys dimidiatus homericus
Holotype: BMNH 99.11.6.77 (skin and skull).

## Acomys flavidus

Holotype: BMNH 91.11.1.11 (skin and skull).
Tatera indica

## Dipus indicus

Holotype: BMNH, not catalogued (skin and broken skull).

## Meriones taeniurus

Syntypes (4): NMW B1283, B1284, B1285,
B1286 (skins and broken skulls).

## Tatera bailwardi

Holotype: BMNH 5.10.4.30 (skin and skull).

## Tatera persica

Holotype: BMNH 6.1.2.5 (skin and broken skull).

## Tatera bailwardi monticola

Holotype: BMNH 5.10.4.33 (skin and skull).

## Tatera persica scansa

Holotype: BMNH 4.6.1.3 (skin and skull).

## Tatera pitmani

Holotype: BMNH 19.12.24.1 (skin, skull and broken mandible).

## Meriones tristrami

## Meriones tristrami

Holotype: BMNH 64.8.17.35 (alcohol specimen with extracted broken skull).

## Meriones blackleri

Holotype: BMNH 3.6.1.1 (skin and skull).
Meriones blackleri lycaon
Holotype: BMNH 8.7.1.28 (skin and skull).

## Meriones blackleri intraponticus

Holotype: ZMB 47990 (skin and skull without mandible).

## Meriones crassus

## Meriones charon

Holotype: BMNH 5.10.4.38 (skin and skull).

## Meriones libycus

Meriones syrius
Holotype: BMNH 5.7.2.2 (skin and skull).

## Spalax leucodon

Spalax monticola thermaicus
Holotype: BMNH 17.11.19.1 (skull).

## Spalax monticola insularis

Holotype: BMNH 17.8.15.3 (skull).

## Spalax xanthodon

## Spalax monticola corybantium

Holotype: BMNH 11.21 .1 (skin and skull).

## Spalax monticola captorum

Holotype: BMNH 19.9.20.23 (skull).

## Spalax ehrenbergi

## Spalax ehrenbergi

Syntypes (6): ZMB 15203, 15205, 15207, 15208, 15210, 15212 (bodies in alcohol), 15202, 15204, 15206, 15209, 15211(skulls).
Note that skulls and wet carcases of the same individuals are catalogued under separate numbers.

## Hystrix indica

Hystrix hirsutirostris mersinae
Holotype: ZMB 70850 (skull).

Own material and data collected in the field. We frequently travelled to Turkey between 1992 and 1995 and again in 2004 and 2005 for at least one month/visit. In addition, the material collected on various expeditions to the Near East by the students of Charles University was at our disposal. This material is kept in the mammal collection of the Department of Zoology, Charles University, Prague, Czech Republic.

Animals were caught using snap traps (commer-
cial kill traps and a modified version of the museum special break back traps) as well as live traps (Elliot, Chmela, Rödl, Longworth). The traps were invariably set in the late afternoon or in the evening and collected the next morning; in exceptional cases they were left in place during the next day. Our aim was to obtain representative samples of the local small mammal faunas. Consequently, the traps were placed where captures were likely to occur. The traps were usually arranged in lines and spaced c. 5-7 m apart. Cotton wick roasted with a mixture of sunflower oil and flour, a mixture of tinned fish and oat flakes, or peanut butter was used as bait. Road kills also contributed voucher specimens. Each specimen was measured and then either prepared immediately in the field or stored in a $4 \%$ solution of formaldehyde or ethanol for later laboratory processing. Skulls were cleaned by Dermestes beetle larvae.

Part of the material was karyotyped; chromosomes were prepared directly from the bone marrow of colchicine-treated animals and flame dried (Ford \& Hamerton, 1956). Tissue samples were stored in liquid nitrogen or in alcohol for subsequent ellectrophoretic and molecular studies.

The following measurements were taken:
H\&B head and body length (from the snout to the anus)
TL tail length (from the anus; terminal hair excluded)
HF hind foot length (claws excluded)
E ear length (terminal hair excluded)
W weight
The measurements were taken to the nearest millimetre (H\&B, TL) or to the nearest 0.1 mm (HF, E); weight was scored to the nearest gram.

All specimens were examined for their reproductive condition. In males we checked the position of testes (scrotal or abdominal). Females were inspected for the presence of nipples, the condition of their uterus and number and size of embryos were recorded.

All field procedures involving handling of animals in this study were in compliance with guidelines approved by the American Society of Mammalogists (Gannon et al., 2007).

## Order: Rodentia

For an introduction to the order, see our previous compilation (Kryštufek \& Vohralík, 2005: 19-20) and for a recent taxonomic and nomenclatural review cf. Wilson \& Reeder (2005). In total, 2,277 species were recognized in 2005, and in comparison to the earlier global review (Wilson \& Reeder, 1993) taxonomic classification changed on all levels. Rodents of Turkey and Cyprus are now in ten families, which are keyed below.

## Key to families

1 Size large: adult body mass $>5 \mathrm{~kg}$
1* Size small: adult body mass $<1 \mathrm{~kg}$

2 Infraorbital foramen small; coronoid process prominent

Castoridae
2* Infraorbital foramen much enlarged; coronoid process vestigial or absent

3 Back covered with spines
Hystricidae
3* Back covered with hair
Myocastoridae
4 Postorbital process prominent; infraorbital foramen small

Sciuridae
4* Postorbital process missing; infraorbital foramen medium sized or large;

5 One premolar present in maxilla; four pairs of chewing-teeth in upper jaw

5* Premolars absent in maxilla; three pairs of chewing-teeth in upper jaw (all molars)

6 One premolar present in mandible (four chew-ing-teeth)

Gliridae

6* Premolars absent in mandible (three chewingteeth, all molars)

Dipodidae
7 Tail absent; eyes entirely covered by skin
Spalacidae
7* Tail present; eyes evident

8 Tail shorter than two thirds of head and body length

Cricetidae
8* Tail longer than two thirds of head and body length

9 Upper molar cusps in three longitudinal series, or laminate

Muridae
9* Upper molar cusps in two longitudinal series Calomyscidae

Rodents of Turkey and Cyprus fall into four suborders (Wilson \& Reeder, 2005):

Suborder: Sciuromorpha Brandt, 1855
Family: Sciuridae
Family: Gliridae
Suborder: Myomorpha Brandt, 1855
Family: Dipodidae
Family: Cricetidae
Family: Muridae
Family: Spalacidae
Family: Calomyscidae
Suborder: Hystricomorpha Brandt, 1855
Family: Hystricidae
Family: Myocastoridae
Suborder: Castorimorpha A.E. Wood, 1955
Family: Castoridae

Sciuromorpha, Dipodidae, and Arvicolinae (Cricetidae) were covered in our previous volume (Kryštufek \& Vohralík, 2005).

## Family: Cricetidae Fischer, 1817

In its current scope, the family Cricetidae includes two subfamilies from the region. The subfamily Arvicolinae was reviewed in our previous volume (Kryštufek \& Vohralík, 2005); cf. also annotated checklist above.

## Key to subfamilies:

1 Molar crowns flat, showing pattern of alternating enamel fields; no check pouches

Arvicolinae
1* Molars cuspidate; check pouches present
Cricetinae

## Subfamily: Cricetinae Fischer, 1817

Herbivorous and omnivorous muroids with short feet and short tail. There are cheek pouches in the mouth which sag to the shoulders during foraging. The body is mainly robust and thickset with a broad head and a short, bluntly rounded muzzle. The eyes are moderately large while the ears are fairly long. The skull is usually robust and broad, but it is narrow with weak zygomatic arches in Cricetulus. Rooted molars are bunodont with two longitudinal series of cusps. A recent molecular phylogenetic reconstruction strongly supports the monophyly of Cricetinae (Neumann et al., 2006).

Cricetinae were traditionally one of two main divisions of Muridae, and included as such all murid genera occurring in the region, except those which are placed into the subfamily Murinae (cf. Table 30 on p. 123 in Kryštufek \& Vohralík, 2005). In their current definition and scope (Musser \& Carleton, 2005), Cricetinae is one of six subfamilies of Cricetidae, including only 18 species of hamsters in seven genera, all of which are of Palaearctic occurrence. Cricetines are mainly associated with open steppic habitats. Three species in two genera occur in Turkey.

Recently, Seçkin \& Coşkun (2006) reported the common hamster Cricetus cricetus (Linneaus, 1758) for Diyarbakır Province in South-Eastern Anatolia. Identification, which is based on Asio otus prey remnants, is clearly erroneous and specimens belong to Cricetulus migratorius (cf. Fig. 2/III on p. 274 in

Seçkin \& Coşkun, 2006). Publication, however, is of some interest because of its reminiscence of the $19^{\text {th }}$ century reports of the common hamster for Anatolia. A specimen collected by Th. Kotschy along the River Cydnus (= Tarsus) was identified in Vienna as Cricetus frumentarius (Pallas, 1811) and subsequently reported as such (Kotschy, 1858). Note that Mus frumentarius Pallas, 1811, was a nomenclatural act of renaming Mus cricetus Linnaeus, 1758 (Ellerman \& Morrison-Scott, 1951) and is thus synonymous with C. cricetus. Although Danford \& Alston (1877) suggested that Kotschy’s specimen more likely belongs to Cricetus nigricans Brandt, 1832, which is a member of Mesocricetus (see under M. brandti), they still listed C. frumentarius in their subsequent paper (Danford \& Alston, 1880). Miller (1912) was mislead by these reports and cited the range of $C$. cricetus to include also Asia Minor. Neuhäuser (1936) accepted the above opinion by Danford \& Alston (1877) regarding the identity of Kotschy's material. Despite this, J. R. Ellerman (in Ellerman \& Morrison-S cott, 1951, 1966) still considered the occurrence of the common hamster in Asia Minor as a possibility: "Asia Minor according to Kuznetzov and Miller, but I have never been able to verify its occurrence there which I am inclined to doubt". Kumerloeve (1975) rejected the possibility that the common hamster could live in Anatolia. During the Middle Pleistocene Cricetus cricetus did occur in Anatolia (Montuire et al., 1994) and was reported also from Israel (Tchernov, 1968b).

Hamsters are rare in museum samples. In our material, obtained by trapping, hamsters contributed merely $4.1 \%$ to the rodent total in a pooled sample from the Taurus Mts., central and eastern Anatolia, and their abundance was even lower elsewhere (Kryštufek \& Vohralík, 2008). In Turkey, hamsters are out-numbered by voles (Arvicolinae) and mice (Murinae), at least in samples obtained by snap trapping (Kryštufek \& Vohralík, 2008). Owl pellet samples suggest them to be much more abundant. In Bubo bubo pellets from Turkey, Obuch (1994) reported the following proportions of hamsters in rodent assemblages: 80.0 \% in Demir Kaziköy ( $\mathrm{N}=50$ ), $76.5 \%$ in Sarikamiş ( $\mathrm{N}=1,180$ ), 55.0\% in Tatvan ( N $=20$ ), 37.9\% in Yaprakhisar ( $\mathrm{N}=58$ ), and $18.3 \%$ in Muradiye ( $\mathrm{N}=1,410$ ). Similarly, Hír (1991, 1992) found in a subfossil material from Bolkar Dağ one
quarter (= 24.3\%) of rodent specimens to be hamsters $(\mathrm{N}=600)$.

## Key to genera

1 Ventral side with black or black and white transverse band across chest; tail shorter than hind foot; oblique blackish or brownish subauricular stripe from cheeks to shoulders; 16 nipples in females; size large (condylobasal length of skull >30.0 mm);

## Mesocricetus

1* Ventral side plain white or grey white; tail longer than hind foot; no oblique contrasting stripe from cheeks to shoulders; 8 nipples in females; size small (condylobasal length $<28.0 \mathrm{~mm}$ ); skull essentially of murine shape and proportions

Cricetulus

## Genus: Cricetulus Milne-Edwards, 1867

Small hamsters with moderately long tail; belly is white. Back is uniformly grey or with darker spinal
stripe. Skull is relatively narrow and not pronouncedly angular. Molar pattern shows no peculiarities. Allocricetulus and Tscherskia, which were frequently associated with Cricetulus, are now considered to be independent genera (Musser \& Carleton, 2005). In its current scope, Cricetulus contains six species; one of them occurs also in Turkey. The genus is perhaps not truly monophyletic and C. migratorius, which is closely related to Tscherskia, Cricetus and Allocricetulus, might be better placed in a monotypic genus on its own right (Neumann et al., 2006).

## Grey dwarf hamster - Cricetulus MIGRATORIUS

Mus migratorius Pallas, 1773. Type loc.: Inderskij Region, Gur'ev District, Western Kazakhstan.
Cricetulus migratorius vernula Thomas, 1917. Type loc.: Khotz (=Çosandere), Trabzon, Turkey.

## Taxonomy

Various names were used for grey dwarf hamsters of Turkey in the past: Cricetus accedula (Pallas, 1779) (Dickson \& Ross, 1839; Danford \& Alston, 1877), Cricetus phaeus (Pallas, 1779) (Danford \& Alston, 1880), and Cricetulus phaeus (Mill-


Figure 2. Grey dwarf hamster Cricetulus migratorius. Drawing: J. Hošek.
er, 1912). Since Aharoni (1932) and Neuhäuser (1936) the name Cricetulus migratorius is used uniformly and consistently.

## Description

External characters. Body slender, with relatively long ears but short hind foot; the two are approximately of same length. Tail is short (16-42\% of head and body length; mean = 28\%), however still evidently longer than in Mesocricetus. Eyes are small (4.14.9 mm in diameter) and whiskers are long (up to 35 mm ). Cheek pouches large, extending backward to the shoulders. Feet small, front one with four digits and five well developed palmar tubercles; hind foot with five digits and six plantar tubercles. Tail annulations ill-defined and thickly covered by short hairs; terminal hairs exceeding tip for approximately 1 mm . Claws are weak and short. Pelage soft, $7-8 \mathrm{~mm}$ long on dorsal side (winter hairs up to 9 mm ), 5-6 mm long on the belly.

A dark mid-ventral glandular band, mentioned already by Neuhäuser (1936), is shifted slightly towards posterior half of the belly. We found it only in adult and sexually active males; it was $9-15 \mathrm{~mm}$ long and $1-2 \mathrm{~mm}$ wide.

Colour. Dorsal side light ash-grey, clearly darker between ears and along spine, very exceptionally with indistinct blackish grey strip approximately 4 mm wide. Contrary to a statement made by Qumsiyeh (1996), there is no conspicuous dark stripe, nor pronounced facial markings. Back frequently with


Figure 3. Grey dwarf hamster Cricetulus migratorius from Yellibeli Geçidi, district Karaman. Photo: A. Kryštufek.


Figure 4. Skin of Cricetulus migratorius in dorsal and ventral view. Based on a male from Karabulut at Akșehirgölü, district Konya. Photo: C. Mlinar.
buff tints which are particularly intense on the posterior side. In extreme cases, ochre dominates over grey colour. Winter pelage is greyish and contrasts brownish summer colour (Osborn, 1965). Belly grey white; intensity of grey tints depends on how wide the slate base colour of hairs is. Chin, throat and chests are pure white to hair bases, but sides are of same colour as the rest of belly. White ventral patch on chest and throat is most variable in extent, narrowed to a belt in some specimens, expanded in others. Demarcation line along flanks is faded and shifted dorsally compared to other muroid rodents. A narrow band of same colouration as back extends towards shoulders. Ears are grey; feet nearly white; tail indistinctly bi-coloured, pale grey above, whitish below.

Nipples. There are eight nipples, two pairs of each, pectoral and inguinal, respectively.

Penis. The glans penis is cylindrical, short and wide, flattened dorso-ventrally. The terminal crater encompasses lappets and a longer central projection. Epidermal spines decrease in size from the base toward the tip (Voroncov, 1982). Harrison \& Bates
(1991; Fig. 376 on p. 263) figured baculum of a specimen from Iran. Proximal baculum is stalk-like; its base is broadly expanded. Distal baculum is of three small processes; the lateral processes exceed the medial one in length. An earlier figure of the baculum (Argyropulo, 1933b; Fig. 10 on p. 132) differs in some details: central distal processus is longer than the lateral ones and the base of the proximal stalk is notched.

Skull is essentially of murine shape and proportions; brain-case and interorbital region are smooth. Dorsal profile evenly convex, occipital region rounded with expanded condyles, and nasals just protruding over incisors. Rostrum broad but long; nasals narrow, gradually expanding towards a rounded tip. Protuberance formed by the proximal root of upper incisors weak; anterior margin of masseteric plate concave. Zygomatic arches moderately expanded (zygomatic width equals 50.8-59.2\% of condylobasal length). Braincase short relative to rostrum, rounded and nearly entirely covered by parietals. Incisive foramens relatively large and wide, not reaching posteriorly the line of $1^{\text {st }}$ molars. Hard palate terminates just posterior to the line of $3^{\text {rd }}$ molars; pterygoid
processes slightly divergent or bent posteriorly; interpterygoid fossa longer than wide. Bullae relatively small. Mandible long, low and slender with well developed processes.

Teeth. Incisors moderately strong, covered by yellow-orange (upper) and yellow enamel (lower). Root of lower incisors forms with its base a protuberance below the coronoid process. Molar row equals about half the length of diastema. In the upper row, $1^{\text {st }}$ molar is the largest and $3^{\text {rd }}$ molar is the smallest; mandibular cheek-teeth are subequal. Molars are brachyodont and cuspidate, with two longitudinal series of cusps. There are three pairs of cusps on $1^{\text {st }}$ molars, two pairs on the remaining cheek-teeth. Cuspidation pattern is most distorted on $3^{\text {rd }}$ upper molar. Second and $3^{\text {rd }}$ molars have a low antero-lateral enamel ridge. For a detailed description of molar variation in a subfossil material from the eastern Taurus Mts. see Hír (1993). Pradel (1981) described variation in a recent population from Syria.

Upper molars have (anterior to posterior) 4, 4, and 3 roots, respectively, and same number of alveoli. In some specimens the anterior pair fuse into a single root on $2^{\text {nd }}$ and $3^{\text {rd }}$ upper molars, thus reducing


Figure 5. Skull and mandible of Cricetulus migratorius, based on an adult male from Gücük near Sarkışla, district Sivas. Scale bar $=5 \mathrm{~mm}$.

a

b

Figure 6. Upper (a) and lower molars (b) in Cricetulus migratorius from Erence, district Erzurum.
Scale bar $=1 \mathrm{~mm}$.
number of alveoli to 3 and 2, respectively (Pradel, 1981; Fig. 7).

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 69 | 103.0 | $82-115$ |
| Tail | 69 | 28.7 | $16-41$ |
| Hind foot | 68 | 16.2 | $14.0-20.0$ |
| Ear | 69 | 17.8 | $14.0-22.0$ |
| Weight | 36 | 29.7 | $20-40$ |
| Condylobasal length | 55 | 25.8 | $23.5-28.0$ |
| Zygomatic breadth | 50 | 14.0 | $12.3-15.3$ |
| Maxillary tooth-row | 69 | 4.2 | $3.6-4.6$ |

Table 2. External and cranial dimensions of Cricetulus migratorius from Turkey. Based on Neuhäuser (1936), specimens in BMNH, FMNH, SMF and ZFMK, and our own material.


Figure 7. Variation in alveolar pattern of maxillary molars in Cricetulus migratorius from Krak des Chevaliers, northern Syria. Lingual side is to the left, anterior is at the top. Redrawn from Pradel (1981).

Dimensions are given in Table 2. We found no differences between sexes in our pooled data which is in accord with Mendelssohn \& Yom-Tov (1999) regarding the lack of secondary sexual dimorphism in the grey dwarf hamster. In Central Anatolian samples, females tend to have a narrower skull.

Volf \& Volf (1993) reported maximum body mass of 75 g for a 15-month old captive female.

Chromosomes. Diploid number of chromosomes is $2 \mathrm{~N}=22$ and the fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=40$. Autosomal set consists of five metacentric and five subtelocentric pairs. Heterosomes are large isomorphic subtelocentrics and differ in distribution of centromeric heterochromatin (Zima \& Král, 1984). Identical standard karyotype is reported from the vicinity of Ordu (Doğramacı \&

Kefelioğlu, 1991b) and from Central Anatolia (Arslan \& Akan, 2008). Gharkheloo (2006) found in a population from Zanjan (Iran) the fundamental number of $\mathrm{NF}_{\mathrm{a}}=38$. For details on banding stained karyotype see Romanenko et al. (2007) and Arslan \& Akan (2008).

## Variation

Neuhäuser (1936) recognised two subspecies in Turkey, the paler C. m. cinerascens (Wagner, 1848) (type loc.: Syria) with shorter belly hairs, and the darker and larger C. m. vernula. In doing so, she evidently followed an earlier taxonomy by Aharoni (1932). Subspecific division by Ellerman (1948) was basically same, however, cinerascens was synonymised with the nominate subspecies. In addition, Ellerman (1948) also noted that "There is a general tendency in skins from Erzurum, N.W. of Konya, Murad-dagh, Smyrna (in part), and Changria, Turkey, and Menzil in Northern Persia, to integrate between the two subspecies here retained, in colour,


Figure 8. Box and whiskers plots for tail length and zygomatic breadth in two subspecies of Cricetulus migratorius as defined by Doğramacı (1989). 1 - C. m. vernula, 2 - C. m. cinerascens. Given are mean (triangle), standard deviation (box) and range (whiskers).


Figure 9. Extreme morphotypes in relative zygomatic width in Cricetulus migratorius from Turkey. a - dolichocephalic female from Erence; $\mathbf{b}$ - brachycephalic male from Burdur. Scale bar $=5 \mathrm{~mm}$.
making the limits of vernula somewhat problematic ..." Lack of clear discontinuity in variation confused also subsequent students of geographic variation in the grey dwarf hamster (e.g. Felten et al. 1971b). Besides, Osborn (1965) noted that various authors allocated the same museum specimens to different subspecies. In his conclusion, animals from steppes were paler and smaller while those from the mountains were bigger and darker (Osborn, 1965). Doğramacı (1989b) maintained two-subspecies division but also introduced into diagnostic characters tail length and braincase width. Noteworthy, his study benefited from large samples. In his conclusion, ssp. vernula (larger, darker and with longer tail) is restricted to northern coast of Anatolia and to Turkish Thrace, while the rest of Turkey is inhabited by a smaller and paler ssp. cinerascens which also has shorter tail. Note that hamsters from the Balkans (Bulgaria) possibly represent the subspecies atticus Nehring, 1902 (type loc.: Pentelikon, Attica, Greece) (Peshev et al., 2004).

We found tail length to vary tremendously, both in absolute terms and relative to head and body length. It seems that specimens from the Aegean coast are particularly short-tailed, while those from North-Eastern


Figure 10. Skins of Cricetulus migratorius from Turkey: a - Yellibeli Geçidi, district Karaman; b - Erence, district Erzurum. Note difference in tail length. Compare with a pale morphotype in Fig. 4. Not to scale. Photo: C. Mlinar.

Anatolia have long tails. Doğramacı (1989b) proposed a tail length of 23 mm as a cut-off point in distinguishing the two Turkish subspecies. In our opinon, the tail length shows geographic trends, however the overlap prevented us from recognising two discrete allopatric morphotypes (Fig. 8). Similarly,
we found zygomatic width to vary between populations, with clearly brachycephalic specimens in one extreme and dolichocephalic on the other (Fig. 9). Again, samples overlapped in this trait as well.

Specimens along the Black Sea coast (ssp. vernula sensu Doğramacı, 1989b) have on average significantly larger cranial dimensions than those from rest of Anatolia, ascribed by Doğramacı (1989b) to C. m. cinerascens, but ranges largely overlap also in this trait (Table 3). We checked our data set for possible variation among variously defined regions of Anatolia, but found no clear trends. We are therefore suspicious whether division of the Turkish grey dwarf hamsters into a subspecies is meaningful.

## Distribution

Range extends from south-eastern Europe (Greece, eastern Bulgaria, Romania) and southern European Russia, eastward to southern Mongolia and northern China. Southern border encompasses the Near and Middle East, Northern Pakistan and Northern India (Musser \& Carleton, 2005). South of Turkey, the grey dwarf hamster spreads along the eastern Mediterranean coast, reaching Jordan (Amr, 2000) and Israel (Mendelssohn \& Yom-Tov, 1999); there are no known records regarding south of $31^{\circ}$ northern latitude. Along the left bank of the River Tigris, the range of $C$. migratorius expands into Iran (Harrison \& Bates, 1991), where the species is "omnipresent" (Lay, 1967). The grey dwarf hamster is also widespread in higher elevations in Transcaucasia, but is largely absent from the lowlands (Šidlovskij, 1976; Bukhnikashvili, 2004).

As evident from Fig. 11, the grey dwarf hamster is widespread in Thrace and Anatolia. Distributional

|  | Thrace |  |  | Trabzon province |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | $\operatorname{mean}$ | $\min -\max$ |
| Head and body | 6 | 109.1 | $96-116$ | 9 | 107.5 | $102-117$ |
| Tail | 6 | 27.1 | $24-33$ | 9 | 26.8 | $24-30$ |
| Hind foot | 6 | 17.2 | $17.0-19.0$ | 9 | 17.0 | $16.0-19.0$ |
| Ear | 6 | 18.2 | $16.0-20.0$ | 9 | 17.7 | $16.0-21.0$ |
| Weight | 6 | 33.1 | $26-41$ | 9 | 32.4 | $25-41$ |
| Condylobasal length | 6 | 27.0 | $26.4-29.6$ | 9 | 26.7 | $26.3-27.5$ |
| Zygomatic breadth | 6 | 14.6 | $14.0-15.7$ | 9 | 14.3 | $13.8-14.6$ |
| Interorbital constriction | 6 | 4.2 | $4.1-4.3$ | 9 | 4.3 | $4.2-4.4$ |

Table 3. External and cranial dimensions of Cricetulus migratorius vernula for four geographic samles from Turkey. From Doğramacı (1989b). Table continues on p. 41.

|  | Antep (= Gaziantep) |  |  | Van \& Hakkari |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |
| Head and body | 17 | 102.9 | $97-112$ | 10 | 106.5 | $91-116$ |
| Tail | 16 | 21.9 | $17-24$ | 10 | 22.3 | $16-29$ |
| Hind foot | 17 | 16.5 | $13.0-18.0$ | 10 | 16.7 | $15.0-18.0$ |
| Ear | 17 | 15.9 | $14.0-18.0$ | 10 | 17.8 | $16.0-20.0$ |
| Weight | 16 | 30.8 | $24-40$ | 10 | 32.1 | $28-38$ |
| Condylobasal length | 17 | 25.8 | $23.3-27.6$ | 10 | 25.9 | $23.5-27.9$ |
| Zygomatic breadth | 16 | 13.9 | $13.0-14.7$ | 10 | 14.0 | $13.1-14.8$ |
| Interorbital constriction | 17 | 3.9 | $3.7-4.2$ | 10 | 4.2 | $4.0-4.7$ |

border is poorly resolved in south-eastern Anatolia, where Ceylanpınar is most likely on the very southern edge of distribution. There are no further records available further south from Mesopotamia and the Syrian desert.

Cricetulus migratorius is absent from the islands offshore Turkish coasts.

Palaeontology. Cricetinae first appeared in the Early Miocene while Cricetulus dates back to the Late Miocene; the oldest records for both the subfamily and the genus are from Europe (Kowalski, 2001; Musser \& Carleton, 2005). Cricetulus probably appeared in Anatolia during Ruscinian
(Sümengen et al., 1990), and was recovered from a pre-pottery Neolithic faunal assemblage of Göbekli Tepe near Şanliurfa, dated about 9,500 years before the present (Peters \& Schmidt, 2004).

Cricetulus migratorius appeared in the Middle Pliocene (Topačevskij \& Skorik, 1992) and is known since the Early Pleistocene from Greece (van der Meulen \& Doukas, 2001) and Bulgaria (Peshev et al., 2004). The earliest records from Turkey are from the Middle Pleistocene when the animal was found on both sides of the Marmara straits: Emirkaya-2 in Central Anatolia (Montuire et al., 1994), Yarimburgaz in Turkish Thrace (Santel \&


Figure 11. Distribution of Cricetulus migratorius in Turkey and adjacent regions. For further details on records see Appendix 1.

Koenigswald, 1998) and the Aegean Island of Chios (Storch, 1975). In Yarimburgz it was by far the most abundant rodent and small mammal (S antel, 1994). Storch (1988) found C. migratorius in the Upper Pleistocene layers of Antalya (Taurus), where from it disappeared at the Quaternary - Holocene boundary, remained absent during the entire Chalkolithic period, and then re-appeared, probably fairly recently. The remaining Holocene records from the Taurus Mts. are not precisely dated. Those from Finike are presumably less than 7,000 years old (Corbet \& Morris, 1967) while the age of the Mt. Bolkar material is not known (Hír, 1993). Further south C. migratorius is known from the end of the Upper Pleistocene ( $14,400 \pm 760$ years BP) in Iraq (Turnbull, 1975) and from the Upper Pleistocene (Early Mous-
terian, 75,000 years ago) strata of Israel (Tchernov, 1992); records from the Middle Pleistocene are reported as Allocricetus bursae Schaub, 1930 (Tchernov, 1975, 1994). The Upper Pleistocene Israeli material was ascribed also to Allocricetus jesreelicus Bate, 1943 (Tchernov, 1968a). Cricetulus migratorius is known from the Late Glacial and Holocene of northern Iran (Storch, 1974, 1980). Grey hamsters of the Upper Pleistocene age and reported as Cricetulus af. migratorius were found also from the southern slopes of the Caucasus in western Georgia and were present during historical times in several localities in Armenia along the Turkish frontier (Vereščagin, 1959).

Cricetulus migratorius was widespread across Europe during dry periods of the Quaternary (Kow-


Figure 12. Habitat of Cricetulus migratorius. a - Yellibeli Geçidi, $1,900 \mathrm{~m}$ a.s.l., district Konya; b - Cihanbeyli, district Konya; c - Gücük, Sarkışla, 1,400 m a.s.l., district Sivas; d - delta of the River Çendik, Suludere, district Burdur. Photo: B. Kryštufek (a, c, d); A. Kryštufek (b).
alski, 2001) and survived in the north-western Balkans into the Early to Middle Holocene ca 6,500 5,400 years BC (Toškan \& Kryštufek, 2004). Fossil material is mainly reported as Allocricetus bursae (Cricetulus bursae sensu Kurtén, 1968) which Kowalski (2001) synonymised with C. migratorius; cf. Pradel (1988) and Hír (1993) for the opposite opinion.

## Habitat

Two very different types of habitats are preferred in Anatolia: rocky places and fields. Association with rocks is a common, albeit by no means fundamental feature of the grey dwarf hamster's habitat requirements. Hence, also in cultivated areas we trapped specimens along rocky walls between fields. Other habitats include rocky slopes with sparse grasses and scattered shrubs, dense tall shrubs, tall, weedy vegetation, and rocky outcrops in the Anatolian steppe. Neuhäuser (1936) and Osborn (1965) did not find grey dwarf hamsters in the natural steppe. In our experience, these animals do occur also in uncultivated steppic habitats where they are tied to rocky boulders. Reports from forests are uncommon for Turkey and in two cases (Uludağ and Pazarköy) specimens were captured in pine stands (Osborn, 1967; Felten et al., 1971b).

Uncultivated gentle slopes covered with sparse grass and weeds, grain fields and rocky waste ground are the main habitat also along the eastern Mediterranean coast (Lewis et al., 1967; Atallah, 1977). Well drained soil is preferred in Israel (Mendelssohn \& Yom-Tov, 1999). In Georgia, open arid landscape is reported to be the main habitat (Bukhnikashvili \& Kandaurov, 1998) and Harrison (1956b) found the grey hamster to be abundant in high rock-strew mountain slopes with short shrubs and vegetation in Iraqi Kurdistan. Range of selected habitats seems to be wider in Iran where Lay (1967) considered the grey dwarf hamster to be omnipresent, from deserts to lush forests. Along western Caspian coast it was found also on moving sands (Ejgelis, 1980).

Many authors report that grey dwarf hamsters readily enter houses and store houses in Turkey (Danford \& Alston, 1877, 1880; Osborn, 1965; Felten et al., 1971b), Transcaucasia (Bukhnikashvili \& Kandaurov, 1998), and Iran (Lay, 1967). Danford \& Alston (1880) explicitly underline that
it was abundant in houses in Kayseri at the time of their visit. In Pakistan, C. migratorius is one among few rodents, besides Tatera indica, Mus domesticus and Rattus species, which are inclined to be commensal (Roberts, 1997).

Altitude of records is between close to sea level (about 200 m a.s.l. near Bergama) and 2,300 m a.s.l. (around Gümüşhane, Erzurum, Kars, Artvin, and Bitlis); the majority of records are above 1,000 m of elevation. Similar range is reported for Lebanon (800-2,900 m; Atallah, 1977). The only Anatolian records at low elevations are from the Aegean coast (İzmir, Bergama) while all the remaining sites in western Anatolia are at elevations between 1,215 and 2,100 m a.s.l. (Felten et al., 1971b). Localities from Turkish Thrace are at much lower elevations (around 300 m a.s.l.) compared to those in Anatolia. Altitudinal range is wider in Iran, (from sea level to 3,656 m; Lay, 1967) and in Georgia (300-400 to 4,000 m; Bukhnikashvili \& Kandaurov, 1998).

Associates. Rocky habitats, where the grey dwarf hamster is occasionally abundant in Turkey, are preferred also by Apodemus mystacinus and Chionomys nivalis (e.g. in Cığlıkara; Felten et al., 1971a), and populated also by Apodemus witherbyi and Crocidura leucodon. In open habitats, hamsters are frequently interspersed with Spermophilus xanthoprymnus, Meriones tristrami or Microtus hartingi/guentheri. We also captured in the same trap lines as the grey dwarf hamster Crocidura suaveolens, C. leucodon, Sorex satunini, Dryomys nitedula, D. laniger, Microtus levis, M. arvalis, M. subterraneus, M. daghestanicus, Mus macedonicus and, very exceptionally, also Mesocricetus brandti. Grey dwarf hamsters were found in the midst of large colonies of Meriones tristrami or Microtus guentheri in Lebanon (Atallah, 1977).

Density. We found the grey dwarf hamster only exceptionally to be abundant in small mammal assemblages and single individuals were mainly captured. Higher abundances were invariably associated with edges of corn fields and with rocky habitats. Owl pellet contents suggest very different picture on the abundance of this animal. Namely, in the results by Obuch (1994) it was one of small mammals most frequently preyed upon by two big owls, Bubo bubo and Strix aluco. In a large B. bubo sample from Sarikamiş ( $\mathrm{N}=1,193$ ) as many as $42.5 \%$ of small mammals were grey dwarf hamsters.

The grey dwarf hamster is rare also in eastern Transcaucasia where trapping mainly yielded $0.4-$ 0.8 individuals per 100 trap nights (Ejgelis, 1980). Populations remain fairly stable across years with at most 3 -4-fold increase in density (Ejgelis, 1980; Fig. 13). Contrary to this, Bašenina (1951) reports remarkable oscillation in abundance from European Russia.


Figure 13. Variation in relative density (number of individuals per 100 trap nights) in Cricetulus migratorius between 1961 and 1970 in a high density (bold line) and low density (interrupted line) habitat in eastern Transcaucasia. Modified from Ejgelis (1980).

## Biology

Activity. Although frequently regarded to be strictly nocturnal (Lewis et al., 1967), the grey dwarf hamster is active also during the day at low ambient temperatures (Mendelssohn \& Yom-Tov, 1999) and is preyed upon by diurnal raptors (Flint, 1966). It is active all year round and does not hibernate in European Russia (Bašenina, 1951) or in Transcaucasia (Šidlovskij, 1976); Ferguson (2002) reports hibernation to be intermittent. Danford \& Alston (1977) state that it is sometimes found on the snow in winter and Atallah (1977) captured specimens in Lebanon during winter and spring (October through May). We noticed subcutaneous fat deposits in specimens trapped in mid-October and early November. In Central Anatolia, we collected specimens in early November when night temperatures dropped well below the freezing point.

Burrows are simple and shallow (up to 76 cm below the surface; Bašenina, 1951), with up to five
exits in addition to blind-galleries or chambers for nest and storing food (Šidlovskij, 1976; Harrison \& Bates, 1991). Most frequently, the burrow system has two openings about $1-2 \mathrm{~m}$ apart (Bašenina, 1951; see Fig. 14). A burrow system from Transcaucasia is figured by Sosnichina (1950). The grey dwarf hamster digs its own burrows but prefers natural holes and fissures in the soil (Mendelssohn \& Yom-Tov, 1999). In European Russia, 71.4\% of 65 occupied burrows were excavated by other rodent species, and in hard soil C. migratorius nearly did not burrow (Bašenina, 1951). While Lewis et al. (1967) state that burrow entrances are indistinguishable from those by Meriones, Atallah (1977) on the other hand claims them to be distinct, "with entrances descending almost perpendicular to the surface."

Reproduction. Detailed information on reproduction is available for hamsters bred in captivity (Volf \& Volf, 1993). Reproductive activity was year-round and litters were frequent; e.g. during eleven months a single female produced eleven litters with a total of 57 cubs. Mean litter size in a captive colony was 5.1 (range $=2-8 ; \mathrm{N}=15$ ). Gestation period was $17-17.5$ days. Young were born blind, nude and helpless (body mass $=1.66-2.20 \mathrm{~g}$ ). When 10 days old they weight on average 8.9 g , and at 30 days they weight 30.4 g . Adult colouration was gained when 4-5 months old. Females first copulated when 37 days old and delivered first litter at the age of 54 days. Longevity was up to 2 years and 4 months (Volf \& Volf, 1993).


Figure 14. Summer (above) and winter (below) burrow system of Cricetulus migratorius in European Russia. $\mathbf{N}$ - nest; cache is shaded. Summer nest was 30 cm deep and winter nest was 43 cm deep. Redrawn from Bašenina (1951).

For Israel Mendelssohn \& Yom-Tov (1999) gave the following details on reproduction: gestation period 16-19 days, litter size 3-5, and 2-3 litters annually. Reproductive period in the Ukraine normally lasts from April (but starts already in March in corn ricks) to September, and can be prolonged into November and December; litters contain 1-10 young, mostly 5-7 (mean = 5.5; Bašenina, 1951).

In Anatolia we captured scrotal males (testes up to $10 \times 6.5 \mathrm{~mm}$ ) in June, July, October and November, and juveniles in April - May and in September. A sample of eight adults collected in June in Central Anatolia suggests intensive reproduction in early summer. In Lebanon, Lewis et al. (1967) captured a pregnant female in March, lactating females in October and males with swollen testes ( $10-11 \times 6-7 \mathrm{~mm}$ ) in December. For Iran, Lay (1967) reports pregnant females from August, November, December and January. Mendelssohn \& Yom-Tom (1999) suggest that the potential for grey dwarf hamsters to breed all year round in captivity is largely realised under natural conditions. As a matter of fact, Ejgelis (1980) found reproduction to last throughout the year in eastern Transcaucasia with peaks in May (27.2\% of females pregnant) and in August (21.3\% pregnant). Six females from Anatolia had 4-8 embryos (mean $=6.3$; Felten et al., 1971b, and our own data) and a similar count is reported also from Iran (4-7; mean $=5.8$, $\mathrm{N}=6$; Lay, 1967). Litter size in eastern Transcaucasia is $2-10$ (mean $=5.7$ ), but varied among years between 5.3 and 6.3 (Ejgelis, 1980). Number of embryos and placental scars in Bulgaria is 4-7 (Peshev et al., 2004). Sex ratio is male biased in eastern Transcaucasia throughout the year (Ejgelis, 1980).

Food. The hamster stuffs small food particles (leaves, seeds, small fruits) into its cheek pouches which sag to the shoulders during foraging (Fig.


Figure 15. Grey dwarf hamster with cheek pouches stuffed with food particles. Redrawn from Flint (1966).
15). Food is taken into the burrow, removed from pouches by pressing with paws and stored (Mendelssohn \& Yom-Tov, 1999). Hassinger (1973) reports 4.5 g of legume leaves, seeds and seedpods in cheek pouches from a 28 g heavy hamster. Food is stored seasonally; in European Russia winter stores mostly contain 400-500 g of food, mainly cultural plants (particularly wheat, barley and maize). Reproductively active females gather 100-200 g of food during summer, plug burrow entrance with soil and stay with their young underground for several days (Bašenina, 1951).

Various authors report that grey dwarf hamster feeds on seeds, fruits, green plants, insects, snails and small vertebrates (Bašenina, 1951; Šidlovskij, 1976; Harrison \& Bates, 1991; Mendelssohn \& Yom-Tov, 1999; Peshev et al., 2004). In European Russia, Bašenina (1951) identified from stores and check-pouches content plants of 37 different species; most abundant were Melilotus officinalis, M. alba, Convolvulus arvensis, Reseda lutea, Agropyrum repens, Bromus squarrosus, Medicago falcate, Atriplex patulum, Galium tricornae, Artemisia austriaca, and Euphorbia gerardiana (Bašenina, 1951). Animals we captured in Anatolia had pouches stuffed with seeds and green leaves (frequently alfalfa) which accords with observation by Lewis et al. (1967) from Lebanon. Captive hamsters are reported to viciously kill jerboas and frogs and partially eat them (Lay, 1967). According to Šidlovskij (1976), the grey dwarf hamster is a pest in grain storehouses.

Predation. Owls are possibly one of the most important predators of the grey dwarf hamster in Turkey and its surroundings. In Anatolia, Obuch (1994) found C. migratorius to be one of small mammals most frequently preyed upon by Bubo bubo and Strix aluco. In addition, Tyto alba (Niethammer, 1989; Kasparek, 1988; Brinkmann et al., 1990), Athene noctua, Asio flammeus (Kasparek, 1985), and Asio otus (Seçkin \& Coşkun, 2006) also prey on grey dwarf hamsters. Note that Seçkin \& Coşkun (2006) report their pellet material from Diyarbakır as Cricetus cricetus, but their figure clearly points on Cricetulus migratorius.

The barn owl Tyto alba is also known to prey on the grey dwarf hamster in Syria and Israel (Rifai et al., 1998). In southern Syria, hamsters constituted $8.9 \%$ of the animals preyed upon by this owl (She-
hab, 2005), but the figure was lower in the north (3.65\%; Shehab \& Al Charabi, 2006). Several reports about predation upon the grey dwarf hamster are from unidentified owl species: in Turkey (Steiner \& Vauk, 1966; Nadachowski et al., 1990) and in Syria (Pradel, 1981; Nadachowski et al., 1990; Shehab et al., 2004).

In Iran, Lay (1965) encountered grey dwarf hamsters "wandering inexplicably in wide open, unprotected places" where they are more frequently preyed upon "by foxes and jackals than any other single rodent species."

Conservation. The grey dwarf hamster is rare along its distribution margin, particularly so in the Balkans. Its status in Turkey is little known. While trapping results suggest it to be rare in general, it was occasionally the principal prey of owls. Opinions on its rarity differ also in Israel (cf. Qumsiyeh, 1996).

## Genus: Mesocricetus Nehring, 1898

Robust hamsters with a short tail, relatively long ears and specialised fur colour pattern of contrasting dark and light areas. Validity of the four small range Mesocricetus species (Musser \& Carleton, 2005) is strongly supported by molecular evidence (Neumann et al., 2006). Allopatric ranges of these species are scattered along the coasts of the Black Sea, Caspian Sea and the north-eastern Mediterranean. In the past, Mesocricetus was mainly reported as monotypic, with M. auratus as the only species recognized in the genus (Neuhäuser, 1936; Ellerman, 1948; Ellerman \& Morrison-Scott, 1951; Osborn, 1965; Steiner \& Vauk, 1966; Lay, 1967; Sickenberg, 1971; Atallah, 1977; Corbet, 1978; Harrison \& Bates, 1991; Qumsiyeh, 1996). Not all authors accepted such a prac-


Figure 16. Turkish hamster Mesocricetus brandti. Drawing: J. Hošek.
tice of oversimplification and recognized $M$. brandti as another distinct species (Aharoni, 1932; Argyropulo, 1933b; Šidlovskij, 1976; Lehmann, 1969; Felten et al., 1971b; Spitzenberger, 1972; Steiner, 1972; Kumerloeve, 1975; Storch, 1975; Lyman \& O’Brien, 1977; Hosey, 1982; Kittel, 1984). Current taxonomy is largely based on a revision by Hamar \& Schutowa (1966). Mesocricetus auratus and $M$. brandti are reproductively isolated. No offspring have resulted from captive mating between the two species, though copulation has been observed (Lyman \& O’Brien, 1977).

Argyropulo (1933b) synonymised Mesocricetus with Cricetus, which was adopted mainly by Russian authors (e.g. Bobrinskij et al., 1965), but only rarely by students of Turkish mammals (Neuhäuser, 1936).

Vereščagin (1959) believed that Mesocricetus is among the endemic forms which evolved on the Caucasus in Pontian times (Pliocene). Hosey (1982), on the other hand, tentatively placed the origin of the genus to Palestine, and suggested that the European M. newtoni dispersed over the Bosporus land bridge during the Pleistocene and subsequently evolved in


Figure 17. Variation in throat and chest colouration in Mesocricetus auratus (a-c) and M. brandti (d-f). a - type of M. auratus; b - Tel Hadida, Aleppo, Syria; c - captive stock; d - Van; e - Gücük, Sarkışla, Sivas; f - Erzurum. Based on specimens in BMNH (a, b, f), NMNH (c), ZFMK (d), and our own material (e). Greyish pelage is light shaded, buff pelage is dark shaded.
allopatry. A gradual reduction in diploid chromosome number can be followed along the putative colonization route (cf. also Yerganian, 1972): M. auratus and $M$. raddei $(2 \mathrm{~N}=44) \rightarrow$. . brandti $(2 \mathrm{~N}=42)$ $\rightarrow M$. newtoni $(2 \mathrm{~N}=38)$. Under the scenario which assumes that simple translocations were the main mechanism of chromosomal changes (Popescu \& Di Paolo, 1980), M. auratus and M. raddei possibly posses the ancestral diploid number. Molecular evidence is in line with this scenario and estimates a divergence between $M$. brandti and $M$. newtoni to occur during the Early Pleistocene (1.7-1.8 million years ago; Neumann et al., 2006). Recent interpretation of karyotypes however suggests a different evolutionary scenario. Hence, Romanenko et al. (2007) showed that M. brandti holds the basal position in a cladogram based on chromosomal character states, while M. auratus and M. raddei display the most derived karyotypes. Relatively late postulated emergence of $M$. newtoni is in accordance with fossil evidence (cf. chapter on Palaeontology under $M$. brandti).

## Identification

The two species living in Turkey were largely distinguished on the basis of colouration (Ellerman, 1948). Despite considerable intraspecific variation, dorsal colouration and some peculiarities of colour pattern are helpful for identification purposes and we considered them in the determination key below. Ellerman (1948) assumed that M. auratus lacks "clear black chest-spot or shoulder stripe, or these vestigial". As a matter of fact, the throat pattern is most variable in $M$. auratus and some specimens display an extensive black chest-spot (Fig. 17). Black subauricular stripe is largely absent in M. auratus; but some specimens (e.g. BMNH specimen 86,1770 from Tel Hadida, Syria) show a broad and well defined stripe.

Hamar \& Schutova (1966) figured differences in the shape of parietal ridges, which we found to be of little help. Yiğit et al. (2000b) suggest shape of interpterygoid fossa to be a stable taxonomic character. Pterygoids are reportedly parallel and orthogonal to a posterior hard palate in M. brandti; the interpterygoid fossa is hence rectangular ( U -shaped in terminology by Yiğit et al., 2000b). Pterygoids converge anteriorly and meet at the posterior hard palate in M. auratus; interpterygoid space is therefore con-


Figure 18. Variation in shape of the posterior margin of the hard palate in Mesocricetus auratus (a-d) and M. brandti (eh). a - Turkey; b - type of M. auratus; c - Aleppo, Syria; d - Ebla, Syria; e - captive stock, originating from Pirbadan, Kurdestan, Iran; f - Erevan, Armenia; $\mathbf{g}$ - Mt. Ararat, Turkey; h - Yazlıkişla, Yozgat, Turkey. Based on BMNH specimens (b, c, e-h); a - redrawn from Yiğit et al. (2000b); d - redrawn from Shehab et al. (1999b). Not to scale.

a

b

Figure 19. Baculum in (a) Mesocricetus auratus and (b) M. brandti. Scale bar $=2 \mathrm{~mm}$. Redrawn from Yiğit et al. (2000b).
stricted anteriorly and triangular in shape (V-shaped in terminology by Yiğit et al., 2000b). We used this character in the key although it is certainly more variable than suggested by Yiğit et al. (2000b). For extreme variants cf. Fig. 18. In a captivity-bred sample of M. auratus (BMNH) 70.7 \% of specimens were of auratus type, 8.6 \% were of brandti type and the remaining 20.7 \% were intermediate $(\mathrm{N}=58)$. Shape of interpterygoids hence does not allow safe allocation of each specimen into the proper species category. Mesocricetus brandti has on average longer masseteric plate (ca. 3.0 mm ) than M. auratus (ca. 2.4 mm ), but the material we saw was too limited for a firm conclusion on the taxonomic validity of this trait. There are significant differences between the two hamsters in the length of baculum (Fig. 19; Yiğit et al., 2000b).

## Key to species

1 Back rich reddish brown; area around ears of same colour as back; interpterygoid fossa mainly triangular (Fig. 18a, b); total baculum shorter than 5 mm (Fig. 19a); diploid number of chromosomes $2 \mathrm{~N}=44$
M. auratus

1* Back pale sandy brown to tawny-olive; area around ears paler and more buff than back; interpterygoid fossa mainly rectangular (Fig. 18f-h); total baculum longer than 5 mm (Fig. 19b); diploid number of chromosomes $2 \mathrm{~N}=$ 42
M. brandti

## Golden hamster - Mesocricetus auratus

Cricetus auratus Waterhouse, 1839. Type loc.: Aleppo, Syria.

The history of golden hamster research in nature was summarised by Gattermann et al. (2001). The earliest report was probably by Russel \& Russel (1797).

## Description

External characters. General form heavy and thick
set. Tail is rudimentary, broad at base and nearly concealed in fur. Ears are large (longer than hind foot) and rounded. Mystacial vibrissae are largely black, rarely white, up to 27 mm long. Fore foot is broad and short, with four fingers; thumb is reduced. Hind foot is short and narrow, with five toes. Soles and palms are nude, with five and six tubercles, respectively. Fur is long (up to 12.2 mm in mid-back), dense and soft.

Colour. Back is reddish or fawn with rusty brown tints along spine and more yellowish along sides. Head is more rufous than back; occasionally there is blackish or dark brown spot between ears. Hair base are dark slate. Belly is greyish or nearly white but always washed by slate grey undercolour. Flanks are grey and well demarcated. There is an oblique narrow blackish to brownish subauricular stripe from cheeks to shoulders. Hairs around lips are greyish white. Colouration of throat and chest is highly variable. Throat is grey to white, followed in some specimens
by rufous transverse band across chest and lying in front of fore feet. Middle part of this band is usually with blackish and white areas of variable extent. In one extreme, anterior part of chest is largely blackish, in another it is split into two by a wide white longitudinal belt (Fig. 17a-c). Fore feet are white and hind feet are covered dorsally by short white hair. Ears are grey and tail is sparsely covered with whitish hair.

Nipples. There are eight pairs of nipples, evenly spaced from pectoral to inguinal region.

Penis. Mesocricetus has the simplest structure of glans penis among Cricetinae (Voroncov, 1982). Yiğit et al. (2000b) found no differences in glans between M. auratus and M. brandti; cf. under that species. Baculum of an individual from Turkey is figured by Yiğit et al. (2000b: Fig. 4a on p. 171). The three processes of a distal baculum are long and widely expanded in their middle portion, but the lateral two converge with the central element into a pointed apex. Lateral processes are longer than the central


Figure 20. Golden hamster Mesocricetus auratus from Turkey. Photo: C. Kern.
one, and the stalk is grooved ventrally. The baculum shows three or four ossification centres: one primary for the stalk, one secondary centre for each of the two lateral prongs, and sometimes a fourth centre for the medial distal process (Callery, 1951). Processes ossify with the proximal stalk into a single bony element with advanced age. The proximal base is expanded (Fig. 19a). The entire baculum is about 4.3 mm long, and 1.3-1.4 mm wide at its most expanded proximal and distal part, respectively (measurements estimated from Yiğit et al., 2000b). In the female, the os clitoridis ossifies from a single centre and attains its maximum length by 50 days. The bone is spatulate in shape with two pairs of spinous projections directed ventro-laterally (Callery, 1951).

Skull is robust and heavy, dorsal profile is slightly convex; brain-case is diamond shaped, short and deep. Squamosals are much expanded dorsally which leaves parietals and interparietal reduced. Rostrum is long and heavy, nasals long and pointed anteriorly. Interorbital region is constricted and much narrower than rostrum, with high lateral ridges and well marked medial groove which is constricted just behind the interorbital portion. Lambdal crest is strong, occipital region is inclined towards condyles which
are shifted backward. Zygomatic arches are heavy and expanded (zygomatic breadth is 53.2-57.8 \% of condylobasal length; mean = 55.1 \%); anterior margin of masseteric plate is concave and masseteric protuberance is large. Incisive foramen moderately long and wide, posteriorly not reaching molar line. Pterygoids converge anteriorly and meet at the posterior hard palate; interpterygoid fossa is thus triangular in a majority of specimens (Fig. 18a-d). Auditory bullae are relatively large. Mandible is similar to that of Cricetulus migratorius, but more robust; all processes are well developed and heavy.

Teeth. Incisors are robust but show no peculiarities in comparison to Cricetulus migratorius. Enamel on front surface is orange (upper incisors) and yellow (lower incisors). Molars essentially as in C. migratorius but the two posterior molars less reduced in relation to the $1^{\text {st }}$ molar. The anterior-posterior trend of reduction in molar size remains pronounced only in the maxillary row. First molar has six tubercles, $2^{\text {nd }}$ and $3^{\text {rd }}$ are with four cusps. Anterior pair of cusps is rudimentary in $1^{\text {st }}$ lower molar. For molar measurements see Shehab et al. (1999b). Alveolar pattern is same as in Cricetulus migratorius: 4, 4, 3 (maxillary row) and 2, 2, 2 (mandibular row).


Figure 21. Skull and mandible of Mesocricetus auratus. Based on a partly reconstructed type specimen; mandible is of an adult female from Tal Hadida, Aleppo, Syria (both BMNH). Scale bar $=5 \mathrm{~mm}$.

a

b

Figure 22. Upper (a) and lower molars (b) in Mesocricetus auratus. Based on a type specimen (BMNH). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

Dimensions are given in Table 4. Body mass of free-living hamsters from northern Syria in spring was $99.5 \pm 5.9 \mathrm{~g}$ in six males and $76.0 \pm 13.7 \mathrm{~g}$ in three females (Gattermann et al., 2001). In captive two-year-old hamsters body mass varied from 97 to 113 g (mean = $105 \mathrm{~g} ; \mathrm{N}=111$; Altman \& Dittmer, 1964) which is less than in free living animals (cf. Table 4).

Сhromosomes. The karyotype consists of 44 chromosomes, and the fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=78$. Of the 21 pairs of autosomes, 18 pairs are bi-armed and three pairs are acrocentric. The X chromosome is the largest metacentric in the set and the Y chromosome is a large metacentric (Doğramacı et al., 1994; Yiğit et al., 2000b). For banding chromosomes see Romanenko et al.
(2007). Laboratory hamsters share same diploid number (Popescu \& Di Paolo, 1980).

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 9 | 145.9 | $128-165$ |
| Tail | 12 | 18.5 | $13.0-20.8$ |
| Hind foot | 17 | 20.1 | $19.0-22.0$ |
| Ear | 17 | 21.2 | $18.0-22.5$ |
| Weight | 9 | 93.0 | $82-175$ |
| Condylobasal length | $22(8)$ | 33.1 | $30.1-38.6$ |
| Zygomatic breadth | $24(7)$ | 18.1 | $17.2-19.8$ |
| Maxillary tooth-row | $57(40)$ | 5.3 | $5.0-6.6$ |

Table 4. External and cranial dimensions of Mesocricetus auratus from Turkey and Syria. Sources: Aharoni (1932), Atallah (1977), Shehab et al. (1999b), Yiğit et al. (2000b), Shehab \& Al Charabi (2006), and specimens in BMNH and NMNH. Sample size for ranges is parenthesized.

## Variation

A monotypic species. Mean heterozygosity in Turkish population is $H_{o}=0.029$ (Yiğit et al., 2007).

## Distribution

Known only from a small area along the TurkishSyrian border (Gattermann et al., 2001).

Previous reports for Lebanon and Israel (e.g. Musser \& Carleton, 1993) are clearly erroneous (Shehab et al., 2004). In Syria, M. auratus is confined to the Aleppinian plateau (Gattermann et al., 2001) where it is known in eight localities; further records occur in south-eastern Anatolia to the south of Gaziantep and near Ceylanpınar. According to Eisentraut (1952), a gravid female was captured in 1949 about 20 km east of Antakya, however, presence of the species in Hatay province was subsequently not confirmed (Fig. 23).

Palaeontology. Mesocricetus auratus was reported from various sites in Israel and fossil record dates back, with some intermittence, into the Upper Pleistocene (Achelo-Yabrudian; about 160,000 years ago); it is absent however from the Late Auchelian strata (Tchernov, 1992, 1994). In earlier papers Tchernov (1968a, 1975) recognised a sequence of the fossil M. aramaeus Bate, 1943, and the extant M. auratus, which were supposed to co-occur briefly during the Upper Mousterian (about 40,000 years ago). If fossil remnants from Israel do belong to $M$. auratus, than the range of this hamster shrunk dur-


Figure 23. Distribution of Mesocricetus auratus. Dubious record is plotted as diamond. Records: $\mathbf{1}$ - Kilis, Gaziantep; 2a - Nizip, Gaziantep; 2b - Kesiktas, Nizip, Gaziantep; 3 - Ceylanpınar, Şanlı Urfa ; 4-20 km east of Antakya (=Hatay); 5 - Arnaz; $\mathbf{6}$ - Biliramun; 7 - Aleppo; $\mathbf{8}$ - Azaz; 9 - Albel; 10 - Shaykh-Riek; 11 - Jarablus; $\mathbf{1 2}$ - Ebla (=Tell Mardikh). Corresponding referrences: Eisentraut (1952): 4. Doğramacı et al. (1994): 2a. Shehab et al. (1999b): 12. Verimli et al. (2000): 1. Gattermann et al. (2001): 2b, 5-11. Yiğıt et al. (2003): 3.
ing the Holocene, similarly as was the case in the region with several other small mammals (e.g. Myomimus roachi and Talpa davidiana; cf. Kryštufek et al., 2009c).

## Habitat

In northern Syria, main habitats are on sandy clay sediments (terra rossa and terra fusca) overlying limestone (Gattermann et al., 2001). Steppic habitats with Hordeum sp., Eryngium sp., Securigera sp., Peganum sp., and Agropyron sp. (Yiğit et al., 2003) on loose soil are occupied in Turkey (Yiğit et al., 2000b). In northern Syria, burrows were mainly found in irrigated fields with annual crops (weed, barley, chickpea, lentil, melon, tomato, cucumber and hibiscus; Gattermann et al., 2001); edges of arable land are also occupied in Turkey (Yiğit et al., 2000b). Plots under leguminous cultures are also frequented (Aharoni, 1932).

Climate within the golden hamster range in northern Syria is continental with large seasonal and di-
urnal fluctuations and low rainfall ( 335 mm annually). Although mean annual temperature is about $20^{\circ}$ C, winters are cool with 35 frosty days and absolute minimum temperatures of -4 to $-9^{\circ} \mathrm{C}$ (Gattermann et al., 2001). Annual precipitation for two Turkish sites is reported as 330 and 528 mm , respectively (Yiğit et al., 2003).

Altitude. Elevation of two Turkish records is 400 and 650 m a.s.l, respectively (Yiğit et al., 2003). The main distribution area in the Aleppinian plateau (Syria) is 280-380 m above sea level (Gattermann et al., 2001).

Associates. Yiğit et al. (2003) reported the following rodents to be associated with golden hamster in south-eastern Anatolia: Cricetulus migratoris, Meriones tristrami, Dipodilus dasyurus, Microtus guentheri, Spalax ehrenbergi, Apodemus mystacinus, Apodemus cf. witherbyi, and Allactaga euphratica. In northern Syria social voles are its abundant associate (Gattermann et al., 2001). Owl pellet sample from northern Syria contained social voles, Cricetu-


Figure 24. Habitat of Mesocricetus auratus. Photo: P. Nová.
lus migratorius, Mus sp., Spalax sp., Rattus sp., Suncus etruscus, and Crocidura sp., in addition to M. auratus; social voles were the most abundant (Shehab et al., 1999b; Shehab \& Al Charabi, 2006).

Density. Gattermann et al. (2001) found in agricultural fields in northern Syria six occupied burrows in an area of 30 ha which suggests low density ( 0.2 per ha). The closest distance between occupied burrows was 118 m . Densities are presumably higher in grassy embankments (Gattermann et al., 2001). Studies of owl diet suggest much higher densities (cf. below under Predation) and induced Shehab \& Al Charabi (2006) to a conclusion that M. auratus "is still common at its type locality (around the city of Aleppo)."

## Biology

The golden hamster is a common experimental animal and a popular pet in the West. The entire captive population originates from a single female with 11 cubs which I. Aharoni excavated near Aleppo on April 12, 1930. A group of a single male and three females from this stock (note that the reverse sex ratio is stated in Gattermann et al., 2001) gave three consecutive litters of 6,8 , and 10 cubs, respectively; this brother-sister pairing multiplied to 150 animals in a single year (Aharoni, 1932). A further 12 wild animals were captured in 1971 and brought to the USA were they were added to a captive colony (Murphy, 1985).

The biology of the golden hamster was studied extensively in the laboratory (e.g. Siegel, 1985) but data from nature remains scarce (Gattermann et al., 2001).

Activity. Solitary (Gattermann et al., 2001) and nocturnal (Aharoni, 1932). Possibly hibernates between November and mid-February in northern Syria (Gattermann et al., 2001) though laboratory studies did not provide convincing evidence that the tendency towards hibernation is seasonal in this species (Lyman \& O’Brien, 1977).

Burrows were studied by Gattermann et al. (2001) in northern Syria. Total length of tunnels per burrow was between 90 cm and $>9 \mathrm{~m}$. Burrow depths varied between 36 cm and 106 cm , while nesting chamber ( $10-20 \mathrm{~cm}$ wide) was $36-93 \mathrm{~cm}$ deep (Gattermann et al., 2001). Yerganian (1972) reports nest chambers to be $2-2.5 \mathrm{~m}$ deep. The burrow entrance (diameter 4-5 cm) leads into a vertical tunnel $18-45 \mathrm{~cm}$ long (Gattermann et al., 2001). Nest is mainly of dry plant matter, occasionally with some textile material, bird feathers and shredded pieces of plastic sacks. At least two tunnels divide from the nesting chamber. A short and blind tunnel is presumably used for urination but there is no evident latrine (Gattermann et al., 2001).

Reproduction was extensively studied in captive animals. Pregnancy lasts 16 to 19 days and litters contain 6-10 young. Although many females are already pregnant when 7-8 weeks old, they reach full adult size at the age of 154 days to (Harrison \& Bates, 1991). In northern Syria, reproductive activity probably starts in February (Gattermann et al., 2001). A pregnant female was excavated in March by Gattermann et al. (2001) and another one again in spring (Eisentraut, 1952); nests with cubs were found in April (Aharoni, 1932) and March (age of cubs 2-3 weeks; Gattermann et al., 2001; BMNH specimen tag no. 1986.1770); a lactating female was collected in April (NMNH specimen tag no. 327.750). Number of cubs from the above evidence was 3 (Gattermann et al., 2001), 5 (BMNH), 6 (Gattermann et al., 2001), and 11 per litter (Aharoni, 1932).

Food. The golden hamster obtains grain by standing on its hind legs, grasping the stalk with its front feet or pushing it down, and cutting the stalk with its incisors. The animal then eats the fallen grain or puts it in its cheek pouches (Lyman \& O’Brien, 1977). Omnivorous in captivity.

Predation. Found in owl pellets in northern Syria (Shehab et al., 1999b, 2004). In a barn owl Tyto alba sample from Yahmool near Syrian-Turkish bor-
der, M. auratus (10.2\% of all animals) was one of the most frequently preyed-upon small mammal, next to Microtus cf. socialis (59.5\%) and Mus domesticus (10.5\%; Shehab \& Al Charabi, 2006).

Conservation. The golden hamster shows at least two criteria of a 7-form rarity model by Rabinowitz (1981), namely small range and low densities. Species displaying both restricted distribution and low density are those most at risk of extinction (Arita et al., 1990). Range in northern Syria is estimated at 10,000-15,000 km² (Gattermann et al., 2001), and inclusion of Turkish area does not essentially increase this figure. Turkish habitats are possibly still a pristine steppe (cf. chapter on Habitat). Syrian populations, however, are restricted to agricultural land where they face extensive control measures, including poisoning (Gattermann et al., 2001). The golden hamster is classified as an endangered species in Turkey (Yiğit et al., 2006c).

## Turkish hamster - Mesocricetus brandti

Cricetus brandti Nehring, 1898. Type loc.: near Tbilisi, Georgia.
Mesocricetus koenigi Satunin, 1900. Type loc.: Kasikoporan (= Göle, Kars district).

## Taxonomy

Danford \& Alston $(1877,1880)$ reported Turkish hamster under the name Cricetus nigricans which is a junior synonym of Mesocricetus raddei (Musser \& Carleton, 2005). Aharoni (1932) also considered $M$. brandti to be just a subspecies of $M$. raddei. The remaining authorities dealing with Turkish mammals have treated the Turkish hamster either as a species on its own right (Šidlovskij, 1976; Lehmann, 1969; Felten et al., 1971b; Spitzenberger, 1972; Steiner, 1972; Kumerloeve, 1975; Storch, 1975, 1988; Lyman \& O’Brien, 1977; Hosey,


Figure 25. Turkish hamster Mesocricetus brandti from Anatolia. Photo: C. Kern.

1982; Kittel, 1984, and all subsequent authors) or a subspecies (or a junior synonym) of $M$. auratus (Argyropulo, 1933b; Neuhäuser, 1936; Ellerman, 1948; Ellerman \& Morrison-Scott, 1951; Osborn, 1965; Steiner \& Vauk, 1966; Lay, 1967; Sickenberg, 1971; Atallah, 1977; Corbet, 1978; Harrison \& Bates, 1991; Qumsiyeh, 1996).

Brandt’s hamster is currently proposed as a vernacular name for M. brandti (Musser \& Carleton, 2005). We prefer the name Turkish hamster, used already by Lyman \& O’Brien (1977).

## Description

External characters. The Turkish hamster is of same shape and proportions as the golden hamster, but is on average significantly larger. Claws are weak and short, longer on front feet. Mystacial vibrissae are up to 34.5 mm long. Fur is long ( $8-11.5 \mathrm{~mm}$ in mid-back), dense and soft.

Colour is sand brown to tawny-olive on the back, never rich reddish as in M. auratus. Head is of same colouration as back but there is always a large blackish brown spot between ears. Hair base are dark slate. Belly is grey-white to white, invariably washed with


Figure 26. Skin of Mesocricetus brandti in dorsal, lateral and ventral view. Based on a female from Sirbasan, district Kars. Photo: C. Mlinar.
slate grey undercolour. Flanks are yellowish and demarcation line is indistinct. There is a well defined oblique black subauricular stripe from cheeks to shoulders. Yellowish area on cheeks expands below ears towards shoulders; hairs around ears are invariably more yellowish (and therefore paler) than back. Lips and chin are occasionally white. Across the chest and lying in front of forefeet is a wide, black transverse band. This band is bordered by white stripe in some specimens; more rarely it is split into two by a median white stripe. Fore feet are yellowish; hind feet are grey and covered by short buff hair. Ears are grey, covered by buff hair. Tail is whitish or yellowish at the tip.

Nipples are as in M. auratus (8 pairs).
Penis. Yiğit et al. (2000b) found no differences in glans penis between M. auratus and M. brandti. The glans in M. brandti (figured by Voroncov, 1982) is short, wide and deep, densely covered by spines over its entire surface, except for a short ventral groove at the base. Terminal crater encompasses three urethral lappets; the central one is shorter than the two on its lateral sides. Baculum is essentially like in $M$. auratus, except being larger and less expanded in its
medial part; its distal portion is relatively longer in relation to the proximal stalk (Yiğit et al., 2000b). The entire baculum is about 5.5 mm long, 2 mm wide across its basal shaft and 1.6 mm wide across distal processes (estimated from Yiğit et al., 2000b).

Skull is essentially as in M. auratus. Zygomatic arches are expanded and relative width of zygoma is similar as in M. auratus (zygomatic breadth is 52.458.2 \% of condylobasal length; mean = $55.5 \%$ ). The main difference between the two species is in the shape of mesopterygoid fossa and possibly in width of masseteric plate (wider in M. brandti). Pterygoids tend to be parallel in $M$. brandti and join orthogonally the posterior margin of hard palate. Interpterygoid fossa is thus mainly rectangular, its shape, however its shape is subjected to individual variation (cf. Fig. 18e-h).

Teeth. Growth of lower incisors is on average 1 cm per month (Lyman \& O’Brien, 1977). Enamel on front surface is yellow to orange (upper incisors) and yellow (lower incisors). Molars are essentially as in M. auratus (Fig. 28). See Hír (1992) for molar measurements. Alveolar pattern as in M. auratus.

Dimensions are given in Table 5. The only estimate


Figure 27. Skull and mandible of Mesocricetus brandti, based on an adult animal from Seyfe Gölü, Kırşehir, Turkey (ZFMK). Scale bar $=5 \mathrm{~mm}$.


Figure 28. Upper (a) and lower molars (b) in Mesocricetus brandti (same specimen as in Fig. 27). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
for body mass from a wild living individual available to us is 118 g . Šidlovskij (1967) reports the largest body mass to be 296 g in Transcaucasia. Two-yearold captive hamsters have a body mass 137-259 g (mean = $163 \mathrm{~g} ; \mathrm{N}=21$; Lyman \& O’Brien, 1977).

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 15 | 147.9 | $135-166$ |
| Tail | 15 | 18.7 | $10-27$ |
| Hind foot | 15 | 19.8 | $17.5-22.0$ |
| Ear | 15 | 21.5 | $17.5-24.0$ |
| Condylobasal length | 18 | 34.5 | $31.1-38.2$ |
| Zygomatic breadth | 14 | 19.1 | $17.6-21.4$ |
| Maxillary tooth-row | 19 | 6.4 | $5.9-7.0$ |

Table 5. External and cranial dimensions of Mesocricetus brandti from Turkey and Transcaucasia. Sources:
Neuhäuser (1936), Nadachowski et al. (1990) and specimens in BMNH, NMNH, and ZFMK.

Сhromosomes. The diploid number of chromosomes is $2 \mathrm{~N}=42$ and consists of 20 bi-armed autosomal pairs. Because of the subjective evaluation of shape of the smallest chromosomes in a set, different fundamental numbers of autosomal arms are reported $\left(\mathrm{NF}_{\mathrm{a}}=76-80\right.$; Zima \& Král, 1984). The X chromosome is a large metacentric, while the Y chromosome is either a medium-sized or the smallest submetacentric (Zima \& Král, 1984).

Several authors karyotyped hamsters from Turkey (Popescu \& Di Paolo, 1980; Doğramacı et al., 1994; Yiğit et al., 2000b, 2006a) and reported fundamental numbers of autosomal arms to be 76, 78, or 80, respectively. Todd et al. (1972) and Lyman \& O'Brien (1977) found $2 \mathrm{~N}=42\left(\mathrm{NF}_{\mathrm{a}}=78\right)$ in a population from Malya, and $2 \mathrm{~N}=44\left(\mathrm{NF}_{\mathrm{a}}=80\right)$ in a sample from Ankara, both Central Anatolia. The difference in diploid number between the two samples results from the absence of the acrocentric pair no. 19 in the Malya hamsters. Hybrids showed $2 \mathrm{~N}=43$ and $\mathrm{NF}_{\mathrm{a}}=79$ (Lyman \& O'Brien, 1977).

Popescu \& Di Paolo (1980) provided details on G-, C- and Ag-I banding; for banding pattern see also Romanenko et al. (2007).

|  | C. Anatolia <br> $\mathrm{N}=53$ | NE Anatolia <br> $\mathrm{N}=11$ |
| :--- | :---: | :---: |
| Total length | 154.4 | 170.0 |
| Tail | 19.8 | 21.1 |
| Hind foot | 20.1 | 21.4 |
| Ear | 21.7 | 23.0 |
| Weight | 80.4 | 108.7 |
| Condylobasal length | 32.0 | 33.5 |
| Zygomatic breadth | 18.0 | 18.4 |
| Maxillary tooth-row | 6.2 | 6.4 |

Table 6. Means for external and cranial dimensions in two samples of Mesocricetus brandti from Anatolia: Central Anatolia (samples from Eskişehir and Afyon in the west to Kayseri in the east) and north-eastern Anatolia (Kars and Ardahan). Modified from Yiğit et al. (2000b).

## Variation

Satunin (1900) based description of Mesocricetus koenigi on a skull with widely expanded zygomatic arches. This taxon was largely synonymised with $M$. brandti, and subsequent authors did not recognise it to be a valid subspecies (Argyropulo, 1933b; Ellerman \& Morrison-Scott, 1951). Turkish ham-
sters however are known to be larger and darker near Kars in north-eastern Turkey (Lyman \& O’Brien, 1977; Yiğit et al., 2000b). Size differences are largely of average (Table 6) and there is no proof of discontinuity. If these hamsters are subspecifically distinct, then the name koenigi is applicable for them.

Lyman \& O’Brien (1977) stated that hamsters from Iranian Kurdestan are paler, possibly representing another subspecies. Neuhäuser (1936) reported a reddish specimen from Uşak.

Mean heterozygosity in Turkish population is $H_{o}$ $=0.080$ (Yiğit et al., 2007).


Figure 29. Distribution of Mesocricetus brandti in Turkey and adjacent regions. Records: $\mathbf{1}$ - Çardak, Denizli; 2 - Uşak; 3 Afyon; 4 - Gökçekısık, Eskişehir; 5 - Akşehir, Sultan Dağ, Konya; 6 - Kösrelik, 25 km north-west of Ankara; 7 - Emir Lake, near Ankara; 8 - Temeyeniçe, Ekinbogin Tepe, ca 100 km north of Ankara; 9 - Tosya, Kastamonu; 10 - Halys (=Bafra), Samsun; 11 - 4 km north-east of Beyşehir; 12 - Konya; 13 - Divanlar, Konya; 14 - Kılbasan, Karaman; 15 - 20 km west of Ulukısla, Niğde; 16 - 20 km north of Arslanköy, Mersin; 17 - Mersin; 18 - Demir Kaziköy, Ala Dağları, Adana; 19 - Niğde; 20 - Yaprakhisar, Ihlara, Aksaray; 21 - Nevşehir; 22 - Aksaray; 23 - Inevi (=Cihanbeyli), Konya; 24 - Şerefli Koçhisar, Ankara; 25 - Kırşehir; 26 - Seyfe Gölü, Kırşehir; 27 - Malya (=Malye), Yenidoğanl, Kirşehir; 28 - Kayseri; 29 - between Buroon-kysla (=Boğazlıyan) and Jazli-tash (= Yazlıtaş, today Yazlıkişla), Yozgat; 30 - Boğazkale, Çorum; 31 - Merzifon, Amasya; 32 - Yıldızeli, Sivas; 33 - Gücük, Şarkışla, Sivas, 1,400 m a.s.l.; 34 - Hafik, Celalli köyü, Sivas; 35 - Darende, Malatya; 36 - Erzincan; 37 - 4 km south-east of Güzyurdu, Gümüşhane; 38 - Sümela, Trabzon; 39 - 5 km east of Bayburt, 1,900 m a.s.l.; $\mathbf{4 0}$ - Erzurum; $\mathbf{4 1}$ - Yazlıtaş, Horasan, Erzurum; 42a - 3 km north of Sirbasan, Kars, 2,200 m a.s.l.; 42b - 3 km west of Handere, Kars, ca 2,600 m a.s.l.; 43 - Sarıkamış, Kars; 44 - Kasikoparan (=Gaz Koparan; now Göle), Kars; 45 - Kars; 46 - Ardahan; 47 - Aralysch (=Aralık), Iğdır; 48 - Mt. Ararat (=Büyükağrı Dağı), Iğdır; 49 - Bendimahi, Muradiye, Van; 50 - Güzeldere köyü, Özalp, Van, 2,480 m a.s.l.; 51 - Van; 52 - 19 km south of Van; 53a - Tatvan, Bitlis; 53 b - 3 km south of Tatavan, Bitlis. Corresponding referrences: Danford \& Alston (1877): 29. Satunin (1900): 44. Aharoni (1932): 10, 17. Neuhäuser (1936a): 2, 9, 23, 47, 48, 51. Ellerman (1948): 40, 41. Osborn (1965): 7, 24, 28. Lehmann (1966a): 30. Steiner \& Vauk (1966): 11. Lehmann (1969): 5, 53a. Sickenberg (1971): 6, 8, 13. Spitzenberger (1972): 15, 16, 31. Lyman \& O’Brien (1977): 27. Obuch (1994): 18, 20, 43, 49, 53b. Doğramacı et al. (1994): 34, 39, 50. Yiğit et al. (1997a): 3, 12. Yiğit et al. (2000b): 19, 21, 22, 25, 36, 45, 46. Yiğit et al. (2003): 1, 4, 14, 32, 35, 38, 52. ZFMK: 26. Our own data: 33, 37, 42a, b.

## Distribution

The Turkish hamster has the largest distributional area in the genus Mesocricetus. It occurs in Anatolia, Transcaucasia (Armenia, Georgia, and Azerbaijan; Šidlovskij, 1967) and in north-western Iran (to Qazvin in the east and to Lurestan in the south; Lay, 1967). Reports for northern Iraq, Syria, Lebanon, and northern Israel (Musser \& Carleton, 2005) are erroneous (Shehab et al., 2004). Majority of the range is in Turkey and north-western Iran.

In Anatolia, the Turkish hamster spreads to the line Çardak (Denizli) - Uşak in the west and does not cross the line Uşak - Bafra (Samsun) in the northwest. Therefore, the species is absent from the Aegean and Marmara regions. Occurrence in the Mediterranean and Black Sea coast is only exceptional, and the animal is also absent from south-eastern Anatolia. Records are the densest in central and north-western Anatolia. The Turkish hamster does not occupy any of the islands offshore from the Turkish coast.

Palaeontology. An early form Mesocricetus primitivus de Bruijn, Dawson and Mein, 1970, occurred in the Aegean - Anatolian region already in the Upper Pliocene (Upper Ruscinian): Isle of Rhodes (de Bruijn et al., 1970) and Çalta in Central Anatolia (Şen, 1977). Surprisingly, last molars in M. primitivus, both maxillary and mandibular ones, were shorter relative to $2^{\text {nd }}$ molar than in extant $M$. auratus and M. brandti (Ș en, 1977). During the Late Pliocene period, hamsters (Cricetinae) were the most abundant rodent group in Rhodes (36.0 \%), but rare in Çalta ( 5.9 \%), and absent from Turkobounia-1 in southern Greece (Şen \& de Bruijn, 1977).

The Lower Pleistocene (Early Biharian) material from the Dodekanese island of Kalymnos is linked to a fossil M. aramaeus described from Palestine (Kuss \& Storch, 1978). Specimens from the Middle Pleistocene are already ascribed to a recent $M$. brandti (Island of Chios; Storch, 1975), or is their species identity left open (Emirkaya-2; Şen et al., 1991; Montuire et al., 1994). Both Aegean islands, inhabited by Mesocricetus during the Early and Middle Pleistocene, are characterised by a non-endemic fauna with strong affinities to Asia Minor. Contrary to this, a large endemic hamster (Mesocricetus rathgeberi Pieper, 1984) occurred on another two Aegean islands, Armathia and Kasos, where it survived into the Holocene (Pieper, 1984; Kotsakis, 1990).

Middle Pleistocene fossils of Mesocricetus, which were not aligned to a species, are known from western Georgia and Apšeron Peninsula in eastern Azerbaijan (Vereščagin, 1959). For the Upper Pleistocene, Storch (1988) reports M. brandti from Karain site near Antalya. The Turkish hamster likely disappeared from the western Taurus Mts. at the Quaternary - Holocen boundary with no subsequent re-colonisation (Storch, 1988). Corbet \& Morris (1967) did not come across Mesocricetus in a sample from Finike, presumably less than 7,000 years old. Further eastward in the Taurus Mts., the Turkish hamster continued its existence into the Holocene and Hír (1991) found it to be common in his undated sample from Bolkar Dağ. Historical 3,000-4,000 years old records are known from Armenia (about 100 km southeast of Erevan; Vereščagin, 1959). During the Upper Pleistocene, Mesocricetus occurred also in northeastern Iraq (Palegawra Cave, 14,400 $\pm 760$ years old and identified as M. cf. armatus) and Iranian Kurdestan (Mousterian layers; reported as M. cf. auratus; Turnbull, 1975).

Hamsters from the Middle Pleistocene layers of Yarimburgaz in Turkish Thrace are tentatively ascribed to M. newtoni (Nehring, 1898) (Santel \& Koenigswald, 1998). This species is currently restricted to a small area along the River Danube in south-eastern Romania and northern Bulgaria and along the Black Sea coast in Bulgaria (MitchellJones et al., 1999; Popov et al., 2007). Its fossil range exceeded the recent one, encompassing also Serbia and Greece; M. newtoni is known since the Middle Pleistocene (Holsteinian; Kowalski, 2001).

## Habitat

Main habitat in Turkey and Transcaucasia consists of dry, rocky steppe country sometimes bordering cultivated fields. Avoided are wooded and bushy regions, damp and wet areas, and desertified places (Lyman \& O’Brien, 1977; Šidlovskij, 1976). The area within the distributional borders of $M$. brandti in Anatolia receives $<500 \mathrm{~mm}$ of precipitation annually; excessively dry are spring ( $<50 \mathrm{~mm}$ of precipitation) and summer (<30 mm; Yiğit et al., 2003). The following plants are typical of Turkish hamster’s habitat in Central Anatolia: Astragalus sp., Medicago radiata, Festuca sp., Cynodon sp., Thymus sp., Polyogonum sp., Salvia cryptantha, S. aethiops, Senecio
vernalis, Hyoscyamus niger, Centranthus longiflorus, Parietaria judaica, Torilis leptophyla, Eryngium campestre, Ziziphora capitata, and Teucrium polum. Habitats in east Anatolia are typically with Festuca valesiaca, Eremopoa songarica, Bromus danthoniae, Ornithogalum sp., Equisetum ramosimum, Atraphaxis billardieri, Crepis sp., Medicago sp., various crucifers (Brassicaceae), Bromus tomentellus, Astragalus microcephalus, Agroppyron repens, Echinops ritrio, and Eryngium campestre (Yiğit et al., 2003). Preferred habitats in eastern Transcaucasia are grassy sites, places of stony debris, loose bushes, as well as fields of cereals and multi-annual crops. In dry steppic regions hamsters are restricted to mesic sites. As a consequence the range is patchy in arid habitats and contiguous in subalpine meadows (Ejgelis, 1980).

Altitude. Turkish records range from the sea level (Bafra, Mersin) to $2,600 \mathrm{~m}$ a.s.l. (Handere) and majority of them lie between 1,100 and $2,200 \mathrm{~m}$ a.s.l. The highest record from the Taurus Mts. is at $2,200 \mathrm{~m}$ (Spitzenberger, 1972). The Turkish hamster goes up to $2,800 \mathrm{~m}$ in the Caucasus (Šidlovskij, 1967); altitudinal range in Georgia is between 250 and 3,000 m a.s.l. (Bukhnikashvili \& Kandaurov, 1998).

Associates of Turkish hamster in Central Anatolia are Spermophilus xanthoprymnus, Cricetulus migratorius, Meriones tristrami, Microtus guentheri, M. socialis, M. levis (replaced by M. arvalis in east Anatolia), Spalax xanthodon, Apodemus spp. (mainly witherbyi and occasionally mystacinus), Mus macedonicus and Allactaga williamsi (replaced by A. elater in the east). In eastern Anatolia, a further two voles (Ellobius lutescens and Prometheomys schapo-


Figure 30. Habitat of Mesocricetus brandti at Gücük, Sarkışla, 1,400 m a.s.l., district Sivas. Photo: B. Kryštufek.


Figure 31. Variation in relative density (number of individuals per 100 trap nights) in Mesocricetus brandti between 1961 and 1970 in two habitats in eastern Transcaucasia: a high mountain steppe (interrupted line) and a subalpine pasture (bold line). Modified from Ejgelis (1980).
schnikowi) and one jird (Meriones vinogradovi) occupy same habitat as M. brandti. Mesocricetus brandti is nowhere sympatric with M. auratus (this volume) or with M. raddei (Bukhnikashvili, 2004).

Density. Rare throughout its range; e.g. not a single Turkish hamster was captured in Iran during the Street expedition of 1962-1963 (Lay, 1967). Relative abundance in small mammal assemblages as perceived through trapping is $0.3-1 \%$ in Georgia (Bukhnikashvili \& Kandaurov, 1998). Ejgelis (1980) reports a trapping success in eastern Transcaucasia to be $0.2-1.2$ hamsters per 100 trap nights; higher abundances (2.0-2.1 per 100 trap nights) are exceptional. Despite its rarity, M. brandti is widespread and Yiğit et al. (2003) found it in nine of 19 localities sampled throughout Anatolia. Fluctuations in population densities are uncommon and when they occur, peaks are followed by sharp declines (Ejgelis, 1980; Fig. 31).

Owl pellet samples suggest much higher abundances of the Turkish hamster. In Bubo bubo pellets from Turkey, Obuch (1994) found the following percentages of $M$. brandti in rodent assembages: 68.0 \% in Demir Kaziköy ( $\mathrm{N}=50$ ), $45.0 \%$ in Tatvan ( $\mathrm{N}=20$ ), $33.6 \%$ in Sarikamiş ( $\mathrm{N}=1,180$ ), $22.4 \%$ in Yaprakhisar ( $\mathrm{N}=58$ ), and $13.8 \%$ in Muradiye ( $\mathrm{N}=$ 1,410). Similarly, Hír $(1991,1992)$ found M. brandti to be one of the most common rodents in a subfossil
material from Bolkar Dağ (14.4 \% of rodent individuals; $\mathrm{N}=600$ ).

## Biology

Activity is nocturnal. Hamsters feed principally at night although may be seen also at dawn and dusk (Argyropulo, 1939).

The Turkish hamster presumably does hibernate in nature and hibernation was confirmed in captive animals (Lyman \& O’Brien, 1977). In any case, M. brandti is a better hibernator than M. auratus. Laboratory animals did not undergo the period of autumnal fattening and lethargy under normal conditions, but when exposed to cold ( $5 \pm 2^{\circ} \mathrm{C}$ ), 92 \% of animals hibernated readily; approximately one tenth of population entered hibernation within 24 hours. Once the hibernation started, it lasted for about five months. The longest period of uninterrupted hibernation was 28 days (Lyman \& O’Brien, 1977). In Transcaucasia hibernation lasts from October to March and animals leave their burrows during warm winter days (Šidlovskij, 1976). Wild hamsters from Anatolia hibernated under captive conditions for 8-63 days (between November 2 and May 5). Most frequently they displayed 4-8 day bouts of torpor (with body temperature at $7-9^{\circ} \mathrm{C}$ ), interrupted with 1-3 day intervals of euthermia. Their pre-hibernating body mass (108-175 g) dropped during hibernation by 24 \% (Yiğit et al., 2008c).

Burrows. The Turkish hamster is a keen digger. The rapidly moving front feet are used to displace the earth and loose soil accumulates under the chest and abdomen. This dirt is moved by hind feet which are thrust backward together, while the front feet are braced. During this activity, the hamster arches its back and lifts its head. As the tunnel becomes longer, excavated earth is moved to the tail by a series of parallel kicks of the hind feet. After each set of kicks, the hamster moves backward about one-half the length of its body and resumes moving the earth (Lyman \& O’Brien, 1977).

Burrows have from one to three entrances (Gromov \& Erbajeva, 1995). On a flat surface the main entrance is an almost vertical shaft descending a meter or more deep. Afterwards the shaft curves abruptly to a horizontal plane; galleries and chambers branch from this main shaft. One or more of chambers are used for food storage, and one chamber is a nest-


Figure 32. Burrow system of Mesocricetus brandti in Transcaucasia. Excavated soil is shaded. $\mathbf{N}$ - nest. Redrawn from Argyropulo (1939).
ing area filled with dried grass (Fig. 32). One of the chambers is used as a latrine (Argyropulo, 1939). Although burrow systems in captivity resemble most closely those in nature, latrines were not used under artificial conditions (Lyman \& O’Brien, 1977). Nest chamber can be up to 2 m below the surface (Gromov \& Erbajeva, 1995).

Reproduction. Data from nature are scarce but reproduction was extensively studied in laboratory animals (Lyman \& O’Brien, 1977). Turkish hamsters exposed to a natural day length were usually not in breeding condition between November and March.

The youngest female to produce litter was 50 days old at her first delivery. Seven to eight-week-old animals reproduced successfully though they had not yet attain full growth. They reached peak of fecundity at about one year of age. Female oestrous cycle becomes less regular in the second year of life when her reproductive success starts to decline. Gestation is 15 days and litter size varies from one to 13 cubs (average is six). Animals born after June do not attain sexual maturity until the following spring (Lyman \& O’Brien, 1977). Females produce two litters annually in nature (Gromov \& Erbajeva, 1995) and never more than three in laboratory (Lyman \& O’Brien, 1977). Sex ratio is balanced in eastern Transcaucasia (Ejgelis, 1980).

Cubs are born blind and naked, but they quickly grow a protective coat. By the $12^{\text {th }}$ to $13^{\text {th }}$ day, the eyes open and they start eating solid food. They are weaned before the $20^{\text {th }}$ day (Lyman \& O'Brien, 1977). Growth in young hamsters is shown in Table
7. Mean body mass at birth is 2.6 g (Yiğit et al., 1997a) and 6-7 weeks old animals weight 50-141 g (mean $=91 \mathrm{~g}$; Lyman \& O’Brien, 1977). The medium life expectancy in laboratory animals is 670 days (Lyman \& O’Brien, 1977).

| Age (days) | N | mean | $\min -\max$ |
| :--- | :---: | :---: | :---: |
| 0 | 38 | 40.5 | $36-45$ |
| 7 | 35 | 57.6 | $51-73$ |
| 14 | 32 | 74.6 | $64-91$ |
| 21 | 30 | 92.4 | $71-118$ |
| 30 | 27 | 110.1 | $96-129$ |
| 38 | 27 | 119.7 | $106-140$ |
| 45 | 27 | 126.1 | $110-145$ |

Table 7. Changes in total length (mm) during postnatal development in Mesocricetus brandti. From Yiğit (2003).

Yiğit et al. (1997a) reported reproductive period in Turkey to last from late March to mid-summer. They collected pregnant females in March (3 females), May (1), June (2) and July (2). An additional female collected on July 7 had 6 placental scars. Young hamsters in museum collections were captured in Turkey between March and September. Of interest is a juvenile specimen obtained on March 7 near Tatvan (ZFMK). Its body mass ( 61 g ) place estimated birth date to early February and a conception to the second half of January. We captured the smallest juvenile ( 39 g ) on September 17 which documents copulatory activity still occurring in early August. On
these grounds, we estimate the reproductive period to last from late January till mid-August. Length of reproductive period in eastern Transcaucasia is 5-5.5 months, from June (possibly April) to October with a peak in July (Ejgelis, 1980).

Yiğit et al. (1997a) reported embryo counts for eight females collected in Turkey; range $=5-12$, mean $=8.5$. Mean litter size in east Transcaucasia is 6.6-7.5; exceptionally litters contain up to $15-16$ (even 19) cubs (Ejgelis, 1980).

Food. Diet consists of plants and insects, but voles are also consumed (Šidlovskij, 1976). Grain and grasses are stored in burrows (Argyropulo, 1939). Captive Turkish hamsters were kept on laboratory rat chow as a staple diet with addition of a slice of raw apple and 30 g rolled oats weekly (Lyman \& O’Brien, 1977).

Predation. Obuch (1994) found Turkish hamster to be a common prey of the eagle owl Bubo bubo. Kasparek (1985) reports a further two owls who prey on this species in Central Anatolia: Athene noctua and possibly Asio flammeus.

Conservation. Over the last two to three decades the area of occupancy was cut into half in the Mtkvari valley, Georgia. Expansion in agriculture reduced the range and pest control caused decline in population density (Bukhnikashvili \& Kandaurov, 1998). In Turkey extensive transformation of the pristine steppe to arable land likely pose a threat and Yiğit et al. (2006c) classified the species as Vulnerable.

## Family: Muridae Illiger, 1811

In its current scope, the family Muridae includes three subfamilies in the region. Dental formula is $1 / 1$, $0 / 0,0 / 0,3 / 3=16$.

## Key to subfamilies

1 Back clearly spinous; mesopterygoid fossa triangular, shifted much posterior to $3^{\text {rd }}$ molars; coronoid process vestigial

Deomyinae
1* Dorsal hairs not spinous; mesopterygoid fossa rectangular, its anterior margin not shifted much behind $3^{\text {rd }}$ molar; coronoid process present

2 Tail fully haired with terminal brush; mastoids and auditory bullae inflated; upper incisors grooved; molars hypsodont

Gerbillinae
2* Tail sparsely haired, almost naked and scaly, with no terminal brush (pencil of longer hairs at most); mastoids and auditory bullae not inflated; incisors not grooved; molars brachiodont

Murinae

## Subfamily: Murinae Illiger, 1811

Small to moderately large murids with no special external modifications. Molars tuberculate, brachiodont and rooted. Cuspidation of molars is highly characteristic, displaying a pattern of three parallel cusp rows. In Nesokia cusps fuse into transverse laminae. See Fig. 33 for the nomenclature of the molar pattern. In the Old World, the murins are amongst the dominant rodent group, both in terms of number of species and abundance. Species richness peaks in the tropics and declines sharply in temperate regions; murins are nearly absent from boreal habitats. Seven hundred thirty species are recognised currently, classified into 150 genera (Musser \& Carleton, 2005). Five genera occur in the study area, and three of them are largely synanthropic. Murins are the main rodent group in Cyprus.

Rodents dominate small mammal assemblages all over Turkey and mice (Murinae) are their most abundant component. The proportion of mice in rodent samples we collected by traps was particularly high (>80\%) in Thrace, the Black Sea Mts., Aegean Anatolia and the Taurus Mts.



Figure 33. Occlusal surface of upper (a) and lower molar series (b) in murines to show terminology of the cusps (after Niethammer \& Krapp, 1978d). Lingual side is to the left, anterior is at the top. $\mathbf{t}$ - cusps of the upper molars; $\mathbf{m}$ mesial; m-la - mesio-labial; m-li - mesio-lingual; c-la -centro-labial; c-li - centro-lingual; d - distal; d-la - distolabial; d-li - disto-lingual. Cusplets are indicated by arrows.

## Key to genera

1 Molars laminate
Nesokia
1* Molars cuspidate

$$
2
$$

2 Size large (head and body >150 mm, condylobasal length $>38 \mathrm{~mm}$ ); lower molars with 4 ( $1^{\text {st }}$ molar), and 3 roots ( $2^{\text {nd }}$ and $3^{\text {rd }}$ molars)

Rattus
2* Size small to medium (head and body <140 mm , condylobasal length $<29.0 \mathrm{~mm}$ ); lower molars with 2 or 3 roots ( $1^{\text {st }}$ molar), and 2 roots ( $2^{\text {nd }}$ and $3^{\text {rd }}$ molars)
$31^{\text {st }}$ and $2^{\text {nd }}$ upper molars with 2 tubercles on lingual side; $1^{\text {st }}$ lower molar with 2 roots; upper incisor frequently with a notch on its cutting edge

## Mus

$3^{*} 1^{\text {st }}$ and $2^{\text {nd }}$ upper molars with 3 tubercles on lingual side; $1^{\text {st }}$ lower molar with 2 or 3 roots; upper incisor without a notch on its cutting edge

4 Size small (head and body $<75 \mathrm{~mm}$, condylobasal length $<18.0 \mathrm{~mm}$ ); tail prehensile; rostrum short and broad (rostral breadth anterior to masseteric plate exceeds its length); $1^{\text {st }}$ upper molar with 5 roots, $1^{\text {st }}$ lower molar with 3 roots

Micromys
4* Size larger (head and body $>78 \mathrm{~mm}$, condylobasal length $>20.0 \mathrm{~mm}$ ); tail not prehensile; rostrum longer and narrower (rostral breadth anterior to masseteric plate less than or equal to its length); $1^{\text {st }}$ upper molar with 4 roots, $1^{\text {st }}$ lower molar with 2 roots

Apodemus

## Genus: Micromys Dehne, 1841

A monospecific genus of wide Palaearctic range, occurring marginally also in the Oriental region. In the region under study, the Eurasian harvest mouse is restricted to European Turkey.

## EURASIAN HARVEST MOUSE - MICROMYS MINUTUS

Mus minutus Pallas, 1771. Type loc.: Simbirsk (= Uljanovsk), Russia.

## Description

External characters. The smallest western Palaearctic mouse and the only one with a prehensile tail. Body slender, head relatively short and rounded, eyes of moderate size, ears short and rounded; vibrissae relatively short (about 13 mm ). Tail slightly shorter than head and body (82-98 \%; mean = $91 \%$; Özkan et al., 2003); annulations distinct, more so on the ventral than on the dorsal side; distal dorsal rings of the truly prehensile part of the tail are completely broken. Tail is sparsely haired, terminal tuft inconspicuous. Fore feet short, palm with four fingers; hind


Figure 34. Eurasian harvest mouse Micromys minutus. Drawing: J. Hošek.
foot long but broader than in Apodemus, with five fingers. Palm and sole naked with five and six tubercles, respectively; posterior tubercle enlarged, particularly the palmar one. Claws curved, sharp, short (2.4-2.6 mm ) and pale. Pelage is soft and relatively long (up to 7 mm on the back in Turkish material).

Colour (Fig. 35). In specimens from Turkish Thrace collected in June and possibly of subadult age, the dorsal pelage is vivid reddish brown in its posterior part, grey on head, shoulders and across the anterior half of the body, inconspicuously sprinkled with black-tipped hairs throughout; flanks are ochre-buff with yellowish ochre ventral stripe; belly


Figure 35. Skin of Micromys minutus in dorsal and ventral view. Based on an adult male from Edirne, Turkish Thrace (TUE). Photo: C. Mlinar.
is white with slate grey hair bases; demarcation line along flanks is sharp. Few adults we saw from northeastern Greece and Macedonia have monochromatic vivid reddish brown back and belly white to hair base. Bicoloured back indicates moult from juvenile to adult pelage (Corbet \& Harris, 1991) and is thus only a temporary feature. Ears are of same colour as back, slightly more greyish; feet are pale, whitish ochre; fingers, sides and soles are grey. Tail is blackish grey, indistinctly bicoloured, darker above than below.

Nipples. There are eight nipples, two pairs of inguinal and pectoral, respectively.

Penis. Glans penis and baculum are figured in Özkan et al. (2003). The glans is long and relatively narrow, covered by spines, with prominent protrusion at its tip. Proximal baculum is stick shaped and narrow, with oval basal expansion; the ventral side of the expansion is concave. Distal cartilaginous portion is triangular and small. Baculum is bent dorsally.

Skull (Fig. 36) is small and delicate with very short rostrum and large, oval brain-case. Dorsal profile is evenly convex; there are no ridges and the occipital region is smooth and rounded. Nasals are short (slightly longer than interparietal suture), not much expanded anteriorly, rounded at the tip. Interorbital region is broad; zygomatic arches are weak and parallel. Frontal, parietal and interparietal bones are large. Incisive foramen is long relative to diastema, reaching posteriorly line connecting $1^{\text {st }}$ molars. Hard palate terminates posterior to $3^{\text {rd }}$ molars. According to a report by Özkan et al. (2003), the mesopterygoid space is triangular in specimens from Turkish Thrace; Miller (1912) and Böhme (1978b) state for the posterior margin of hard palate to be straight or rounded. In our material from the Balkans, this character appears to be prone to individual variation. Pterygoids are either parallel or converge anteriorly, thus resulting in a triangular interpterygoid fossa; we observed also intermediate stages (Fig. 37). Because museum skulls are frequently damaged in this region, no firm conclusion could be reached on possible geographic trends, but triangular fossa seems to be more common in the south of the Balkan Peninsula and rectangular one in the north. Bullae are relatively large. Mandible is weak but rather deep; all three processes are evident.


Figure 36. Skull and mandible of Micromys minutus, based on an adult male from Edirne, Turkish Thrace (TUE).
Scale bar $=2 \mathrm{~mm}$.

Teeth (Fig. 38) in general resemble condition in Apodemus (see below). Molar row is short (approximately one sixth of a profile length) and teeth are small. Molars retain all main cusps seen in Apodemus. Tubercle t9 is small and frequently ridge-like on $1^{\text {st }}$ and $2^{\text {nd }}$ upper molars; postero-labial accessory cusp is occasionally also present on these cheek-teeth (Fig. 39). First lower molar with a mesial cusp; narrow enamel ledge along labial margin of $2^{\text {nd }}$ lower molar bears a small accessory cusplet.


Figure 37. Variation in shape of interpterygoid vacuity in Micromys minutus from the Balkans. a - Virpazar, Montenegro; b - Sečovlje, north-western Istria, Slovenia. Anterior is at the top. M3 - third upper molar; hp - hamular process; pa - palatine. Scale bar $=1 \mathrm{~mm}$.

Number of alveoli in upper molars: 5 ( $1^{\text {st }}$ molar), 4 ( $2^{\text {nd }}$ molar), 3 ( $3^{\text {rd }}$ molar); lower molars: 3 ( $1^{\text {st }}$ molar), 2 ( $2^{\text {nd }}$ and $3^{\text {rd }}$ molars) (Niethammer $\&$ Krapp, 1978).

Dimensions are given in Table 8. Males were slightly lighter than females in late autumn sample from eastern Austria (Haberl \& Kryštufek, 2003). Size varies seasonally in the western Balkans; adults are the lightest in March and April (body mass $=4-5$ grams), while subadults in the autumn reach body mass of 5.5 grams (Kryštufek \& Kovačić, 1984).

Chromosomes. Diploid number of chromosomes is $2 \mathrm{~N}=68$, and the fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=132$ (Özkan et al., 2003). The autosomal complement consists of one strikingly large submetacentric pair, 3 pairs of small metacentrics, and 29 pairs of subtelocentric chromosomes. The karyotype reported from Turkish Thrace by Özkan et al. (2003) does not deviate from conditions reported elsewhere in Europe (Zima \& Král, 1984).

## Variation

An exaggerated number of more than twenty subspe-


Figure 38. Upper (a) and lower molars (b) in Micromys minutus from Edirne, Turkish Thrace (TUE). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
cific forms accumulated in Europe over time, clearly a result of ignorance over individual and seasonal variability. For a critical review of colour variation see Szunyoghy (1958). Simionescu (1974) recognized only three subspecies throughout the Palaearctic range, and described a new species M. danubialis from the Danube delta in Romania (Simiones-


Figure 39. First and $2^{\text {nd }}$ upper molars in Micromys minutus from the Balkans. a - Gephyra, district Thessaloniki, Greece; b - Karlukovo, district Loveč, Bulgaria. Lingual side is to the left, anterior is at the top. Scale bar $=0.5 \mathrm{~mm}$.
cu, 1971). Danubian harvest mice are characterised by large size (mean condylobasal length $=19.1 \mathrm{~mm}$ ) and long tail relative to head and body (125 \%; Simionescu, 1974); M. danubialis, however, is currently uniformly synonymised with $M$. minutus (Corbet, 1978; Musser \& Carleton, 2005).

Size varies in the Balkans (Kryštufek \& Kovačić, 1985) and larger populations from the southern margin are occasionally ascribed to a subspecies $M$. m. brauneri Martino, 1930 (type loc.: Kraljevo, Serbia); its taxonomic validity is under question ( $\mathrm{Pe}-$

|  | Turkish Thrace |  |  | NE Greece |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |
| Head and body | 8 | 66.8 | $56-70$ | 9 | 66.9 | $63-74$ |
| Tail | 8 | 60.3 | $53-63$ | 10 | 66.5 | $58-80$ |
| Hind foot | 8 | 14.9 | $13-16$ | 10 | 15.6 | $14.4-16.6$ |
| Ear | 8 | 9.3 | $8-11$ | 9 | 9.4 | $9.0-10.0$ |
| Weight | 8 | 9.9 | $7-14$ | 9 | 7.9 | $7-13$ |
| Condylobasal length | 8 | 16.9 | $16.5-17.5$ | 7 | 17.4 | $16.6-19.0$ |
| Zygomatic breadth | 8 | 9.3 | $9.0-9.4$ | 7 | 9.6 | $9.2-10.3$ |
| Maxillary tooth-row | 8 | 2.9 | $2.8-3.0$ | 13 | 3.1 | $3.0-3.2$ |

Table 8. External and cranial dimensions of Micromys minutus from Turkish Thrace (from Özkan et al., 2003) and from north-eastern Greece (our own material).
trov, 1992) or this name is ignored in some reviews (Böhme, 1978b). Differences in size are slight however. The largest recorded body mass in the southern Balkans is 14 g (Table 8) while adults from southern Pannonia reach 12 g (Haberl \& Kryštufek, 2003). Özkan et al. (2003) applied subspecific name brauneri to a population from Turkish Thrace, evidently on geographic grounds. Dimensions of Thracian harvest mice correspond closely to those from the adjacent lowlands of north-eastern Greece (Table 8), and from the western Balkans (Kryštufek \& Kovačić, 1984). Variation in shape of interpterygoid fossa requires further investigation.

## Distribution

The harvest mouse has a broad range, extending from north-eastern Spain and Britain across woodland and moister steppe zones of Asia to the Ussuri region, Korea and Japan. Geographic isolates occur in Oriental China, Assam, Burma and Taiwan (Corbet, 1978). European range extends as north as central Finland and reaches Mediterranean coasts in the south; the
harvest mouse is absent from the Mediterranean islands (Böhme, 1978b). Range in the Balkans is restricted mainly to northern lowlands and to hilly regions; the southernmost records are from southern Albania (Bego et al., 2008), northern Greece and Turkish Thrace.

In Turkey, the harvest mouse is known only in Thrace, where first reported by Kurtonur (1975). Seven localities are currently known, all of them from the lowlands (Özkan et al., 2003).

Zeybek \& Tokay (1990) reported the harvest mouse for the Ankara district. We were unable to trace this reference, which remains available to us only through the Zoological Record. Özkan et al. (2003) did not comment this record, and Demirsoy (1996) did not plot it onto species’ distribution map. Kurtonur et al. (1996) reported the harvest mouse only from Thrace, while Doğramacı (1989a) missed this species in his list of Turkish mammals.

The harvest mouse is closely approaching Anatolia in the east along the Black Sea coast. The species is rare in Georgia (Bukhnikashvili \& Kandau-


Figure 40. Distribution of Micromys minutus in Turkey and adjacent regions. Records: 1 - Değirmenyeni, Edirne; 2a - Güllapoğlu, Edirne; 2b - Tayakadın, Edirne; 2c - Havsa, Edirne; 3 - Babaeski, Kırklareli; 4 - Karacaköy, İstanbul; 5 - Küçük Çekmece Lake, 3 km north-west of Halkali, İstanbul. Corresponding references: Kurtonur (1975): 5. Özkan et al. (2003): 1, 2a-c, 3, 4, 5.
rov, 1998), and Bukhnikashvili (2004) cites only six localities. Noteworthy, Anakhva, as the southernmost locality in Georgia, is only 50 km to the north of Turkish-Georgian border. Presence of M. minutus in coastal north-eastern Turkey is thus quite probable, even more so since Bukhnikashvili \& Kandaurov (1998) presume a southward spread over the last half a century. In eastern Transcaucasia, the species is restricted to the Caspian coast in north-eastern Azerbaijan north-east of Kuba (Ejgelis, 1980).

Palaeontology. For Europe, Kowalski (2001) lists records of Micromys throughout the entire Pleistocene. Several fossil species (M. steffenei, M. bendai, M. kozaniensis, M. praeminutus), which predate the Pleistocene (Ruscinian and Villanyian), were reported for various Balkan countries (van der Meulen \& van Kolfschoten, 1986). The Early Pleistocene material is mainly ascribed to Micromys praeminutus Kretzoi, 1959, which was also reported for the Early Villanyian (Pleistocene) fauna of the Greek Island of Evia (Kotsakis, 1990). Differences between M. praeminutus and the extant species are not clear however, and the validity of fossil harvest mice requires revision (Kowalski, 2001). E.g., the Early Pleistocene (Lower Biharian) material from Volos, Greece, was identified as Micromys cf. minutus (van der Meulen \& van Kolfschoten, 1986). Santel \& Koenigswald (1998) did not recover Micromys from the Middle Pleistocene layers of Yarımburgaz, Turkish Thrace.

## Habitat

A wide variety of open habitats are utilized across Europe. In England, where the species range from salt marshes and grassy coastal dunes, to high moorland, the majority of its nests ( $52.2 \%$ ) were recorded in hedgerows, in bramble, along field edges and ditches, and in reedbeds (Harris, 1979). Disturbed habitats (rubbish dumps, road verges, abandoned coal mines), cultivated areas and urban environments are also occupied (Harris, 1979; Haberl \& Kryštufek, 2003). Harvest mice are rapid colonizers of ruderal fields (Churchfield et al., 1997). In a habitat mosaic at Lake Neusiedl (Austria), the harvest mouse strongly prefers reed stands and also inhabits temporarily flooded regions (Haberl \& Kryštufek, 2003).

Mesic habitats are preferred in the Balkans: reedbeds, other marshy situations with tall grass, and rice


Figure 41. Rice fields in Turkish Thrace, inhabitated by Micromys minutes. Photo: B. Özkan.
fields. Specimens were collected also from poplar and willow stands but much more exceptionally in flooded oak forests (Kryštufek \& Kovačić, 1984). In Turkish Thrace, Kurtonur (1975) captured a single specimen in a rubbish tip near the lake shore, and B. Özkan (personal communication) collected several in rice fields. Rice fields with Typha sp., Phragmites australis, Scirpus maritimus, and Juncus sp., are also frequently occupied by the harvest mouse in Bulgaria (Peshev et al., 2004) and in eastern Macedonia. Open landscape with grassy or bushy vegetation is the main habitat in Transcaucasia (Šidlovskij, 1976). In eastern Transcaucasia, the harvest mouse is widespread, albeit not abundant, in the zone of lowland forests (Ejgelis, 1980).

Altitude. Known in Turkish Thrace only in the lowlands. The majority of records from the Balkans are also from low elevations (below 500 m a.s.l.), although the species exceptionally appears well above $1,000 \mathrm{~m}$ a. s. l. (up to $1,700 \mathrm{~m}$; Kryštufek \& Kovačić, 1984; Peshev et al., 2004). Georgian records are from altitudes between 300 and 500 m (Bukhnikashvili \& Kandaurov, 1998).

Associates. No information is available from Turkey, but in the rest of the Balkans the harvest mouse was collected alongside Crocidura suaveolens, C. leucodon, Suncus etruscus, Microtus levis, Mus macedonicus, M. domesticus, M. spicilegus, Rattus rattus, R. norvegicus, Apodemus sylvaticus, and Apodemus agrarius.

Density. Densities and trapping success vary tremendously. Haberl \& Kryštufek (2003) reported
a density of up to 100 individuals per ha for southern Pannonia.

## Biology

Biology was studied in Europe and in Asia (cf. Böhme, 1978b; Corbet \& Harris, 1991); in the Balkans, data are available from Bulgaria (Peshev et al., 2004), however, not from Turkey.

Activity. The harvest mouse is an agile climber and exploits a three dimensional habitat. Typically, spherical summer nests, built of a wide variety of monocotylodonous plants, are located above ground in vegetation. Breeding nests are built by females in late pregnancy. Nests (diameter 5.5-9 mm) are 4585 cm above ground (Peshev et al., 2004). Winter is spent in underground burrows. This mouse is also a keen swimmer and enters water readily (Haberl \& Kryštufek, 2003). It is predominantly nocturnal but also diurnal during the winter (Corbet \& Harris, 1991).

Reproduction. Males outnumber females in
southern Pannonia (1 male : 0.66 females; Haberl \& Kryštufek, 2003). In southern Bulgaria, reproductive activity starts in April and terminates in October or November. Testes in sexually active males weigh at least 30 mg . Gestation lasts 18-20 days and number of embryos varies between five and twelve. Mean number of embryos increases during the reproductive season: 6.66 in April, 7.0 from July to August, and 7.2 in September and October. Young wean at the age of 15 days and females attain sexual maturity at 1.5 months old (Peshev et al., 2004).

Food requirements are high due to high costs of thermoregulation (Corbet \& Harris, 1991). Green leaves, seeds and insects were found in the stomachs of harvest mice from Bulgaria (Peshev et al., 2004).

Predation. One specimen was found in the pellets of a barn owl (Tyto alba) from eastern Greek Thrace not far from the Turkish border. Near Burgas (southeastern Bulgaria) Simeonov et al. (1981) also found the harvest mouse at low proportion in barn owl pellets ( $0.2 \%$ in total 4,727 small mammals).

## Genus: Apodemus Kaup, 1829

The genus Apodemus comprises small to medium sized murines with a relatively long hind foot and with no clear external modifications. Tail is long and with distinct annulations, moderately haired; pelage is soft; palms and feet are naked with five and six tubercles, respectively. Skull is deep, with no special modifications; rostrum is long. First upper molar has four roots. These mice are absent from Cyprus, but in Turkey they are the dominant and the most abundant small mammal in nearly every habitat.

Taxonomy of the genus has caused a long-standing source of confusion and disagreement, which started to stabilise only in the last decade or so, following the progress in genetic studies (Musser \& Carleton, 2005).

Zimmermann (1962) split Apodemus into three subgenera (Apodemus, Sylvaemus, Alsomys) and his
division was a widely, albeit not uniformly accepted. Musser et al.(1996) preferred a division into three species groups (Apodemus, Sylvaemus, and argenteus group) and in the recent revision by Musser \& Carleton (2005), the genus is divided into two subgenera (Apodemus and Sylvaemus), while two geographically extralimital species (A. argenteus (Temminck, 1844) and A. gurkha Thomas, 1924) are not allocated to a subgenus. Sylvaemus and Apodemus are occasionally considered as independent genera (Mezhzherin, 1990; Vorontsov et al., 1992; Filippucci et al., 1996; Zagorodnyuk et al., 1997; Shehab et al., 2004); Sylvaemus was sometimes spelled as Sylvimus (e.g. Mezhzherin, 1987) or Silvaemus (e.g. Mezhzherin, 1993). The two major groups of Apodemus clearly differ morphologically (Musser et al., 1996) and genetically (Mezhzherin, 1987; Mezhzherin \& Zykov, 1991; Filippucci et al., 2002; Michaux et al., 2002; Bellinvia, 2004).


Figure 42. Field mouse Apodemus. Drawing: J. Hošek.

Apodemus agrarius is a sister group to the clade of the remaining five species occupying Turkey, and is the only western Palaearctic member of the subgenus Apodemus. Further division of Sylvaemus is less unequivocal, but $A$. mystacinus emerged in all analyses as a sister group to the remaining Sylvaemus cluster; occasionally it is placed into a subgenus Karstomys (see below). For the sake of convenience, we use the group name Sylvaemus for "brown" field mice (sylvaticus, flavicollis, witherbyi, uralensis); A. mystacinus is therefore in the Karstomys section, whatever its rank (see further discussion under that species). As long as Turkish Sylvaemus mice are in question, the molecular markers suggest $A$. witherbyi to hold a basal position and A. flavicollis to be a sister species to A. uralensis (Michaux et al., 2002; Bellinvia, 2004). Various electrophoretic studies yielded incongruent results, but mainly suggested the basal position of $A$. uralensis (Filippucci et al., 2002). For comparisons of biochemical results between different authors see Hille et al. (2002).

The number of species in Sylvaemus has varied tremendously over time, however, a great majority of traditional divisions underestimated the species' diversity (Ellerman, 1941, 1948; Ellerman \& Morrison-Scott, 1951, 1966; Corbet, 1978). The group was usually split into two species, the larger A. flavicollis and the smaller A. sylvaticus (e.g. Ellerman \& Morrison-Scott, 1966). Such a taxonomy, which was applied also by students of Turk-


Figure 43. Possible phylogenetic relations among six Apodemus species from Turkey. Note that branch lengths do not intended to correspond to divergence metrics (temporal or genetic). See text for further details.
ish field mice, caused permanent confusion since the two size classes frequently cut across other traits, e.g. colouration. As a consequence, Lehmann (1966a) believed that $A$. sylvaticus and A. flavicollis in Turkey were hybrids and designated them as "semi-species". The first detailed study of the Anatolian Apodemus by Neuhäuser (1936) was followed by Osborn (1965) and by Doğramacı (1974). Doğramacı in particular elaborated large samples from all over the country. Since he was unable to go beyond a two-species taxonomy of Sylvaemus, his results do not deviate from the remaining cotemporary attempts and therefore are of little use.

There were some early attempts towards more novel taxonomic solutions, i.e. by recognising more species than merely A. flavicollis and A. sylvaticus. Ellerman (1948) in his monograph of the rodents of south-western Asia noted under A. sylvaticus: "Nearly always European races may be distinguished from Asiatic ones by their proportionally longer palatal foramina". Shortly afterwards, Felten (1952) reported that in Germany the smaller $A$. sylvaticus has incisive foramen of same length as the larger $A$. flavicollis. As subsequently shown by Tvrtković \& Džukić (1979), A. microps (= A. uralensis) actually has a short incisive (palatal) foramen, a character which is of taxonomic importance (see text below). Steiner (1978a) produced fertile hybrids between field mice from Rize (Anatolia) and the Austrian A. microps over six generations and confirmed in similar cross-breeding trials the presence of A. flavicollis in north-eastern Anatolia. Sadly, Steiner's discoveries remained entirely ignored by later students of Sylvaemus taxonomy.

Taxonomic difficulties on the Caucasus were already fully realised by Russian authors in the 1950s, however, their work remained unknown in the West. Papers by Larina (1958a) and Larina \& Golikova (1959) provide clear evidence on the existence of three Sylvaemus groups, differing in morphology and in habitat preferences. Larina (1958a) showed that morphospace is more relaxed to the north of the Caucasus (with two Sylvaemus species) and becomes more saturated in the Caucasus where the third morphotype of intermediate morphology appears; her results were recently confirmed by Frynta et al. (2006). Larina (1958a) applied the following taxonomic names for the three morphological groups:
the larger $A$. tauricus (=flavicollis), an intermediate group which was not named, and the smaller A. sylvaticus; she supposed that the intermediate type was of hybrid origin. We believe that Larina's names can be easily translated into a current taxonomy by Musser \& Carleton (2005), namely as being identical to A. ponticus, A. witherbyi, and A. uralensis, respectively.

The real breakthrough towards a better understanding of taxonomic diversity in Sylvaemus was achieved by application of various genetic tools, firstly by electophoretic analyses of allozymes. Vorontsov et al. $(1989,1992)$ revealed on the Caucasus the presence of all three Sylvaemus species that also occur in Anatolia, but taxonomic complexity has been signalised already by Mezhzherin (1987). The first paper, focusing on taxonomy of Anatolian populations is by Filippucci et al. (1996) and was followed by studies of Macholán et al. (2001) and Filippucci et al. (2002). The results of electrophoretic studies were mainly confirmed by molecular markers: nuclear IRBP gene, cytochrome $b$ and 12S rRNA (Michaux et al., 2002), and the mitochondrial control region (Bellinvia, 2004). For the time being, six Apodemus species are known for Turkey: A. agrarius, $A$. mystacinus, and four sibling species of Sylvaemus (A. sylvaticus, A. flavicollis, A. witherbyi, A. uralensis).

## Identification

The four Sylvaemus species closely resemble each other, which makes their morphological identification a demanding task. Frynta et al. (2001), who subjected cranial measurements of genetically identified material from Turkey and Iran to a discriminant function analysis, found considerable overlap between $A$. witherbyi and $A$. flavicollis, while $A$. uralensis emerged clearly distinct. An early determination key for the Caucasian species by Vorontsov et al. (1992) was subsequently extended geographically by Zagorodnyuk et al. (1997). Although all these authors did spot the taxonomic traits, character states were loosely defined and their variation was not assessed. Therefore, Hille et al. (2002) encountered problems in sorting species from the Caucasus in a simultaneous application of traditional morphometric, biochemical and genetic techniques.

Morphological characters enabling identification
of Sylvaemus species in western Anatolia were defined by G. Storch (in Filippucci et al., 1996) and our results largely follow this paper. In total, we examined over 1,000 specimens from all the regions of Turkey and additional material from the neighbouring countries (the Balkans, the Caucasus, Iran, Syria). Part of our material was identified as a particular species by one or the other genetic techniques (Filippucci et al., 1996; Macholán et al., 2002; Hille et al., 2002). This allowed us to cross-check the identifications based on different data sets and to draw conclusions on the reliability of determination


Figure 44. Bivariate plot of maxillary tooth-row length against length of bullae for three Anatolian field mice (Apodemus). Polygons enclose extremes for a species.


Figure 45. Bivariate plot of maxillary tooth-row length against length of bullae for Apodemus flavicollis and A. witherbyi from the Taurus Mts. Polygons enclose extremes for a species.
performed on the museum material alone. In the case of complete voucher specimens (skin and complete adult skull with unworn molar pattern), the match between identifications based on morphology and genetics was nearly perfect. Incomplete specimens caused more problems, because characters overlap and firm identification often required examination of more than one trait (colouration, molar cusp pattern, skull dimensions). In our results, the species overlap morphologically to a larger extent than reported in the literature. Despite this we are convinced that morphological identification of cryptic Sylvaemus species in the Near and Middle East is possible and provides reliable results.

Bi-variate plot of maxillary-tooth row length (measured on crowns) against length of bulla provides reasonably good separation, in spite of some overlap (Fig. 44). Apodemus flavicollis has the longest bulla and only marginally overlap with $A$. witherbyi. Only four specimens of A. witherbyi (= 1.3 \% out of total 319) had bulla longer than 4.7 mm , and in a single Anatolian A. flavicollis (of total 103) bulla was shorter than 4.8 mm . When only those parts of Anatolia were considered where A. flavicollis and A. witherbyi are the only Sylvaemus species (Aegean and Taurus regions), overlap was no longer detected (Fig. 45).

Identification of the material from northern Anatolia, where A. flavicollis, A. witherbyi and A. uralensis are broadly sympatric, is more challenging. Al-


Figure 46. Bivariate plot of maxillary tooth-row length against length of bullae for three field mice (Apodemus) from Marmara and the Black Sea Mts. Polygons enclose extremes for a species.
though $A$. witherbyi and $A$. uralensis broadly overlap in maxillary tooth-row length in a pooled Anatolian sample (Fig. 44), the overlap diminishes when only the material from the Black Sea coast is considered (Fig. 46). On the basis of molar-row length, we safely identified $64.8 \%$ of $A$. witherbyi (maxillary toothrow longer than 3.75 mm ) and $64.3 \%$ of $A$. uralensis (maxillary tooth-row shorter than 3.6 mm ). The remaining specimens ( $31 \%$ out of total 422) of both


Figure 47. Variation in shape of interpterygoid sinus in four Apodemus species from Turkey. Anterior is at the top. Apodemus sylvaticus: a-d, f - Karakasım, Edirne, $\mathbf{e}$ - Edirne. Apodemus flavicollis: a, d-Longoz, Iğneada, Istranca Mts., b-5 km south-east of Velika Köy, Demirköy, Istranca Mts., c, e-7 km north-east of Sivrileri, Istranca Mts., f-8 km north of Yenice, Zonguldak. Apodemus witherbyi: a, b, f - Çayır, Zonguldak, c - 5 km north of Safranbolu, Zonguldak, d, e-8 km north-west of Yenice, Zonguldak. Apodemus uralensis: a, b, d - 8 km north-west of Yenice, Zonguldak, c, e, f-5 km north of Safranbolu, Zonguldak. Scale bar $=2 \mathrm{~mm}$.
species were in the zone of overlap (length of maxillary tooth-row of $3.6-3.75 \mathrm{~mm}$ ) which required examination of additional characters. Ventral colouration was helpful, particularly so when representative series were available from the same locality. It was frequently possible to distinguish at a glance the darker A. uralensis from the paler A. witherbyi. Examination of the ventral side served as a further test: belly was always grey in $A$. uralensis but typically white in $A$. witherbyi.

Filippucci et al. (1996) reported differences in shape of interpterygoid sinus, a character known already to Vorontsov et al. (1992). Typically, the sinus is narrow in $A$. uralensis and broad in $A$. witherbyi. Furthermore, shape of the posterior margin of hard palate is rounded in A. sylvaticus but mainly straight in $A$. witherbyi and $A$. uralensis. The interpterygoid region is of help when identifying museum material; note however that differences between species are not sharp; character states also overlap and vary geographically (Fig. 47).

Dichotomy No. 3 in the key below splits Sylvaemus species according to the region. We saw no $A$. sylvaticus from Anatolia and therefore cannot judge on the possibility of its morphological recognition on the Asiatic side of the Marmara straits. As far as we are able to conclude from our Thracian sample, $A$. sylvaticus is distinguishable from $A$. uralensis by (1) tooth-row length (usually at least 3.8 mm in A . sylvaticus; one exception among 27 specimens), and (2) by the position of the posterior margin of incisive foramens (in A. sylvaticus mostly posterior to the line connecting the anterior alveolar margins of $1^{\text {st }}$ upper molars; anterior to it in A. uralensis). Apodemus sylvaticus from Thrace differs from the Anatolian A. witherbyi in (1) grey ventral pelage (normally white in A. witherbyi) and (2) in a nearly uniform lack of stephanodonty on $1^{\text {st }}$ upper molar. For comparison with A. flavicollis, see under that species and the account of $A$. sylvaticus.

## Key to species

1 Back with black medial stripe; supraorbital ridges present; $2^{\text {nd }}$ upper molar lacks the ante-ro-labial tubercle ( t 3 )
A. agrarius

1* Back with no black medial stripe; no supraorbital ridge; $2^{\text {nd }}$ upper molar with the anterolabial tubercle (t3)

2 Back normally grey; maxillary tooth-row (measured on crowns) at least 4.3 mm long (mainly $>4.5 \mathrm{~mm}$ ); postero-lingual accessory cusp t12 nearly always present on $2^{\text {nd }}$ upper molar
A. mystacinus

2* Back normally brown; maxillary tooth-row (measured on crowns) at most 4.4 mm long $^{1}$; postero-lingual accessory cusp t12 only rarely present on $2^{\text {nd }}$ upper molar

3 Occurs in Thrace ${ }^{2}$
3* Occurs in Anatolia ${ }^{2}$

4 Belly grey, demarcation towards back indistinct; throat blank or with a spot; posterior margin of incisive foramen mainly exceeds line of the anterior alveolar margins of $1^{\text {st }}$ molars (Fig. 48a); fronto-parietal suture usually angled (Fig. 49a-d); tubercle $t 7$ on $2^{\text {nd }}$ upper molar always cusp-like, never entirely lost
A. sylvaticus

4* Belly white, sharply demarcated towards back; throat with spot or collar, very rarely blank; posterior margin of incisive foramen rarely exceeds line of the anterior alveolar margins of $1^{\text {st }}$ molars (Fig. 48b); fronto-parietal suture usually rounded (Fig. 49d-f); tubercle $t 7$ on $2^{\text {nd }}$ upper molar frequently ridgelike or lost

## A. flavicollis

5 Bulla long (at least 4.7 mm$)^{3}$
A. flavicollis

5* Bulla shorter (at most 4.8 mm$)^{3}$
6

6 Belly normally pure white; maxillary-tooth row at least 3.5 mm long (at least 3.6 mm in majority of specimens); $1^{\text {st }}$ upper molar clear-
ly stephanodont (cusps t1 and t5 connected by a ridge), t1bis occasionally present; t7 normally cusp-like on $2^{\text {nd }}$ upper molar; $3^{\text {rd }}$ upper molar relatively large
A. witherbyi

6* Belly normally grey; maxillary-tooth row at most 3.75 mm long (at most 3.65 mm in majority of specimens); $1^{\text {st }}$ upper molar with no traces of stephanodonty (cusps t1 and t5 never connected by a ridge), t1bis never present; t7 normally ridge-like on $2^{\text {nd }}$ upper molar; $3^{\text {rd }}$ upper molar relatively small
A. uralensis
${ }^{1}$ Maximum in Anatolian material is 4.2 mm
${ }^{2}$ For the islands see text and maps
${ }^{3}$ See also Figs. 44-46.


Figure 48. Ventral side of rostrum to show differences in the position of posterior margin of incisive foramens relative to $1^{\text {st }}$ molar in Apodemus sylvaticus (a) and A. flavicollis (b) from Turkish Thrace. Based on specimens from Edirne (a), and Sivriler, Istranca Mts. (b). Scale bar $=5 \mathrm{~mm}$.

## Long-tailed field mouse - Apodemus sylvaticus

Mus sylvaticus Linnaeus, 1758. Type loc.: Uppsala, Sweden.

## Taxonomy

The morphological distinction between $A$. sylvaticus and A. flavicollis caused confusion in Europe throughout the $20^{\text {th }}$ century (e.g. Niethammer \& Krapp, 1978). Length of incisive foramen relative to length from $3^{\text {rd }}$ upper molar to incisor proved to be a good taxonomic character in Europe (Tvrtković, 1979), including the Balkans (e.g. Kryštufek \&

Stojanovski, 1996). In Thrace, however, the overlap between the two species is considerable (Table 9). Tail is typically shorter in A. sylvaticus and longer in A. flavicollis, both absolutely and relative to head and body length. Again, there is overlap between the two species. In our sample, about one third of Thracian A. flavicollis have a tail shorter than head and body length, and approximately a quarter of $A$. sylvaticus have a tail longer than head and body. Other external and cranial dimensions overlap as well (cf. Tables 10 and 12). As shown by Filippucci et al. (1996), the shape of the fronto-parietal suture differs between the two species, typically being angled in $A$. sylvaticus and curved in A. flavicollis; however, as with all other traits, character states overlap (cf. Fig. 49). Apodemus flavicollis occasionally lacks a tubercle $t 7$ on $2^{\text {nd }}$ upper molar, however at low frequencies ( $<10 \%$ of specimens in majority of populations); t7 is invariably present in A. sylvaticus (Tvrtković, 1976). Best single diagnostic character seems to be the colouration of the ventral side (see Key to species); be aware that young A. flavicollis have a grey belly.


A. uralensis


Figure 49. Variation in shape of fronto-parietal suture in four Apodemus species from Turkey and adjacent Thrace in Greece. Anterior is at the top. Apodemus flavicollis: $\mathbf{a}$ - Cayır, Zonguldak, b, c - 8 km north of Yenice, Zonguldak, d-Longoz, Iğneada, Istranca Mts., e, f-7 km north-east of Sivrileri, Istranca Mts. Apodemus sylvaticus: $\mathbf{a , ~ c , ~ e , ~ f ~ - ~ K a r a k a s ı m , ~ E d i r n e , ~ b ~ - ~ A l e x a n d r o u p o l i s , ~ G r e e c e , ~}$ d - Monastirakio, Evros, Greece. Apodemus witherbyi: a, $\mathbf{f}-8$ km north-west of Yenice, Zonguldak, b, c - Çayır, Zonguldak, d, e-5 km north of Safranbolu, Zonguldak. Apodemus uralensis: a-c, f-8 km north-west of Yenice, Zonguldak, d, e-5 km north of Safranbolu, Zonguldak. Scale bar $=5 \mathrm{~mm}$.

|  | N | FI short | FI medium | FI long |
| :--- | :---: | :---: | :---: | :---: |
| A. flavicollis | 115 | $58.3 \%$ | $29.6 \%$ | $12.1 \%$ |
| A. sylvaticus | 32 | $6.3 \%$ | $6.3 \%$ | $87.5 \%$ |

Table 9. Incidence of three morphotypes according to a foramen length relative to the anterior margin of the $1^{\text {st }}$ molar's alveoli in two Apodemus species from European Turkey. See Fig. 48 for definition of two extreme morphotypes. Character states: FI short - foramen does not reach line of M1 alveoli (Fig. 48b); FI medium - foramen on the line of M1 alveoli; FI long - foramen extends posterior to M1 alveolar line (Fig. 48a). Sample of A. sylvaticus includes specimens from Thrace in Greece and Turkey.

## Description

External characters. Medium sized field mouse with tail normally shorter than head and body length. Body slender, ears relatively long, hind foot long and narrow. Fore foot short, considerably smaller in area than hind foot; palm with four fingers, thumb is reduced to a mere tubercle but still possesses a reduced nail. Hind foot with five fingers, the central three are the longest and sub-equal. Palm and sole naked with five and six tubercles, respectively. Claws curved, sharp, short (2.4-2.6 mm) and pale. Tail long (88$107 \%$ of head and body; mean $=95.5 \%$ ) with distinct annulations; sparse hairs terminate in a short pencil (1.9-2.4 mm). Pelage soft, summer hairs up to 6-7 mm long on mid-back (sparse long hairs up to 9 mm ), approximately 3 mm on the belly. Vibrissae are moderately long (up to 33 mm ).

Colour (Fig. 50). Buffy wood-brown above, tinged in some specimens with yellow on the posterior half of the back. Cheeks, sides of neck, flanks and the outer surface of the fore legs light buff. The throat and belly clouded by the slate grey undercolour; buff wash is exceptional. Delineation line along the flanks is moderately sharp, never entirely faded. Chest between the forelegs with a narrow, ill defined buff spot in approximately half of specimens; the throat is of same colour as the belly in the remaining animals. Ears dull brownish, feet pale to greyish, and tail indistinctly bi-coloured, paler below than above.

Nipples. There are six nipples, two pairs of inguinal and one pair of pectoral, respectively.

Penis was described in detail in long-tailed field mice from Croatia, north-western Balkans (Williams et al., 1980). The glans penis is cylindrical in shape, longer than wide, and divided by a shallow
constriction in the midsection to a definite proximal and distal section. The distal section has a wide ventral groove with longitudinal folds. The dorsal ridge is clearly defined for the entire length of the glans; its sides expand on the proximal part of glans, converge at the constriction and diverge again on the proximal section. The distal portion of the glans consists of a terminal crater that encompasses urethral craters and


Figure 50. Skin of Apodemus sylvaticus in dorsal and ventral view. Based on an adult male from Mahmut köy, Keşan, district Edirne, Turkish Thrace. Photo: C. Mlinar.
lappets. Epidermally, a number of relatively large spines are present along the ventral grove. Glans is $5.81-6.63 \mathrm{~mm}$ long and $2.86-3.36 \mathrm{~mm}$ wide; proximal section is as wide as distal one ( $2.85-3.37 \mathrm{~mm}$ ). At the midsection, the glans is $2.32-2.91 \mathrm{~mm}$ wide and 2.38-2.79 mm deep (Williams et al., 1980). In material from Turkish Thrace, the glans is 5.26-6.05 mm long and 2.63-3.00 mm wide. For a drawing of Turkish specimen see Yiğit et al. (2006c: Fig. 38A).

The baculum is composed of two parts: the cartilagous distal baculum (trilobed in dorsal view) and the osseous proximal baculum. In dorsal aspect, the proximal baculum consists of a distally tapering shaft that expands abruptly at the base. The base is also expanded dorsoventrally. The entire baculum is 4.695.79 mm long; proximal section measures 3.14-4.00 mm in length and is $0.95-1.47 \mathrm{~mm}$ wide at base (Williams et al., 1980).

Skull (Fig. 51). The skull is smoothly rounded and without ridges. Dorsal profile is evenly convex, reaching the most exposed point just anterior to the fronto-parietal suture. Occipital region rounded and nasals protruding anterior to the premaxillary bone.

Rostrum is relatively short, however, its maximal breadth just anterior to zygomatic plate is still less than its length. Nasals are long and narrow, tapered anteriorly and converging towards the frontal bone. Zygomatic arches weak, running parallel or diverging posteriorly. Greatest breadth of skull exceeds one half of condylobasal length (zygomatic breadth equals to 51.4-57.1 \% of condylobasal length; mean = 54.0 \%). Interorbital region is broad, flat and smooth; brain-case is relatively large and rounded. The fron-to-parietal suture is usually angled (Fig. 49). Interparietal bone is large, but narrow. Incisive foramens long (20.7-24.3 \% of condylobasal length; mean = $23.0 \%$ ), their posterior margin extending behind the line of the anterior margins of the alveoli. Hard palate terminates posterior to the tooth-row. Pterygoids concave in the middle, their tips bent laterally; interpterygoid space narrow. Bullae short relative to condylobasal length (18.9-21.4 \%), and rounded. Mandible slender and low; its coronoid process is weak.

Teeth (Fig. 52). Upper incisor strongly curved, its proximal root forming a protuberance posterior to praemaxillo-maxillary suture; at that point the


Figure 51. Skull and mandible of Apodemus sylvaticus, based on an adult female from Karakasım near Edirne, Turkish Thrace. Scale bar $=5 \mathrm{~mm}$.


Figure 52. Upper (a) and lower molars (b) in Apodemus sylvaticus. Same specimen as in Fig. 51. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
rostrum reaches its greatest breadth. Lower incisor much less curved, its root terminating under base of coronoid process where forming a protuberance on the lingual side of the mandibular rhamus. Enamel orange on the upper incisor's anterior surface, paler or yellow on the lower ones.

Maxillary molar-row parallel, clearly shorter than diastema. Molars small relative to size of skull. In
both, the maxillary and the mandibular row, the $1^{\text {st }}$ molar is the largest, with the most complete tubercular pattern, and the $3^{\text {rd }}$ molar is the most reduced, both in size and structure. Upper molars have tubercles arranged into three longitudinal rows; the median row is the largest. Tubercles are connected by cross-ridges forming transverse and crescent laminae. Rarely does the enamel ridge connect the tubercles t1 and t5 (stephanodonty; Fig. 53 a). All main tubercles, nine in total, are evident on the $1^{\text {st }}$ molar. The postero-lingual tubercle (t7) is most reduced; when present it is developed either as a tubercle (Fig 53 a) or a ridge (Fig. 53 b), but can be also entirely lost. The postero-labial accessory tubercle (t12) is rarely large and well defined in Turkish material (Fig. 53 c). Tubercle t9 is mainly large, rarely reduced, but never absent, as is occasionally in A. flavicollis. Small accessory tubercles are frequently present between the anterior cusps t1-t2 and/or t2-t3 (Fig 53 d). Occasionally, there is a small tubercle also on the lingual margin between tubercles t 1 and t 4 (Fig. 53 d ).

Second upper molar lacks the antero-medial tubercle (t2), and its antero-labial tubercle (t3) is much reduced. Central cusps $t 5$ and t8 are well developed, but postero-lateral cusps t 7 and t 9 are small. Third upper molar is scarcely half the size of $2^{\text {nd }}$ molar. Only five cusps are retained of the original number of nine, namely all the lingual ones ( $\mathrm{t} 1, \mathrm{t} 4, \mathrm{t} 7$ ) and two mesial cusps (t5 and t8). Cuspidation is clearly visible only on unworn $3^{\text {rd }}$ molars, which are rare in museum material since the pattern of enamel abrasion is more progressive on $3^{\text {rd }}$ molar than on the remaining teeth.


Figure 53. Variation of $1^{\text {st }}$ upper molar in Apodemus sylvaticus from Turkish Thrace and adjacent Greece. a, d - Karakasım, district Edirne; b - Monastirakio, district Evros, Greece; c - Komara, district Evros, Greece. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

Lower molars consist of a series of paired tubercles that are partly joined by cross-ridges. First molar has three pairs of tubercles, in addition to mesial and distal tubercles. Its labial margin has a narrow enamel ledge bearing small accessory cusplets. Second molar is essentially like the first one, except that lacks mesial and mesio-lingual tubercles. Third molar, which is the smallest, has lost all mesial elements.

Number of roots is 4 ( $1^{\text {st }}$ and $2^{\text {nd }}$ upper molar), 3 ( $3^{\text {rd }}$ upper), and 2 (lower molars; Zejda, 1965; Niethammer \& Krapp, 1978). In upper molars, the typical condition is found in more than $90 \%$ of specimens from central Europe (Niethammer, 1962). Deviations are due to fusions of existing roots or by additions of small, accessory roots. Number of roots thus varies in upper molars, being $3,4,5$ or $6\left(1^{\text {st }}\right.$ molar); 3, 4 or 5 ( $2^{\text {nd }}$ molar); 1, 2, 3 or 4 ( $3^{\text {rd }}$ molar) ( Ni ethammer, 1962; Zejda, 1965).

Dimensions for Thracian sample are given in Table 10. Filippucci et al. (1996) report measurements of two specimens from the Anatolian side of the Marmara straits (in mm): head and body: 91/82, tail: -/88, hind foot: 23.0/22.5, condylobasal length: 23.87/22.98, maxillary tooth-row (on crowns): $3.60 / 3.86$, length of bulla: $4.49 / 4.49$. There is no secondary sexual dimorphism in size.

|  | N | mean | $\min -\max$ |
| :--- | :---: | :---: | :---: |
| Head and body | 26 | 102.3 | $91-109$ |
| Tail | 24 | 97.2 | $91-110$ |
| Hind foot | 26 | 22.9 | $21.5-24.5$ |
| Ear | 24 | 16.4 | $15.0-18.0$ |
| Weight | 25 | 28.7 | $23-39$ |
| Condylobasal length | 21 | 24.0 | $23.1-25.3$ |
| Zygomatic breadth | 22 | 13.0 | $12.1-13.8$ |
| Maxillary tooth-row (alveoli) | 8 | 4.3 | $4.1-4.4$ |
| Maxillary tooth-row (crowns) | 27 | 4.0 | $3.7-4.2$ |
| Bulla length | 27 | 4.8 | $4.4-5.3$ |

Table 10. External and cranial dimensions of Apodemus sylvaticus from Thrace in Turkey and adjacent Greece. Based on our own material.

Chromosomes. The karyotype consists of 48 acrocentric chromosomes of decreasing size ( $2 \mathrm{~N}=48$, $\mathrm{NF}_{\mathrm{a}}=46$ ). The X chromosome is one of the largest elements in the set and the size of $Y$ chromosome is variable (Zima \& Král, 1984). Karyotype was studied in various Balkan countries (Soldatović et al.,
1975), including Bulgaria (Nadjafova et al., 1993) and Thrace in Turkey (Çolak et al., 2005). For details on differential staining of Bulgarian material see Nadjafova et al. (1993).

## Variation

Size and colour vary across Europe (Miller, 1912). Niethammer (1978a) tentatively recognised 32 subspecies, and some twenty of them are island races. Island populations, particularly around Great Britain, attain the largest size. On the mainland, size correlates negatively with latitude (Alcántara, 1991), and field mice from Thrace are on the end of this size cline. Grey bellied animals are common in the north and white bellied in the south; the former also tend to be darker dorsally. From the point of belly colouration, the Thracian population is anomalous.

Partial sequence of the mitochondrial cytochrome $b$ gene revealed two main clades, one comprising samples from western, central and northern Europe, and from northern Africa, and the second one containing samples from Italy and from the Balkans. The divergence between these two lineages is estimated at $1.5-1.6$ million years ago. The later clade was further subdivided into two lineages, the first one comprising specimens from the Balkans and peninsular Italy, and the second one containing Sicilian material. Divergence between the last two lineages is estimated at about $0.8-0.9$ million years (Michaux et al., 2003). Genetic variability is higher in Mediterranean Europe than further north, a legacy of surviving glacial-interglacial dynamics in southern refugia. The Sicilian population is particularly diverse. The source of post-glacial northward colonization was the western refugium in southern France and in Iberia (Michaux et al., 2003).

## Distribution

For the majority of the $20^{\text {th }}$ century, A. sylvaticus was reported to have a broad Palaearctic distribution (Corbet, 1978), including Japan (Ellerman \& Morrison-Scott, 1951, 1966). Within its current scope, A. sylvaticus is nearly endemic to Europe, with an isolate in northern Africa (Morocco, Algeria, Tunisia). In mainland Europe, the long-tailed field mouse is the most widespread Apodemus species, ranging from the Mediterranean coasts in the south as north as $60^{\circ}$ of northern latitude (Niethammer,

1978a; Mitchell-Jones et al., 1999). The eastern border is in eastern Ukraine and western-most Russia in the basin of the River Donetc (Zagorodnyuk, 1994; Mezhzherin, 1997; Mezhzherin et al., 2002). The long-tailed field mouse is widespread on many islands in the Baltic, the Northern Sea, around Britain, in the Mediterranean, and on Ireland and Iceland (Niethammer, 1978a). Its distribution on the Aegean islands is not clear. While it certainly does occur on Crete (Kryštufek, 2002b), some of the earlier reports for the islands offshore Anatolia actually relate to A. witherbyi (Özkan \& Kryštufek, 1999; Kryštufek \& Mozetič Francky, 2005).

The long-tailed field mouse is widespread in Turkish Thrace, but seems to be restricted mainly to disturbed lowland habitats. Yiğit et al. (2003) reported it for Velika on Istranca Mts., however we doubt whether their identification was correct. Namely, three Apodemus species were cited for Velika, in addition to A. sylvaticus: A. flavicollis, A. mystacinus and A. agrarius. In our sample of 130 Apodemus specimens from the same locality and its nearby vicinity,
only A. flavicollis is present. Besides, a report of $A$. mystacinus for European Turkey is most unlikely (cf. Mitchell-Jones et al., 1999). Because of such evident errors and in the absence of any further information on the material and its identification, we subsequently reject the paper by Yiğit et al. (2003) as a reliable source of field mice distributional records.

Filippucci et al. (1996) reported two localities in north-western Anatolia. Identification was based on morphology and electroporetic analysis of 38 protein loci, and subsequently verified by a partial sequence of the mitochondrial cytochrome $b$ gene (Michaux et al., 2003). Contrary to these results, Macholán et al. (2001) did not recognize A. sylvaticus in their study on allozyme variation in Turkish Apodemus species. We examined a large sample ( $\mathrm{N}=171$ ) of field mice from the regions of Bolu and Zonguldak, where the occurrence of $A$. sylvaticus has been reported by Filippucci et al. (1996), but not a single animal matched the morphology of that species. Our examination of many more specimens from other localities in the Marmara region and the western


Figure 54. Distribution of Apodemus sylvaticus in Turkey and adjacent regions. Records: 1 - Edirne, University campus; 2 - Karakasım, Edirne; 3 - Mahmut köy, Kesan, Edirne; 4 - Akcakoca (= Akçakoca), Bolu; 5 - 5 km south of Çaycuma, Zonguldak; 6 - Greece, Island of Crete. Corresponding references: Filippucci et al. (1996): 4, 5. Kryštufek (2002b): 6. Our own data: 1-3. Putative presence in Anatolia is indicated by diamonds.

Pontic Mts. also failed to identify a single A. sylvaticus. Filippucci et al. (1996) provide drawings of A. sylvaticus specimen from Akçacoca (ventral side of skull and both molar rows). This animal clearly differs from our Thracian sample in its short incisive foramen. We therefore conclude that presence of $A$. sylvaticus in Anatolia requires further attention and additional supporting evidence. Yiğit et al. (2006c) mapped A. sylvaticus only for Thrace.

A report of A. sylvaticus from the Island of Gökçeada (Özkan, 1999a) is erroneous (Özkan \& Kryštufek, 1999).

Palaeontology. Genus Apodemus has been known in Europe since the Miocene (Kowalski, 2001) and in Turkey and the eastern Mediterranean since the Late Turolian (Miocene) and Ruscinian (Pliocene; Meulen \& Kolfschoten, 1986; Kotsakis 1990; Sümengen et al., 1990). Apodemus possibly emerged from the fossil Parapodemus Schaub, 1938 (Michaux, 1967); Parapodemus putatively survived much longer in the Near East (till Mindel) than anywhere else (Tchernov, 1979). The Pliocene material from Çalta near Ankara was identified as A. dominans Kretzoi, 1959 (Şen, 1977). These mice, which lived in steppic conditions, had a stephanodont $1^{\text {st }}$ upper molar, with well developed accessory tubercle t12 (Şen, 1978).

Taxonomic identity of the fossil material is frequently vague, and with the exception of A. mystacinus and A. agrarius, fossil histories of recent Turkish species are traced back into time with considerable degree of uncertainty. Whenever two size classes were recognized in the fossil Sylvaemus material, they were ascribed either to two extinct species (the larger A. levantinus and the smaller A. caesareanus), or to two extant species: the larger A. flavicollis and the smaller A. sylvaticus. Apodemus levantinus Bate, 1942, and A. caesareanus Bate, 1942, were both described from the Aucheulian and the Levalloi-so-Mousterian strata of the Tabun cave in the Carmel, Israel (Bate, 1942). Two size-based morphotypes are reported from the Dodecanese Island of Kalymnos (Early Pleistocene; Kuss \& Storch, 1978), Israel (Late Middle Pleistocene to Lower Mousterien; Tchernov, 1975, 1979), eastern Greece and Turkey (Lower Pleistocene; Meulen \& Kolfschoten, 1986), eastern Mediterranean islands (Pleistocene; Kotsakis, 1990), and Antalya in Anatolia (Mid-
dle Pleistocene to Early Late Pleistocene; Storch, 1988).

Taking into account recent progress in the taxonomy of Apodemus, we assume that the fossils A. levantinus and $A$. caesareanus probably correspond to extant A. flavicollis and A. witherbyi, respectively. E.g., the Middle Pleistocene molars from the Island of Chios (Storch, 1975; Fig. 19 on p. 175) show a stephanodont $1^{\text {st }}$ upper molar with an accessory tubercle t 12 . Together with large tubercles t 7 and t 9 on the $2^{\text {nd }}$ upper molar, dental pattern suggests $A$. witherbyi to be in question, rather than A. sylvaticus. Few $1^{\text {st }}$ molars excavated in Israel and whose photographs are published by Tchernov (1979; Plate I on pp. 138-139) also point to $A$. witherbyi.

In conclusion, the molar size suggests a sympatry of at least two Sylvaemus species in Anatolia and the rest of the Eastern Mediterranean throughout the Pleistocene (cf. Tchernov, 1979). Taxonomic identity of these two forms, however, is not fully understood. Presence of A. sylvaticus is not very probable, and the smaller morphotype more likely belongs to A. witherbyi. This conclusion is putatively valid also for the Caucasian region, specifically for the Middle Pleistocene record from the Apšeron Peninsula in Azerbaijan, which was identified as A. sylvaticus (Vereščagin, 1959).

Contrary to the eastern Mediterranean, fossil records of A. sylvaticus are numerous in Europe since the Early Biharian (Early Pleistocene; Kowalski, 2001). Santel \& Koenigswald (1998) reported from the Middle Pleistocene strata of the Yarımburgaz cave on the Istranca Mts. only A. sylvat-


Figure 55. Habitat of Apodemus sylvaticus near Edirne.
Photo: B. Kryštufek.
icus, but not A. flavicollis. Phylogeographic evidence suggests that A. sylvaticus suffered a serious genetic bottleneck in its Balkan glacial refugium (Michaux et al., 2005).

## Habitat

The long-tailed field mouse is a eurytopic species and is common across a wide range of habitats. It seems to be less common and widespread in Thrace than is generally the case in majority of Europe. Note however, that A. sylvaticus is relatively rare throughout the Balkan Peninsula to the south of the rivers Sava and Danube.

In Thrace of Turkey and Greece, we collected long-tailed field mice only in open lowland habitats, mainly in dense and tall vegetation (tall grass, bushes, reeds) between fields or along rivers. On the Istranca Mts., where forests abound with A. flavicollis, we failed to capture a single long-tailed field mouse even in forest clearings and along hedgerows. In Bulgaria, A. sylvaticus mainly occupy disturbed habitats at low altitudes: arable land, bushes, and sparse forests along rivers (Peshev et al., 2004).

Altitude. All Turkish records are from the lowlands, below about 300 m of elevation. In Bulgaria, A. sylvaticus occasionally occurs up to $1,400 \mathrm{~m}$ (Popov, 1993) but is mainly tied to low altitudes (Peshev et al., 2004). In the rest of Europe, the longtailed field mouse also occupies high altitudes (e.g. about $1,900 \mathrm{~m}$ in the Alps; Spitzenberger, 2001).

Associates. The habitat of the long-tailed field mouse in European Turkey is shared by another two mice: A. flavicollis and Mus macedonicus. Hedgerows (Crategus sp., Pirus malus, P. communis, Rubus sp.) are mainly dominated by A. flavicollis. In more open and dry habitats, Mus macedonicus usually outnumbers A. sylvaticus. Other associates of the longtailed field mouse in Turkish Thrace include Crocidura suaveolens, C. leucodon, Microtus levis, Dryomys nitedula, and Myomimus roachi.

Density varies tremendously (from $<1$ individual per ha to $>50$ individuals per ha; Montgomery, 1999a), depending on the habitat and season; densities also oscillate over years. In general, densities of small mammals are high in low Turkish Thrace in late summer and in autumn. In optimal habitats, A. sylvaticus makes approximately up to one quarter of small mammals collected in trap lines. In Bulgaria,
the relative abundance of $A$. sylvaticus is mainly $<5$ individuals per 100 trap nights (Peshev et al., 2004).

## Biology

Literature covering biological aspects of A. sylvaticus is voluminous; for reviews see Niethammer (1978a) and Corbet \& Harris (1991). There is considerably less information available from Thrace.

Activity is nocturnal (Peshev et al., 2004).
Burrows are simple and relatively shallow, e.g. $40-50 \mathrm{~cm}$ deep in Bulgaria. Nest chamber (diameter of $10-12 \mathrm{~cm}$ ) is lined with dry vegetable matter. There are 1-3 caches per burrow (Peshev et al., 2004).

Reproduction. Reproductive activity in Thrace seems to be restricted to vegetation season. First juveniles are recruited in late June, and we found no sign of reproductive activity in late October. Reproductive season in Bulgaria starts at the end of February (mostly in March) and terminates in late September, exceptionally in November or early December (Peshev et al., 2004). In Turkish Thrace the number of embryos is $4-7$ (mean $=5.5 ; \mathrm{N}=11$ ). Similar mean litter (= 5.26 ) is reported from Bulgaria, but the range is much wider ( $=2-11$; $\mathrm{N}=567$ ), doubtlessly a consequence of differences in samples sizes. Within the species' area of distribution, there is a west to east and south to north cline in litter size, with the largest litters in north-east (Frynta \& Vohralík, 1992). Pregnancy lasts 21-23 days (Peshev et al., 2004).

Food. A feeding generalist. No data, apart from macroscopic examinations of stomach contents, are available from Turkish Thrace. Diet was studied in agricultural habitats in Bulgaria. Daily consumption is $7-8 \mathrm{~g}$ of food (= about $24 \%$ of body mass). Main dietary items are seeds (particularly in the autumn), insects, green plant material, buds, and flowers (particularly in the spring); various fruits and nuts are consumed, depending on the season. Food is cached and stores contain up to $1.5-3 \mathrm{~kg}$ of seeds. The animal is considered to be a pest to agriculture and is capable of destroying an estimated $40-60 \mathrm{~kg}$ of crop per ha (Peshev et al., 2004).

Predation. No information is available from Turkish Thrace. Vohralík \& Sofianidou (1992a) report unidentified Apodemus (either A. flavicollis or A. sylvaticus, or both) from the pellets of Tyto alba and Athene noctua, collected in Greek Thrace.

## Yellow-necked field mouse - Apodemus FLAVICOLLIS

Mus flavicollis Melchior, 1834. Type loc.: Sielland, Denmark.
Apodemus flavicollis saturatus Neuhäuser, 1936. Type loc.: Kurayiseba (= Ikizdere), Vilayet Rize, north-east Turkey.

## Taxonomy

Taxonomic relations between A. flavicollis and $A$. ponticus (Sviridenko, 1936) (type loc.: Olgino Village on the Northern Caucasus) have not been resolved. Musser \& Carleton (2005) retain specific status for $A$. ponticus, considering it to be endemic to the Caucasus. Mezhzherin (1997) applied this name for mice from the Caucasus, Asia Minor and the Middle East, and retained A. flavicollis for the European populations. Within such a scope, A. ponticus at least partially overlaps with the Middle and Near Eastern phyllogeographic clade of A. flavicollis sensu Michaux et al. (2004). Therefore, the nomenclatural solution by Mezhzherin (1997) is not appropriate since Mus arianus Blanford, 1881 (type loc.: Qohrud, Isfahan, Iran) which is a junior synonym of $A$. flavicollis (Kryštufek, 2002), holds priority over $A$. ponticus. Electrophoretic evidence provides contradictory results on the taxonomic position of A. ponticus. Different studies suggest this taxon to be a sister group to A. flavicollis or A. falzfeini Mezhzherin \& Zagorodnyuk, 1989 (a junior synonym of $A$. witherbyi; Musser \& Carleton, 2005), or even part of the later (Mezhzherin, 1990, 1997; Mezhzherin \& Zykov, 1991; Hille et al., 2002).

Morphologically, A. ponticus is not adequately diagnosed, and characters given by Mezhzherin (1997) perfectly match the description of Anatolian A. flavicollis. Zagorodnyuk et al. (1997) distinguished between $A$. flavicollis and $A$. ponticus on the basis of molar-row length (shorter in ponticus), tail length relative to head and body (shorter in ponticus), size of pectoral spot (slightly longer in ponticus), and shape of interpterygoid space (broader in ponticus). In our opinion, all these characters are variable an overlap between populations. Further diagnostic characters were provided by Voroncov et al. (1992) who also published drawings of the ventral skull and chest patch, as well as statistics for external
and cranial dimensions. On these grounds, we are unable to see any clear difference between the Caucasian A. ponticus and the Anatolian A. flavicollis. Zaika (2009) claims that ponticus lacks a stephanodonty on $1^{\text {st }}$ upper molar. We examined a sample of $A$. ponticus from Georgia (ZFMK), and found it to be identical to A. flavicollis from Anatolia.

Vorontsov et al. (1992) recognized A. ponticus (and not A. flavicollis) for the Caucasus. Similarly, Bukhnikashvili (2004) mapped for Georgia only A. ponticus, and some of localities are very close to Turkish border. His map contradicts the results derived from the electrophoretic study of allozymes (Macholán et al., 2001; Filippucci et al., 2002) and from sequencing mitochondrial cytochrome $b$ gene (Michaux et al., 2004); all these studies placed field mice from north-eastern Turkey (districts of Gümüşhane and Artvin) and Azerbaijan, to A. flavicollis. Therefore, the taxonomic and geographic scope of $A$. ponticus is evidently not defined unambiguously. At present we see no reason against


Figure 56. Yellow-necked field mouse Apodemus flavicollis from Yeşiltarla, Mt. Uludağ. Photo: A. Kryštufek.
clumping all yellow-necked field mice of Anatolia and the Caucasian region into A. flavicollis. Such a conclusion is also well supported by crossbreeding over two generations between specimens from a district of Rize with Austrian A. flavicollis (Steiner, 1978a).

Mezhzherin (1997) continues to use A. tauricus (Pallas, 1811) as a valid name for A. flavicollis. Such a nomenclatural solution dates back to Heptner (1948) and was adopted widely, albeit not universally, particularly by Russian authors. Mus sylvat-
icus var. tauricus has been described as being from "the mountains of Crimea". As stated by Corbet (1978), the diagnosis of var. tauricus relative to $A$. sylvaticus (multo major et elegantissimi velleris) is not satisfactory enough to indisputably link this name with A. flavicollis. Besides, two more Apodemus species occur in the Crimea, in addition to A. flavicollis (Mezhzherin, 1997): A. witherbyi (reported in the quoted paper as arianus, with fulvipectus, hermonensis, and falzfeini as junior synonyms) and $A$. uralensis. Musser \& Carleton (1993) synonymised Pal-


Figure 57. Skins of Apodemus flavicollis in dorsal and ventral view. a-8 km south-east of Velika Köy, district Kırklareli, Turkish Thrace; b - Kabaca, district Artvin, Anatolia. Photo: C. Mlinar.
las' tauricus with A. sylvaticus, but their conclusion contradicts the fact that A. sylvaticus is absent from the entire peninsula of Crimea (Mezhzherin, 1997; Zagorodnyuk et al., 1997). Corbet (1978) proposed a rejection of var. tauricus of Pallas as being impossible to determine. In an assembly of three sibling Apodemus species, as is the case on Crimea, his proposal sounds reasonable. Pavlinov \& Rossolimo (1987) consider tauricus of Pallas to be nomen oblitum. This does not hold since tauricus Pallas has been used since 1899 as a senior synonym of A. flavicollis. Moreover, the name was not rejected between 6 November 1961 and 1 January 1973 (Article 23.12 of the International Code of Zoological Nomenclature; ICZN, 1999), therefore tauricus Pallas is a potentially valid name (Kryštufek, 2002). Recently Zaika (2009) reported tauricus as a species distinct from flavicollis.

## Description

External characters (Fig. 56). The yellow-necked field mouse is very similar to A. sylvaticus. Ears and eyes are large, and whiskers are long. Feet are essentially as in A. sylvaticus, hind foot, however, is
longer. Tail is on average of same length as head and body ( $101 \%$; range = 87-118 \%; $\mathrm{N}=120$ ); with a short terminal pencil. Anatolian yellow-necked field mice have 31-36 caudal vertebrae (median $=33, \mathrm{~N}$ = 56; Štĕpánková \& Vohralík, 2008). Pelage is soft, summer hairs are up to 7 mm long on mid-back (sparse long hairs up to 9 mm ), approximately 4-5 mm on the belly.

Colour (Fig. 57) is buffy wood-brown above, frequently with russet tints. Ventral side is white and washed by slate grey undercolour; demarcation line along flanks is sharp. Very exceptionally the belly is washed by buff, thus resembling pattern in $A$. sylvaticus (three skins of total 192). Chest between the forelegs is with a clear buff spot or collar, and is very rarely blank white. Collar is common in European Turkey and rare in Anatolia (Table 11). Spot varies in size but is mainly broad (or dot-like when small), rarely narrow and elongate. Tail is indistinctly bi-coloured and feet are pale.

Nipples as in A. sylvaticus: two pairs of inguinal and one pair of pectoral, respectively (six nipples in total).


Figure 58. Skull and mandible of Apodemus flavicollis, based on an adult male from Edirne. Scale bar = 5 mm .

|  | Thrace | Island of <br> Gökçeada | North <br> Anatolia | West \& South <br> Anatolia |
| :--- | :---: | :---: | :---: | :---: |
| N | 91 | 96 | 41 | 60 |
| Blank | $2.2 \%$ | $6.3 \%$ | $2.4 \%$ | $5.0 \%$ |
| Spot | $65.9 \%$ | $68.7 \%$ | $97.6 \%$ | $91.7 \%$ |
| Collar | $31.9 \%$ | $25.0 \%$ | $0.0 \%$ | $3.3 \%$ |

Table 11. Incidence of three morphotypes of the chest pattern in Apodemus flavicollis according to regions of Turkey. Sources: Island of Gökçeada (Özkan, 1995); the rest is based on our own material.

Penis and baculum are essentially as in A. sylvaticus. The dorsal ridge, however, is not as distinct in the yellow-necked field mouse, and there is no apparent ventral groove. Also, the proximal region is more bulbous (width $=2.89-3.50 \mathrm{~mm}$ ). In Croatian material, the glans is $6.21-6.64 \mathrm{~mm}$ long and $2.91-3.34 \mathrm{~mm}$ wide; at the midsection, the glans is $2.49-2.94 \mathrm{~mm}$ wide and 2.31-2.93 mm deep. The entire baculum is $5.14-5.58 \mathrm{~mm}$ long; proximal section measures $3.57-3.95 \mathrm{~mm}$, and base is $1.13-1.49$ wide (Williams et al., 1980). The glans is $6.05-6.32 \mathrm{~mm}$ long and 2.89-3.00 mm wide in specimens from Turkish Thrace; corresponding dimensions in an Anatolian
individual are 5.63 mm and 3.16 mm , respectively. For a drawing of material from Turkey see Yiğit et al. (2006c: Fig. 38F). Larina (1958b) figured baculum of A. flavicollis from Saratov region (lower basin of the Volga); dimensions are as follows: length $=$ $3.8-4.0 \mathrm{~mm}$ in adults and $7.7-7.9 \mathrm{~mm}$ in senile individuals; basal width $=1.3-1.4 \mathrm{~mm}$ (adults), 1.63-2.2 mm (senile animals).

Skull (Fig. 58, 59) closely resembles the condition in A. sylvaticus, but is broader and more robust. Zygomatic breadth relative to condylobasal length is wider (mean $=55.0$ \%; range $=51.6-59.8$ \%). Rostrum is broader and incisive foramen is shorter (18.423.9 \% of condylobasal length; mean $=21.3 \%)$. Interpterygoid space is typically wide, and the posterior margin of hard palate is rounded. Fronto-parietal suture is usually rounded, bullae are relatively short (on average 20.9 \% of condylobasal length; range = 18.9-23.3 \%).

Teeth (Fig. 60) are essentially as in A. sylvaticus, with no categorical differences between the two species which would allow safe identification of every individual. First upper molar shows stephanotont pattern in approximately one tenth of specimens, this


Figure 59. Skull and mandible of Apodemus flavicollis, based on an adult female from Adana. Scale bar $=5 \mathrm{~mm}$.


Figure 60. Upper (a) and lower molars (b) in Apodemus flavicollis from Edirne (same specimen as in Fig. 58). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
however varies among samples. The cusps $t 1$ and $t 5$ are more frequently connected by a ridge (Fig. 60a) than is the case with cusps t3 and t5 (Fig. 61a). Cusps t 1 and t 3 show posterior spurs in more than half of specimens. Tubercle t7 is mainly developed as a cusp


Figure 61. Variation of $1^{\text {st }}$ upper molar in Apodemus flavicollis from Turkey. a, c - Demirköy, Istranca Mts., Turkish Thrace; b-Adana. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
(Fig. 61b), but is ridge-like (Fig. 61c) in approximately one tenth of animals; this percentage varies geographically. Cusp t1 is isolated (Fig. 61b) in more than half of specimens and such condition remains visible even in moderately worn teeth. Postero-labial cusp t12 is present in more than one half of specimens; see Fig. 62 for different morphotypes of t12.

On the $2^{\text {nd }}$ molar, tubercle $t 9$ is only rarely as large as t6 (Fig. 63a). Instead, t9 tends towards reduction and is ridge-like (Fig. 63b) in at least half of animals. In extreme cases, t9 is absent (Fig. 63c), a condition that is diagnostic for A. flavicollis (Tvrtković, 1976). Cusp t 7 is always large and never clearly ridge-like. Incidence of the accessory postero-lingual cusp 112 (Fig. 63d) is lower than on the $1^{\text {st }}$ molar. The $3^{\text {rd }}$ molar is relatively large.

Number of roots is same as in A. sylvaticus and deviations from the typical pattern are less common. Deviant root counts in upper molars are: 3, 5, 6 ( $1^{\text {st }}$ molar); 3 or 5 ( $2^{\text {nd }}$ molar); 1, 2, 4 ( $3^{\text {rd }}$ molar; Niethammer, 1962; Zejda, 1965).


Figure 62. Variation of postero-labial cusp t12 (shown by arrow) on $1^{\text {st }}$ upper molar in Apodemus flavicollis from Turkey. a Demirköy, Istranca Mts., Turkish Thrace, b-8 km west of Yenice, Zonguldak; c-e - Adana. Lingual side is to the left, anterior is at the top. Scale bar $=0.5 \mathrm{~mm}$.


Figure 63. Variation of $2^{\text {nd }}$ upper molar in Apodemus flavicollis from Turkey. a, d - Adana; b - Demirköy, Istranca Mts., Turkish Thrace; c - Longoz, Istranca Mts., Turkish Thrace. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

Dimensions are given in Table 12. Males are on average slightly larger, but the difference is not significant. In a sample from the Istranca Mts., mean condylobasal length in males is 25.34 mm , and in females 25.09 mm .

Chromosomes. The karyotype consists of 48 acrocentric chromosomes of decreasing size ( $2 \mathrm{~N}=48$, $\mathrm{NF}_{\mathrm{a}}=46$ ). The X chromosome is one of the largest elements in a set and the Y chromosome is of medium size (Zima \& Král, 1984). Turkish populations do not deviate in this respect from European samples (Doğramacı \& Kefelioğlu, 1991a; Zima \& Macholán, 1995; Çolak et al., 2005) and same karyotype is reported also from Jordan (Sözen et al., 2008). For differential staining of Bulgarian specimens see Nadjafova et al. (1993).

From one to six supernumerary (or B) chromosomes were reported for the yellow-necked field mouse from various parts of its European range (Zima \& Macholán, 1995). B chromosomes are largely heterochromatic and do not pair with any of
the A chromosomes in meiosis. Their role in the genome and their influence on the organism are not well understood and no unambiguous interrelationship was found between the frequency of B chromosomes and various biological or ecological variables. Zima \& Macholán (1995) suggested their incidence to be mainly due to stochastic effects operating with the specific genetic background of a population. There is some evidence suggesting a selective advantage for males possessing B chromosomes, possibly in relation to survival during winter (Zima et al., 2003). In the central Balkans, the frequency of animals with B chromosomes increases with altitude and is negatively correlated to average temperature and habitat suitability. Therefore, the presence of B chromosomes is putatively widening the genetic variability and hence enabling the species to extend its response to the environment by occupying more habitats (Vujošević et al., 2007). In European Turkey, approximately one quarter of specimens had from one to three supernumerary elements in their karyotype (Zima \& Ma-

|  | Thrace |  |  |  |  | Anatolia |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\mathrm{max}$ |
| Head and body | 87 | 107.4 | $92-121$ | 62 | 102.8 | $93-118$ |
| Tail | 69 | 107.4 | $92-125$ | 52 | 105.8 | $87-122$ |
| Hind foot | 88 | 24.1 | $21.9-26.5$ | 63 | 23.2 | $20.9-25.4$ |
| Ear | 81 | 17.6 | $15.9-19.2$ | 58 | 16.9 | $15.5-18.3$ |
| Weight | 89 | 31.5 | $21-55$ | 53 | 27.9 | $20.5-37$ |
| Condylobasal length | 85 | 25.3 | $23.5-27.6$ | 54 | 24.4 | $23.0-26.0$ |
| Zygomatic breadth | 86 | 13.8 | $12.5-15.2$ | 55 | 13.4 | $12.3-14.3$ |
| Maxillary tooth-row (alveoli) | 98 | 4.4 | $3.8-4.7$ | 13 | 4.3 | $4.2-4.4$ |
| Maxillary tooth-row (crown) | 114 | 4.2 | $3.8-4.4$ | 104 | 4.0 | $3.8-4.2$ |
| Bulla length | 103 | 5.2 | $4.7-5.6$ | 103 | 5.1 | $4.7-5.5$ |

Table 12. External and cranial dimensions of Apodemus flavicollis from Turkey. Based on our own material.
cholán, 1995), but Anatolian populations lacked B chromosomes (Macholán \& Zima, 1997).

Supernumerary chromosomes are absent in the remaining Apodemus species occurring in Turkey (Macholán \& Zima, 1997).

## Variation

Morphological differences between yellow-necked field mice, separated by the Marmara straits, are on average and are not categorical. Thracian animals tend to be larger and heavier (Table 12). The throat collar is rare in Anatolian samples, while it is common in Thrace and on the Island of Gökçeada (Table 11). No interpopulation variation in size was detected in Anatolia (Kryštufek \& Vohralík, 2008). Mice from the Island of Gökçeada differ from the mainland samples in longer incisive foramen and shorter palatinum (Özkan \& Kryštufek, 1999).

Cusp pattern differs between the two major regions of Turkey. On $1^{\text {st }}$ upper molar, the incidence of the accessory postero-lingual cusp t12 is more frequent in mice from Adana than those from Thrace. In the Adana sample, a direct connection is more frequently established between cusps $t 8$ and t 9 (Fig. 62c), and not via t12 (Fig. 62d), what results is an enamel island on the postero-labial side of the tooth (Fig. 63e). In European Turkey, the $1^{\text {st }}$ upper molar tends to have more frequently a ridge-like cusp t7 (Fig. 61a,c), and connected cusps t 1 and t 5 (Fig. 61a). In Anatolian animals, $2^{\text {nd }}$ upper molar shows higher incidence of a cusp-like t9 (Fig. 63a,d), and the incidence of t 12 (Fig. 63d).

Partial sequence of the mitochondrial cytochrome $b$ gene suggests deep divergence between the yellownecked field mouse populations separated by the Marmara straits. The divergence between the two main phylogeographic lineages (Europe vs. Middle East) is estimated at 2.2-2.4 million years ago (Michaux et al., 2004). Genetic evidence from protein electrophoresis contradicts mitochondrial results. Namely, in a study by Filippucci et al. (2002), the Italian population appeared to be the most unique, while no clear geographic structuring was detected in the Balkans and the Middle East. These results point to a relatively recent invasion of the Middle East from southern Europe (Filippucci et al., 2002).

Michaux et al. (2004) suggested that "The Oriental population [of A. flavicollis] is genetically very
differentiated from the European and Russian populations and could be described as a particular subspecies." If so, several names are already available from Asia (see chapter on Taxonomy above).

## Distribution

Widespread from Western Europe to the Ural Mts., but absent from western Iberian Peninsula and western France; introduced to England. Asiatic range encompasses Anatolia, western Iran, and eastern Mediterranean coast as south as Israel (Mendelssohn \& Yom-Tov, 1999) and Jordan (Abu Baker \& Amr, 2008). Presence in the Caucasus is uncertain due to unclear relations between $A$. flavicollis and $A$. ponticus (see comments under Taxonomy above). More rarely present on the islands than A. sylvaticus, but occurs on some islands of the Adriatic, Ioannean, and the Aegean Sea (Montgomery, 1999b).

In Turkey, the yellow-necked field mouse is widespread throughout Thrace. The range in Anatolia follows the coasts and coincides fairly well with the Euxinian mesic forests in the north and with the Mediterranean woodland climax in the west and south. The range in the Taurus Mts. is puzzling, as there is a wide gap in a well-surveyed central part of the mountain range; the yellow-necked mouse is again widespread in Hatay (Kryštufek \& Vohralík, 2008). Apodemus flavicollis occurs on the Island of Gökçeada (Özkan, 1999a; Özkan \& Kryštufek, 1999), as well as on two Greek islands in the proximity to Gökçeada: Thassos and Samothraki (Vohralík \& Sofianidou, 1987, 1992a).

Palaeontology. See comments under A. sylvaticus. The earliest reports from Anatolia are from the Middle Pleistocene of Emirkaya near Seydișehir in Central Anatolia (Late Biharian; Şen et al., 1991; Montuire et al., 1994) and Antalya (Storch, 1988). First upper molars from Emirkaya are characterised by stephanodonty and a well developed tubercle t12, hence, they may belong to $A$. witherbyi. The Middle Pleistocene report for Anatlya (Storch, 1988) is well within the current range of the yellow-necked field mouse. Tchernov (1994) stated an intermittent occurrence of A. flavicollis in the southern Levant over the past 150,000 years; the animal was present only during cold phases. In the Pleistocene of Europe, A. flavicollis is reported since the Biharian, and was continually present for the last 1.6 million years


Figure 64. Distribution of Apodemus flavicollis in Turkey and adjacent regions. Records: 1 - Karakasım, Edirne, 40 m a.s.l.; 2 - University Campus, Edirne 40 m a.s.l.; 3 - Dupnisa Mağarası, Dereköy, Kırklareli, ca 400 m a.s.l.; 4 - Yeniköy, Kırklareli; 5 - Velika Bridge (=Velika Köy), Demirköy, Kırklareli, 800 m a.s.l.; 6 - 7 km north-east of Sivriler, Kırklareli, ca 50 m a.s.l.; 7 - İğneada, Kırklareli, ca 50 m a.s.l.; 8a - Yeşir Tarla, Ulu Dağ, Bursa, ca $1,000 \mathrm{~m}$ a.s.l.; $\mathbf{8 b}$ - Ulu Dağ, Bursa, 1,800 m a.s.l.; 9 - 5 km south-west of İznik, Bursa; 10a - 25 km south of Düzce, Bolu; 10b - Abant Gölü, Bolu, ca 1,000 m a.s.l.; 11 - Akcacoca (=Akçakoca), Bolu; 12 - Çayır, Zonguldak; 13 - 8 km north-west of Yenice, Zonguldak, ca 100 m a.s.l.; 14 - 5 km north of Safranbolu, Zonguldak, ca 500 m a.s.l.; 15 - Bürnük, Kastamonu; 16 - Bektasaga, Sinop; 17 - Kürtler, Samsun, ca 5 m a.s.l.; 18 - Borabay Lake, Taşova, Amasya; 19 - Giresun; 20 - Trabzon; 21 - Khotz (=Çosandere), Trabzon; 22 - Rize; 23 - Kabaca, 8 km south of Murgul, Artvin, ca 800 m a.s.l.; 24 - Damar, 4 km south east of Murgul, Artvin, ca $1,000 \mathrm{~m}$ a.s.l.; $25-4 \mathrm{~km}$ south-east of Güzyurdu, Gümüşhane, ca 2,300 m a.s.l.; 26 - 3 km south-east Derebük, Erzincan; 27 - Island of Gökçeada; 28 - Behran, Ayvacık, Çanakkale; 29 - İzmir; 30 - 4 km south of Akçaköy, Aydın, 190 m a.s.l.; 31 - Göksuyu river, 10 km south-east of Kütahya; 32 - Datça, Marmaris, Muğla; 33-20 km north-west of Fethiye, Muğla; 34 - Olu Deniz (Ölüdeniz), Fethiye, Muğla; 35 - İkizce, Kramık, Antalya, ca 1,000 m a.s.l.; 36 - Ylanli, 11 km south-east of Eğirdir, Isparta; 37-20-25 km south and south-east of Eğirdir, Isparta; 38 - Pozantı, Adana; 39 - Çukurova University Campus, Adana, 100-150 m a.s.l.; 40 - Yukarı Karafakılı, Hatay, ca 600 m a.s.l.; $\mathbf{4 1}$ - Belen Geçidi, Hatay; $\mathbf{4 2}$ - Bedirge, Amik Gölü, Antalya. Corresponding references: Zima \& Macholán (1995): 3, 5, 7. Filippucci et al. (1996): 4, 8b, 10a, 11, $13,14,31,32,33,34,36,37$. Özkan \& Kryštufek (1999): 27. Macholán et al. (2001): 24, 25. Frynta et al. (2001): 23. Michaux et al. (2004): 22. Kryštufek \& Vohralík (2008): 8a, 9, 10b, 12, 17, 26, 28, 30, 35, 39, 40. ZFMK: 19, 20, 38, 41, 42. NMNH: 15, 16, 18, 21, 29. Our own material: 1, 2, 6.
in Bulgaria (Peshev et al., 2004). Records from the rest of the Balkans are scarce (Kowalski, 2001), and Santel \& Koenigswald (1998) did not identify A. flavicollis in the Middle Pleistocene material from the Yarımburgaz cave on the Istranca Mts. In line with phylogeographic evidence, the Balkans and the Italian Peninsula provided the major glacial refu-
gium for the yellow-necked field mouse (Michaux et al., 2005).

## Habitat

The yellow-necked mouse is mainly associated with forests and bushy vegetation. It depends more heavily on a three dimensional habitat than A. sylvaticus
or A. witherbyi. In Turkish Thrace, A. flavicollis is the dominant small mammal in all habitats, except open fields and other disturbed places which provide little cover. The yellow-necked mouse is competitively inferior to A. sylvaticus only in places under herbaceous vegetation without bushes or trees. On the Istranca Mts., we collected the yellow-necked mice with ease in every place with reasonable shelter, but tall closed canopy deciduous forest was the principal habitat. In Thracian lowlands, A. flavicollis is abundant in dense vegetation of low trees and bushes with diverse species composition.

Habitats populated by the yellow-necked field mouse in Anatolia are essentially the same as in Thrace, i.e. bushes on pastures and various types of forests. Forests are a typical habitat in the Black Sea Mts. while shrubby cover is clearly preferred in the zone of the Mediterranean woodlands (Kryštufek


Figure 65. Habitat of Apodemus flavicollis in Turkey.
a - 5 km north of Safranbolu, Zonguldak, ca 500 m a.s.l;
b - Edirne. Photo: B. Kryštufek.
\& Vohralík, 2008). In the north, mesic deciduous and mixed forests of oaks (Quercus), beech (Fagus), willow (Salix), plane trees (Platanus), walnut tress (Juglans), hornbeam (Ostrya) and alder (Alnus), frequently with rich undergrowth of rhododendron, are preferred over coniferous stands of spruce (Picea orientalis) and fir (Abies spp.). In the mountains of north-eastern Anatolia, we also collected yellownecked field mice among rocks and under low juniper shrubs on short-grass alpine pastures. Woody evergreen vegetation of Olea europaea, Quercus coccifera, Erica arborea, and of Arbutus sp. is the principal habitat on the island of Gökçeada (Özkan \& Kryštufek, 1999).

Altitude. From sea level (Marmara, Black Sea coast, vicinity of Adana) and up to $2,300 \mathrm{~m}$ a.s.l. in the eastern Black Sea Mts. Highest records on the Taurus Mts. are at $1,000 \mathrm{~m}$ and in the Marmara at $1,500 \mathrm{~m}$ of elevation. In Turkish Thrace from the lowlands to the top of the Istranca Mts. at about 1,000 m; up to 2,600 m in Bulgaria (Peshev et al., 2004).

Associates. Because of its wide habitat selection, the yellow-necked field mouse was collected along with a number of small mammal species. In Thrace these included: Apodemus agrarius, Microtus subterraneus, Sorex araneus, S. minutus, and Neomys anomalus on Istranca Mts., and Apodemus sylvaticus, Mus macedonicus, Microtus levis, Myomimus roachi, Dryomys nitedula, Crocidura leucodon and C. suaveolens in the lowlands. List of associates is even longer in Anatolia, and includes all Apodemus species living there (A. witherbyi, A. uralensis, A. mystacinus), Mus macedonicus, a number of voles (Myodes glareolus, Arvicola amphibius, Microtus subterraneus, M. daghestanicus, M. majori, M. arvalis, M. levis, Chionomys nivalis), and various shrews (Sorex satunini, Neomys teres, N. anomalus, Crocidura leucodon, C. suaveolens). On the Island of Gökçeada, the yellow necked field mouse co-occurs with Mus macedonicus, rats (Rattus rattus and $R$. norvegicus), Crocidura suaveolens and C. leucodon (Özkan, 1999a; Özkan \& Kryštufek, 1999).

The yellow-necked field mouse is sympatric with all the remaining five Apodemus species occurring in Turkey. For the relations with A. sylvaticus in Thrace, see under that species. In Anatolia, A. flavicollis is syntopic with $A$. witherbyi throughout its range and with $A$. uralensis in the Black Sea Mts.

Sympatry with A. mystacinus is rare (Kryštufek \& Vohralík, 2008). Exceptionally do all four Anatolian Apodemus co-occur in the deciduous lowland forests of the western Black Sea Mts. (e.g. near Safranbolu).

Density. The yellow-necked field mouse was by far the most abundant species in small mammal assemblages in deciduous forests on the Istranca Mts. comprising $75 \%$ of all small mammals collected; locally, its proportion approached $90 \%$. Its relative abundance was lower in stands of tall bushes and trees along streams in Thracian lowlands.

In Anatolia, the yellow-necked field mouse is very exceptionally as abundant as in Thrace. Throughout the Taurus region, A. witherbyi was more abundant and widespread and was outnumbered by A. flavicollis only around Adana and in Hatay. On the campus of the Çukurova University, Adana, about $60 \%$ of small mammals collected in May 1993 were yellownecked field mice. In the Black Sea Mts., A. flavicollis was less abundant than $A$. witherbyi or $A$. uralensis, and became increasingly rare in a west to east direction. This trend is evident from a number of specimens captured and number of localities where A. flavicollis was present. The yellow-necked field mouse was found to be common on the Island of Gökçeada, where it accounted for about $40 \%$ of all small mammals trapped (Özkan \& Kryštufek, 1999).

## Biology

Biology of the yellow-necked field mouse was intensively studied in deciduous forests of central Europe (reviewed by Niethammer, 1978b). Mode of life in Turkey can only be deduced from field notes and specimen tags.

Activity is nocturnal.
Burrows are usually located under trees and shrubs. In Bulgaria, tunnels go up to 1.5 m deep; the system includes a nest chamber (lined with dry vegetable material) and a nest chamber (Peshev et al., 2004). Burrowing is reported also from Levant (Qumsiyeh, 1996).

Reproduction evidently occurs throughout the vegetation period; on the Istranca Mts. we collected pregnant females as late as mid-October. Along the Aegean coast, females were pregnant also during dry and hot summer. Number of embryos varies from three to eight. There are slight differences in count of
embryos between the regions, with Thrace having a higher mean (4.8; range $=4-8 ; \mathrm{N}=17$ ) than Anatolia (4.3; range $=3-6 ; \mathrm{N}=10$ ). In Bulgaria, reproductive season lasts from March till end of October. Females deliver 3-4 litters (up to 2 in the mountains), each with 3-7 embryos; gestation lasts $23-26$ days ( $\mathrm{Pe}-$ shev et al., 2004).

Food. In Bulgaria, main diet is comprised of fruits, nuts and acorns of various trees and shrubs (Crategus, Tilia, Fagus, Quercus, Coryllus), grass seeds, and more rarely green parts of vegetation (Peshev et al., 2004). For Levant, Qumsiyeh (1996) reports diet of acorns, seeds, succulent grasses, buds, insect larvae, and other invertebrates.

Predation. For Thrace see comments under $A$. sylvaticus. Apodemus mice (reported as A. sylvaticus) were found in pellets of various owls (Bubo bubo, Strix aluco, Tyto alba) from within the Anatolian range of the yellow-necked field mouse (Brinkmann, 1990; Obuch, 1994).

## Steppe field mouse - Apodemus witherbyi

Mus witherbyi Thomas, 1902. Type loc.: Sheoul (=Shul), Fars, Iran (Lay, 1967).
Mus sylvaticus tauricus Barrett-Hamilton, 1900. Type loc.: Zebil, Bulgar Dagh (= Bolkar Dağları)
Apodemus sylvaticus iconicus Heptner, 1948. New name for Mus sylvaticus tauricus Barrett-Hamilton, 1900.
Apodemus sylvaticus kilikiae Kretzoi, 1964. New name for Mus sylvaticus tauricus Barrett-Hamilton, 1900.

## Taxonomy

Taxonomy of the steppe field mouse has a long and confusing history, which was further complicated by independent research performed in Turkey, Iran and Levant on the one hand, and in the Caucasus, Ukraine and Russia on the other. There was hardly any exchange of material and ideas between the two sides, consequently different names were used for same taxonomic entities by the two groups of researchers. This parallelism is best demonstrated by an independent description of the steppe mouse by the two groups in the same year: as A. falzfeini in Ukraine (Mezhzherin \& Zagorodnyuk, 1989) and as $A$.
hermonensis in Israel (Filippucci et al., 1989). While the former name was synonymised with A. fulvipectus Ognev, 1924, shortly afterwards (Musser \& Carleton, 1993), the latter one continued to be in use until quite recently. It has been known for more than a decade that $A$. hermonensis is very close to $A$. fulvipectus (Filippucci et al., 1996) and these two names are now synonymised (Musser \& Carleton, 2005).

Given that A. fulvipectus and A. hermonensis are predated by several names, nomenclature was confusing. Mus sylvaticus tauricus Barrett-Hamilton, 1900, is doubtlessly identical with $A$. hermonensis, however, it is predated by tauricus Pallas, 1811 (see account on Taxonomy under A. flavicollis). Two names (nomina nova) were proposed to replace tauricus Barret-Hamilton (see synonymy above). In accordance with the Article 60.2 of the ICZN (1999), the oldest of these names is the valid name of the taxon with its own authorship and date. Following the law of priority, Apodemus iconicus Heptner, 1948, is an older name available for $A$. hermonensis (Kryštufek, 2002). This nomenclatural change was ignored and $A$. hermonensis was favoured instead (Filippucci et al., 2002; Bellinvia, 2004); very few authors accepted the priority of A. iconicus (Çolak, 2003; Shehab, 2004; Yiğit et al., 2006c). Of course, the usage of a particular Linnean binominal is not a matter of personal preference, but a consequence of the nomenclatorial history of the name and norms accepted by the scientific community and available through ICZN.

Musser \& Carleton (2005) synonymised all the above names with $A$. witherbyi. The type of Mus witherbyi is very similar to $A$. iconicus in all aspects


Figure 66. Steppe field mouse Apodemus witherbyi from Bodrum, Turkey. Photo: E. Grimmberger.
of dental morphology, but has shorter maxillary row and longer bullae (Kryštufek, 2002). Musser \& Carleton (2005) demonstrated that the holotype of witherbyi is at one edge of the variation range in $A$. hermonensis from Iran, and evidently conspecific with it. This is in agreement with ellectrophoretic evidence from the region (Macholán et al., 2001). In the past, witherbyi was synonymised with arianus, which was considered to be either a valid subspecies of A. sylvaticus (Ellerman, 1941; Ellerman \& Morrisson-Scott, 1951; Mendelssohn \& YomTov, 1999) or a species in its own right (Musser \& Carleton, 1993). As previously explained, Mus arianus Blanford, 1881, is actually a junior synonym of A. flavicollis (Kryštufek, 2002).

## Description

External characters. Medium sized and slender field mouse, closely resembling the Anatolian $A$. flavicollis. Ears are large and whiskers long (26-33 mm ); eye is large (diameter 4.1-4.9 mm; mean $=4.6$ $\mathrm{mm} ; \mathrm{N}=6$ ). Tail on average slightly longer than head and body (103 \%; range = 83-121 \%; $\mathrm{N}=191$ ); terminal pencil is short. There are 29-34 caudal vertebrae (median $=32, \mathrm{~N}=91$; Štĕpánková \& Vohralík, 2008). Pelage is soft, summer hairs on midback up to 7 mm long (sparse long hairs up to 9 mm ), approximately 4 mm long on the belly.

Colour (Fig. 67). Upper side is generally paler than in A. flavicollis and A. uralensis. In Central Anatolia, the back is light yellowish-brown in the palest specimens, wood-brown in the darkest. Snout and shoulder are buff in some animals. Subadults from the Taurus Mts. are occasionally as grey as $A$. mystacinus. Belly is white (except in north-eastern Anatolia; see below under "Variation"), pure white in some individuals, clouded with grey undercolour in others. Grey wash is in general less pronounced than in A. flavicollis. Yellow wash on the belly is exceptional.. Demarcation line along flanks is clear but less sharp in the pale form, a consequence of its yellowish flanks. Feet are frequently pale, nearly whitish, but tend to be greyish in dark individuals. Tail is fairly clearly bi-coloured.

Chest between fore legs usually has a buff median area. Narrow spot is a norm, found in approximately $75 \%$ of Anatolian animals. In the remaining quarter of specimens, the spot is reduced to a few pale yel-


Figure 67. Skin of Apodemus witherbyi in dorsal and ventral view. Based on an adult male from Abant Gölü, district Bolu. Photo: C. Mlinar.
low hairs or is entirely absent. The spot is $5-20 \mathrm{~mm}$ long and $1.5-6 \mathrm{~mm}$ wide; when long, then expands anteriorly and tapers backward towards a belly. Spot is frequently pale and indistinct, contrary to clearly defined patch in A. flavicollis. Very exceptionally, the spot expands laterally but never forms a collar. In a population from the Island of Bozcaada, the incidence of spot was $71.3 \%$, while the throat was blank in $28.7 \%$ of individuals ( $\mathrm{N}=143$; Özkan, 1995).

Nipples as in A. sylvaticus: two pairs of inguinal and one pair of pectoral, respectively (six nipples in total).

Penis. The glans penis resembles condition in $A$. sylvaticus. The proximal section is longer than the distal one, the ventral groove is long and extends posteriorly onto the proximal glans, and the dorsal ridge is restricted to the proximal part of the glans. Spines are present throughout the surface (Çolak, 2003). In our material from Anatolia, the glans was 4.47-5.00 mm long and $2.11-2.37 \mathrm{~mm}$ wide; its proximal section was $2.21-2.74 \mathrm{~mm}$ long and $1.84-2.05 \mathrm{~mm}$ wide in the midsection. The proximal section of the baculum is 3.74 mm long and 1.74 mm wide at the basal expansion (Çolak, 2003).

Skull (Fig. 68). Except for its smaller size, the skull resembles condition in A. flavicollis. Zygomatic region is as wide relative to condylobasal length (mean $=55.1 \%$; range $=51.5-59.6 \%$ ); bullae, however, are clearly shorter than in A. flavicollis and the difference between the two species is already evident in juveniles. Incisive foramen is slightly shorter relative to condylobasal length than in A. sylvaticus (16.9-22.1 \%; mean = $20.0 \%$ ); its posterior border exceeds the line of the anterior alveoli of $1^{\text {st }}$ molars in $16 \%$ of specimens and does not reach this line in 50 $\%$ of them ( $\mathrm{N}=246$ ). Interpterygoid space is wide; posterior hard palate margin is normally straight, with a medial protrusion.

Tеетн (Fig. 69). Molar row is of approximately same length as in A. flavicollis, and distinctly longer than in A. uralensis. Dentition, although essentially as in A. sylvaticus, differs in some important and easily recognisable aspects. Accessory tubercle t1bis (Fig. 70a) is present in approximately one third of specimens (Filippucci et al., 1996, report this frequency as $68 \%$ ). Stephanodonty was a frequent character state in our $A$. witherbyi material, but it is not a diagnostic character. In the $1^{\text {st }}$ upper molar cusps t1 and $t 5$ are connected with a ridge (Fig. 70a) in 82\% of specimens, but connection between t 3 and t 5 (Fig. 70b) is much more rare (approximately $13 \%$ of animals). Cusp t1 is frequently isolated from t2 ( $64 \%$ of specimens; Fig. 70c). Isolation of t 1 is not as categorical as in A. uralensis since it is obscured by the presence of t1bis in $A$. witherbyi. Tubercle $t 7$ is a cusplike in majority of specimens ( $82 \%$ ), and the accessory postero-labial cusp t12 is clearly evident in $64 \%$ of specimens (Fig. 70a, c). On the $2^{\text {nd }}$ upper molar, t9 is invariably cusplike, and a ridgelike t7 was found only in $6 \%$ of animals. Postero-lingual accessory cusp t12


Figure 68. Skull and mandible of Apodemus witherbyi, based on an adult female from 7 km north-west of Niğde.
Scale bar $=5 \mathrm{~mm}$.
is fairly rare (13\% of specimens; Fig. 71a). Filippucci et al. (1996) report cusp t1 to be connected with $t 5$ in majority of specimens. In one case we observed cusps t 1 and t 3 to fuse anterior to t 5 (Fig. 71c). The $3{ }^{\text {rd }}$ upper molar normally has a deep labial fold.

Number of roots is same as in A. sylvaticus.

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 224 | 97.3 | $86-109$ |
| Tail | 196 | 99.5 | $82-118$ |
| Hind foot | 229 | 21.7 | $19.7-25.0$ |
| Ear | 223 | 15.4 | $13.0-17.0$ |
| Weight | 219 | 24.0 | $15-37$ |
| Condylobasal length | 179 | 23.2 | $21.4-25.3$ |
| Zygomatic breadth | 168 | 12.8 | $11.6-14.1$ |
| Maxillary tooth-row (alveoli) | 21 | 4.0 | $3.8-4.4$ |
| Maxillary tooth-row (crown) | 332 | 3.8 | $3.4-4.1$ |
| Bulla length | 318 | 4.4 | $4.0-4.8$ |

Table 13. External and cranial dimensions of Apodemus witherbyi from Anatolia. Based on our own material.

Dimensions are given in Table 13. Males from Central Anatolia were on average larger but the dif-
ference between sexes was statistically significant only for condylobasal length (mean $=23.6 \mathrm{~mm}$ in males, 22.8 mm in females) and zygomatic breadth (mean $=13.0 \mathrm{~mm}$ in males, 12.7 mm in females).

Chromosomes. The karyotype of 48 acrocentric chromosomes ( $2 \mathrm{~N}=48, \mathrm{NF}_{\mathrm{a}}=46$ ) of decreasing size was reported from several localities in north-western Anatolia (Macholán \& Zima, 1997; Çolak, 2003; Yiğit et al., 2006a), Iran (Yiğit et al., 2006a) and Israel (Zima \& Macholán, 1995). The X chromosome is a large acrocentric, and the Y chromosome is a small acrocentric (Çolak, 2003).

## Variation

In our material, the external characters were subjected more to geographic variation than cranial and dental measurements. The heaviest animals were from Eastern Anatolia (mean body mass $=26.8 \mathrm{~g}$; range $=20-37 \mathrm{~g} ; \mathrm{N}=32$ ) and the lightest were from the Aegean coast (mean $=22.0 \mathrm{~g}$; range $=19.0-25.5$; $\mathrm{N}=16$ ). Populations from the eastern Black Sea Mts. showed the shortest tail relative to head and body length (mean $=98.6 \%$; range $=82.5-108.1 \%$; N


Figure 69. Upper (a) and lower molars (b) in Apodemus witherbyi from Balkusan, district Konya. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
$=20)$. Hind foot was the shortest in the Taurus Mts. (mean $=21.1 \mathrm{~mm}$; range $=19.7-22.8 \mathrm{~mm} ; \mathrm{N}=63$ ), and the longest on the Aegean coast (mean $=22.5$; range $=19.8-24.4 \mathrm{~mm} ; \mathrm{N}=15$ ). Aegean material had the shortest ear length (mean $=14.8 \mathrm{~mm}$; range $=$ $13.4-15.7 \mathrm{~mm} ; \mathrm{N}=15$ ). Therefore, the most unique was a sample from the Aegean coast which was characterised by a slim body, long hind foot and short ear. No overall trend was evident across Anatolia, however.

Specimens from mesic mountains along the Black Sea coast tended to be darker, with wood-brown back and belly clouded by the slate grey undercolour. As such, $A$. witherbyi was externally not always distinguishable from sympatric A. uralensis. Dark specimens with grey belly were the most common in the mountains around Artvin. The pale form, with a pale yellow back, pure white belly and a narrow or ill de-


Figure 70. Variation of $1^{\text {st }}$ upper molar in Apodemus witherbyi from Anatolia. a, c - Balkusan, district Konya; b-3 km west of Handere, district Kars. Note the accessory tubercle t 1 bis between t 1 and t 2 (shown by arrow). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.


Figure 71. Variation of $2^{\text {nd }}$ upper molar in Apodemus witherbyi from Anatolia. a - Cığlıkara, district Antalya; b - Gücük near Sarkışla, district Sivas; c - 10 km north-east of Bardakçi, Manisa. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
fined spot, dominated arid habitats of central Anatolia, along the Aegean coast and the Taurus Mts.

Genetic evidence, based on protein electrophoresis, did not uncover significant phylogeographic structuring of $A$. witherbyi in Anatolia and Iran. Genetic distances correlated only weakly with the geographical distance (Macholán et al., 2001; Filippucci et al., 2002).

## Distribution

Retarded recognition of the steppe field mouse is in sharp contrast with its broad geographic range. It populates eastern Europe (to the east of River Dnepr), the Caucasus, Asia Minor, eastern Mediterranean coasts south to Israel and Jordan; northern and central Iran, southern Turkmenistan, and western and central Pakistan (Musser \& Carleton, 2005). Along with A. mystacinus, the steppe field mouse is the most wide-
ly distributed Apodemus species in Anatolia, but it is absent from Thrace. The range border is loosely defined in south-eastern Anatolia and no localities are known to the south of Şanlıurfa - Lake Van - Hakkari line (Kryštufek \& Vohralík, 2008); Yiğit et al. (2006c) mapped its occurrence throughout Anatolia. The steppe field mouse also occupies at least three islands offshore of western Anatolia: Bozcaada (Özkan \& Kryštufek, 1999), Rhodes (Kryštufek \& Mozetič Francky, 2005), and Kos (our own data). We expect that re-examination of the material from Samos (Laar \& Daan, 1967), which was reported as A. sylvaticus, will also reveal $A$. witherbyi.

Palaeontology. See comments under A. sylvaticus and A. flavicollis. Papers on fossil evidence mainly predate the recognition of $A$. witherbyi as a species distinct from A. sylvaticus and A. flavicollis. Nevertheless, some published data suggest occurrence of $A$. witherbyi during the Middle Pleistocene in the Eastern Aegean islands (Chios; Storch, 1975), in central Anatolia (Emirkaya-2; Montuire et al., 1994), in the Taurus Mts (Antalya; Storch, 1988), and in Israel (Tchernov, 1979).

## Habitat

The steppe field mouse is a eurytopic species and populates a broad variety of habitats that provide at least some shelter. We collected specimens in open habitats with scattered bushes (Fig. 73c) or with rocks, among brushes, and in various types of forests, from low and degraded ones to tall closed-canopy stands (Fig. 73b). In Artemisia and Pistacia-Amygdalus steppe habitats on the highlands of inner and eastern Anatolia the species was captured below bushes and in tall herbaceous vegetation, along irrigation ditches, in poplar stands and at rocky walls. Under these arid conditions, the animal preferred the more mesic environment of lake shores, along streams and around cultivated areas. On the overgrazed mountain pastures, $A$. witherbyi found adequate shelter in strips of tall herbaceous plants along streams (Fig. 73d) or under rocky outcrops. On the Taurus Mts., the steppe field mouse was common in open habitats with scattered bushes, along hedgerows, and among rocks. In Çığlıkara, A. witherbyi was abundant in mature cedar (Cedrus lebanoni) forests (Fig. 73a), but in the rest of the Taurus Mts. it was seemingly replaced by A. flavicollis in tall oak stands and restricted mainly


Figure 72. Distribution of Apodemus witherbyi in Turkey and adjacent regions. For further details on records see Appendix 2.
to shrubs. Habitats along the Aegean coast involve rocky places on pastures and degraded broad-leaved forests.

In the Island of Bozcaada, the steppe field mouse is common in degraded evergreen shrubby vegetation of Olea europaea, Quercus coccifera, Erica arborea, and Arbutus sp. In the Islands of Rhodes and Kos (Aegean Greece) we collected animals only on the edges of evergreen shrubs along fields.

From the southern margin of the species' range in Jordan, Amr (2000) reports woodland dominated by oak with Arbutus sp. and Ceratonia sp. as the only habitat utilised by $A$. witherbyi.

Altitude. From the sea level up to $2,600 \mathrm{~m}$ a.s.l. ( $2,800 \mathrm{~m}$; Yiğit et al., 2006c) in the eastern Black Sea Mts. Highest record in the western Black Sea

Mts. is at $1,100 \mathrm{~m}$, in Marmara at $1,700 \mathrm{~m}$, in the Taurus Mts. at $1,850 \mathrm{~m}$, and in Central Anatolia at $1,850 \mathrm{~m}$ of elevation. With the exception of the western coast, $A$. witherbyi is typically rare close to sea level (Kryštufek \& Vohralík, 2008).

Associates. List of species, obtained in trap lines along with $A$. witherbyi, is a long one. The steppe field mouse is frequently syntopic with at least one of the remaining three Anatolian Apodemus mice. All four Anatolian Apodemus were found in sympatry only in deciduous lowland forests near Safranbolu (western Black Sea Mts.; Fig. 65a). In the Black Sea Mts. and in Marmara, the steppe mouse is usually outnumbered by $A$. uralensis. In central Anatolia, $A$. mystacinus is the only congeneric species that is locally sympatric with $A$. witherbyi. The proportion of these two field


Figure 73. Habitat of Apodemus witherbyi in Turkey. a, b - Cığlıkara, district Antalya; c - Çarrköy, district Zonguldak; d-4 km east of Şerefiye, district Sivas, 1,620 m a.s.l. Photo: A. Kryštufek (a, b); B. Kryštufek (c, d).
mice depends on the rockiness of the habitat, with $A$. mystacinus favouring more rocks. Of 13 local samples from the Taurus Mts., A. witherbyi was the only species of the Sylvaemus-group in nine samples, syntopic with A. flavicollis in three samples, and absent from one sample. Around Adana and in Hatay, A. witherbyi is by far less abundant than A. flavicollis.

List of other associates includes Mus macedonicus, a number of voles (Myodes glareolus, Arvicola amphibius, Microtus subterraneus, M. daghestanicus, M. majori, M. arvalis, M. levis, M. hartingi, M. irani, Chionomys nivalis, C. gud, C. roberti), two hamsters (Cricetulus migratorius and Mesocricetus brandti), a jird (Meriones tristrami), a forest dormouse (Dryomys nitedula) and various shrews (Sorex satunini, S. volnuchini, S. raddei, Neomys teres, $N$. anomalus, Crocidura leucodon, C. suaveolens). In open habitats of Central Anatolia and in alpine pastures in the eastern Black Sea Mts., voles were much more abundant than $A$. witherbyi.

On the Island of Bozcaada, the steppe field mouse co-occurs with Mus domesticus and Rattus rattus (Özkan, 1999a; Özkan \& Kryštufek, 1999). On the Greek islands of Rhodes and Kos, we never collected $A$. witherbyi in the same trap line with $A$. mystacinus, which was the only Apodemus species inhabiting rocky places and cypress forests. Habitats occupied by $A$. witherbyi were invariably infested by

Rattus rattus on both islands.
Density. The steppe field mouse is frequently abundant in small mammal assemblages. In bushy habitats of central and eastern Anatolia and in the Taurus Mts., between one half and three quarters of small mammals we captured were $A$. witherbyi; the proportion was much lower in the Black Sea Mts. (mainly $<10 \%)$. The steppe field mouse is the most abundant small mammal on the island Bozcaada (76 \% of small mammals trapped; Özkan \& Kryštufek, 1999).

## Biology

Activity is nocturnal.
Reproduction. Mean litter size, as estimated from embryos and placental scar counts, is on average 4.5 (range $=1-7 ; \mathrm{N}=37$ ). In central Anatolia, reproductive activity was recorded even during the hottest and driest months of the year.

Food as for $A$. sylvaticus.
Predation. Apodemus mice (reported as A. sylvaticus) were found in pellets of various owls (Bubo bubo, Strix aluco, Tyto alba) from within the Anatolian range of the steppe field mouse (Brinkmann, 1990; Obuch, 1994). Reports by Obuch (1994) from eastern Anatolia (for Bubo bubo and Strix aluco) can be safely ascribed to $A$. witherbyi. The steppe field mouse is also reported in the owl pellets from Syria (Shehab, 2004).


Figure 74. Herb field mouse, Apodemus uralensis. Photo: J. Vogeltanz.

## Ural field mouse - Apodemus uralensis

Mus sylvaticus var. uralensis Pallas, 1811. Type loc.: Troick Region, Čeljabinsk District, Southern Ural Mts., Russia.

## Taxonomy

The Ural field mouse was first recognised as a species on its own right by Kratochvíl \& Rosický (1952) and described as A. microps (type loc.: Šaca, eastern Slovakia; Vohralík, 2002). Tvrtković \& Džukić (1977) were probably the first who suggested that A. microps might be identical to uralensis of Pallas; their opinion, however, has been entirely ignored in subsequent papers. Apodemus uralensis was first established for northern Anatolia (as A. microps) by Steiner (1978a) who successfully crossbred specimens from the district of Rize with the Austrian A. microps over six generations. Steiner's results, however, were also uniformly ignored by all later students of Apodemus in Anatolia and the Caucasus.

Species boundaries of $A$. uralensis are not resolved; cf. Musser \& Carleton (2005) for a thorough discussion.

## Description

External characters (Fig. 74). The smallest Apodemus species in Anatolia, dimensions however overlap with $A$. witherbyi and partly also with A. flavicollis. Tail is relatively the shortest among Anatolian fieldmice, albeit still of same average length as head and body (85-112 \%; mean = 100 \%); there are 29-33 caudal vertebrae in specimens from Anatolia (median $=31, \mathrm{~N}=59$; Štěpánková \& Vohralík, 2008). Ears are moderately long, and eyes fairly small (diameter about 4 mm ). Vibrissae up to 28 mm long; hair soft, up to 6-6.6 mm long in summer pelage (on mid-back); ventral hairs shorter (up to 4 mm ).

Colour (Fig. 75). Upper side dark wood-brown, rarely as russet as in A. flavicollis. Darker along the spine and between ears and eyes; flanks are paler than back, washed with buff or grey. Belly is mainly clouded with slate grey undercolour, more rarely white (see also below under Variation); buff wash is not rare. Feet are brown-grey, tail is clearly bi-coloured.

Chest spot between fore legs found in about 20\% of specimens, therefore the throat is blank and of
same colour as belly in majority of specimens. Incidence of a spot is slightly higher in the eastern Black Sea Mts. than in the western Black Sea Mts. and Marmara. Spot, when present, is small and narrow, frequently reduced to a few hairs.

Nipples as in A. sylvaticus: two pairs of inguinal and one pair of pectoral, respectively (six nipples in total).

Penis. The glans penis resembles condition in $A$. sylvaticus. Spines are present all over the glans; they are smaller on the distal section. In our material from


Figure 75. Skin of Apodemus uralensis in dorsal and ventral view. Based on an adult female from 5 km west of Bağdaşan, district Kars. Photo: C. Mlinar.

Anatolia, the glans is 4.37-4.68 mm long and 2.372.58 mm wide; its proximal section measures 2.372.63 mm in length; width at the midsection is $1.95-$ 2.11 mm . For drawing of a specimen from Anatolia see Yiğit et al. (2006c: Fig. 38E).

Skull (Fig. 76) as in A. witherbyi, but rostrum tends to be narrower and longer; zygomatic width relative to condylobasal length $=50.0-60.0 \%$. Bullae are absolutely and relatively of same size (17.7$21.6 \%$ of condylobasal length) as in A. witherbyi; they are categorically shorter than in Anatolian A. flavicollis and difference does not depend on age. Incisive foramen short (19.0-22.1\% of condylobasal length); its posterior border only exceptionally exceeds line of the anterior alveoli of $1^{\text {st }}$ molar ( $2 \%$ of specimens), and does not reach it in $79 \%$ of specimens ( $\mathrm{N}=301$ ).

Teeth (Fig. 77). Molar row is shorter than in $A$. witherbyi and A. flavicollis, and $3{ }^{\text {rd }}$ upper molar is particularly reduced in size. First upper molar lacks any traces of stephanodonty (cusp t3 occasionally has a spur which does not reach t5) and does not develop the accessory antero-lingual cusp t1bis. Tubercle
t7 is mainly narrow, rarely clearly ridgelike, but only occasionally in the shape of a rounded cusp. Cusp t1 is clearly isolated from t2 in young animals; isolation becomes obscured with progressive tooth-wear. Presence of the accessory postero-labial cusp t12 is exceptional (Fig. 78 a); t12 occurs very rarely also on $2^{\text {nd }}$ upper molar (Fig. 78 b).

|  | N | mean | $\mathrm{min}-\mathrm{max}$ |
| :--- | :---: | :---: | :---: |
| Head and body | 171 | 94.3 | $79-107$ |
| Tail | 136 | 93.9 | $81-111$ |
| Hind foot | 175 | 21.2 | $18.9-23.7$ |
| Ear | 170 | 15.5 | $13.0-21.6$ |
| Weight | 171 | 20.2 | $13.3-31.5$ |
| Condylobasal length | 164 | 22.4 | $21.0-24.0$ |
| Zygomatic breadth | 152 | 12.3 | $11.3-13.7$ |
| Maxillary tooth-row (alveoli) | 21 | 3.7 | $3.5-4.0$ |
| Maxillary tooth-row (crown) | 251 | 3.5 | $3.1-3.8$ |
| Bulla length | 231 | 4.3 | $4.0-4.6$ |

Table 14. External and cranial dimensions of Apodemus uralensis from Anatolia. Pooled are all geographic samples, except those from the western Black Sea Mts. (see Table 15). Based on our own material.


Figure 76. Skull and mandible of Apodemus uralensis, based on an adult male from Hanyatak köyü, Kapiorman Dağları, district Sakarya. Scale bar $=5 \mathrm{~mm}$.


Figure 77. Upper (a) and lower molars (b) in Apodemus uralensis from Sakarya (same specimen as in Fig. 76). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.


Figure 78. Postero-labial cusp t12 (shown by arrow) on $1^{\text {st }}$ upper molar (a) and $2^{\text {nd }}$ upper molar (b) in Apodemus uralensis from Turkey. a - Yalnizçam Geçidi, district Artvin; b - Hanyatak köyü, Kapıorman Dağları, district Sakarya. Lingual side is to the left, anterior is at the top.
Scale bar $=0.5 \mathrm{~mm}$.

Number of roots is same as in A. sylvaticus. Deviations are rare in central European populations (upper molars only): 3 and 5 on $1^{\text {st }}$ and $2^{\text {nd }}$ molar, 1,2 or 4 on $3^{\text {rd }}$ molar (Zejda, 1965).

Dimensions are shown in Table 14. In our material, males were the larger sex in majority of dimensions, significant differences, however, emerged only in a sample from the western Black Sea Mts. (Sakarya and the area of Zonguldak; Table 15).

Chromosomes. The karyotype consists of 48 acrocentric chromosomes $\left(2 \mathrm{~N}=48, \mathrm{NF}_{\mathrm{a}}=46\right)$ of de-

|  | Males |  |  | Females |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |
| Head and body* | 28 | 94.8 | $86-103$ | 13 | 91.5 | $88-103$ |
| Tail | 23 | 94.4 | $80-107$ | 12 | 91.3 | $79-100$ |
| Hind foot | 28 | 21.6 | $19.9-24.2$ | 12 | 21.1 | $20.1-22.5$ |
| Ear | 28 | 15.1 | $13.8-16.3$ | 13 | 14.9 | $14.0-16.8$ |
| Weight* | 21 | 21.0 | $16.5-26$ | 10 | 17.2 | $15.5-20.5$ |
| Condylobasal length* | 29 | 22.7 | $21.1-24.2$ | 13 | 22.2 | $21.2-23.3$ |
| Zygomatic breadth* | 28 | 12.7 | $11.9-13.5$ | 13 | 12.4 | $11.6-12.8$ |
| Maxillary tooth-row (alveoli) | 17 | 3.8 | $3.6-4.0$ | 7 | 3.9 | $3.6-4.1$ |
| Maxillary tooth-row (crown) | 30 | 3.6 | $3.4-3.7$ | 13 | 3.5 | $3.2-3.7$ |
| Bulla length | 29 | 4.4 | $4.2-4.7$ | 13 | 4.5 | $4.2-4.6$ |

Table 15. External and cranial dimensions of Apodemus uralensis from the western Black Sea Mts. (areas of Zonguldak and Sakarya) according to sex. Asterisks indicate parameters that show significant secondary sexual dimorphism (at p<0.05). Based on our own material.
creasing size, and was reported from several localities in north-western Anatolia (Macholán \& Zima, 1997) and from central Europe (Zima \& Macholán, 1995).

## Variation

There seems to be west to east cline along the Black Sea Mts. in tail length, zygomatic breadth and bulla length. Mice from the east are relatively long-tailed, have a narrower skull and shorter bulla. Ventral colouration also varies: grey-bellied animals predominate in the west (approximately $80 \%$ of specimens), where a clear white ventral side is exceptional (less than $5 \%$ of individuals); in the east, $20 \%$ of animals have a pure white belly, $68 \%$ are clearly grey, and
the remaining are intermediate. Interpterygoid space tends to be narrow in the west, but it is frequently wider in the east (Fig. 47). The labial fold between cusps $t 5$ and $t 6$ on $3^{\text {rd }}$ upper molar is absent in majority of western populations but is observed in more than one half of specimens from the eastern Black Sea Mts.

Level of interpopulation genetic variation is low (Macholán et al., 2001), and allozyme variation does not suggest geographic structuring in Anatolia (Filippucci et al., 2002).

Herb field mice show higher counts for tail vertebrae (29-33) in Anatolia than their conspecifics from Central Europe (28-31; Štĕpánková \& Vohralík, 2008).


Figure 79. Distribution of Apodemus uralensis in Turkey and adjacent regions. Records: 1 - Ulu Dağ, Bursa, 850-2,250 m a.s.l.; 2 - Hanyatak, Kapıorman Dağları, Sakarya, ca 400 m a.s.l.; 3a - 25 km south of Düzce, Bolu; 3b - Abant Gölü, Bolu, са 1,000 m a.s.l.; 4-17 km north-west of Bolu; 5 - 8 km north-west of Yenice, Zonguldak, ca 100 m a.s.l.; 6 - 5 km north of Safranbolu, Zonguldak, ca 500 m a.s.l.; 7 - Ilgazdağı Geçidi, Kastamonu, 1,650 m a.s.l.; 8 - Kürtler, Samsun, 5 m; 9 - 2 km east of Seyfe, Amasya, ca 1,100-1,400 m a.s.l.; 10 - Topçam, Ordu, 850 m a.s.l.; 11 - Tamdere, Rize, 1,550 m a.s.l.; 12 - 4 km south-east of Güzyurdu, Gümüşhane, ca 2,300 m a.s.l.; 13 - Sumela (=Meryem Ana), Trabzon; 14 - Çamlik, Rize, 1,380 m a.s.l.; 15 - Çayırtepe, Erzurum, 1,950 m a.s.l.. 16 - Kabaca, 8 km south-west of Murgul, Artvin, ca 800 m a.s.l.; 17 - Damar, 4 km south east of Murgul, Artvin, ca 1,000 m a.s.l.; 18 - Cankurtaran Geçidı, Artvin, 1,050 m a.s.l.; 19a Yalnızçam Geçidi, Artvin, ca 2,500 m a.s.l.; $19 b-5 \mathrm{~km}$ west of Bağdaşan, Kars, ca 2,600 m a.s.l. Corresponding references: Filippucci et al. (1996): 1, 2, 3a, 3b, 4, 5, 6. Frynta et al. (2001): 9, 12, 16, 17, 19a, 19b. Macholán et al. (2001): 13. Kryštufek \& Vohralík (2008): 1, 2, 3b, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19a, 19b.

## Distribution

From central Europe and the Baltic countries to Xinjiang and Mongolia, but borders are unresolved in the east (Musser \& Carleton, 2005). Southern range margin crosses northern Anatolia, where the herb field mouse "is restricted to a narrow belt of relatively humid habitat in the very north" (Macholán et al., 2001). Range in Anatolia largely coincides with the Euxinian mesic forests. The westernmost locality is Mt. Uludağ and we did not collect A. uralensis in similar habitats at the Kaz Dağları Mts. further west. The herb field mouse is widespread in Georgia (Bukhnikashvili, 2004) and was reported recently from Iranian Azerbaijan (Kryštufek \& Hutterer, 2006).

Palaeontology. See comments under A. sylvaticus. Kowalski (2001) does not list A. uralensis as a member of the European Quaternary fauna. Putatively present in Bulgaria throughout the entire Pleistocene, but material requires a careful re-examination (cf. Peshev et al., 2004).

## Habitat

The majority of our specimens (84\%) were captured in forests, both dry and mesic. Therefore, the herb field mouse occupies deciduous (Fagus, Alnus, Salix, Juglans, Acer, Quercus), coniferous (Pices, Abies) and mixed forests; dense undergrowth of Vaccinium or Rhododendron bushes seem to be preferred. In the alpine meadows, mice found shelter under rocks and shrubs and in tall herbaceous vegetation. At Kürtler (Samsun) we captured several herb field mice on a mosaic of pastures and tall bushes, only few metres above sea level.

Altitude. To the west of the Kızılırmak River the altitudinal range is from $<10 \mathrm{~m}$ to $2,250 \mathrm{~m}$ a.s.l., and to the east of the river the range is from 800 to 2,600 m (Kryštufek \& Vohralík, 2008). The highest record at 2,800 m a.s.l., as reported for Bağdaşan (Macholán et al., 2001) is evidently an error; elevation of the site was $2,600 \mathrm{~m}$ a.s.l.

Associates. The herb field mouse is sympatric with $A$. witherbyi and A. flavicollis throughout its range in Anatolia. All four Anatolian Apodemus species were found in sympatry only in the deciduous lowland forests in the western Black Sea Mts (near Safranbolu; Fig. 65a). List of other associates includes a number of voles (Myodes glareolus, Arvi-


Figure 80. Habitat of Apodemus uralensis in Turkey. a - Abant Gölü, Bolu (Photo: B. Kryštufek); b - Meryem Ana, Trabzon (Photo: V. Vohralík).
cola amphibius, Microtus subterraneus, M. daghestanicus, M. majori, M. arvalis, M. levis, Chionomys nivalis, C. gud, C. roberti), two hamsters (Cricetulus migratorius and Mesocricetus brandti), forest dormouse (Dryomys nitedula) and various shrews (Sorex satunini, S. volnuchini, S. raddei, Neomys teres, N. anomalus, Crocidura suaveolens).

Density. Throughout its range, the herb field mouse is one of the most abundant small mammals and the most numerous Apodemus species. In the Black Sea Mts. its proportion was on average 59 \% of all captured murine mice, and locally this proportion approached about $90 \%$.

## Biology

Aspects of life were studied in central Europe where the species was reported in the past as A. microps. For a review see Steiner (1978b)

Activity is nocturnal.

Reproduction. We collected pregnant females in early June and early September. Mean litter size, as estimated from counts of embryos and placental scars (mean = 5.2; range $=3-7 ; \mathrm{N}=30$ ) is higher than in the remaining Apodemus species occurring in Anatolia. Similar range (3-6) was reported also from Bulgaria (Peshev et al., 2004).

Food. In Bulgaria mainly weed and grass seeds, less so green plants, while insects are insignificant in the diet (Peshev et al., 2004).

## Eastern broad-toothed field mouse Apodemus mystacinus

Mus mystacinus Danford \& Alston, 1877. Type loc.: Zebil, Bulgar Dağ, Turkey.
Mus mystacinus smyrnensis Thomas, 1903. Type loc.: Smyrna (= İzmir), Turkey.
Apodemus mystacinus euxinus Allen, 1915. Type loc.: Scalita (= Altindere), Trabzon, Turkey.


Figure 81. Drawing of Apodemus mystacinus in the original description of the species by Danford \& Alston (1877).

## Taxonomy

Apodemus mystacinus differs from the remaining Sylvaemus species in external, cranial and dental traits, and has different mode of life (Niethammer, 1978c). Two group names were proposed in the past to define A. mystacinus against Sylvaemus: Petromys Martino, 1934 (preoccupied by Petromys Smith, 1834), and Karstomys Martino, 1939. Although Karstomys did not attain much attention during the $2^{\text {nd }}$ half of the $20^{\text {th }}$ century, it was frequently considered in current molecular studies, usually as a subgenus of either Apodemus (Michaux et al., 2001; Bellinvia, 2004) or Sylvaemus (Mezhzherin et al., 1992). The monophyly of the A. mystacinus - A. epimelas clade benefits strong support from molecular evidence (mitochondrial D-loop sequence; Bellinvia, 2004) but remained unsupported in electrophoretic study by Filippucci et al. (2002).

Although Miller (1912) retained A. mystacinus as a species distinct from A. epimelas (Nehring, 1902) (type loc.: Agoriani on Mt. Parnassus, Greece), the two were pooled subsequently, therefore $A$. mystacinus remained the only species of Karstomys (Ellerman \& Morrison-Scott, 1951, 1966; Corbet, 1978; Niethammer, 1978c; Musser \& Carleton, 1993). The two subspecies (mystacinus and epimelas) were diagnosed by linear dimensions; the nominate subspecies is smaller on average (Mirić, 1964; Felten et al., 1973). Storch (1977) pointed out dental differences between the two taxa (cf. also below); these traits allow tracing their fossil history back at least into the Middle Pleistocene and Storch (1999) argued that differences indicate two independent species, rather than two subspecies. This view was fully supported in studies of gene markers (Mezhzherin, 1997; Filippucci et al., 2002; Bellinvia, 2004; Michaux et al., 2005) and by multivariate analyses of morphometric data (Vohralík et al., 2002; Kryštufek \& Janžekovič, 2005). The molecular clock estimates the divergence between $A$. mystacinus and A. epimelas at about 4.2-5.1 million years ago (Michaux et al., 2005).

Although A. mystacinus morphologically differs from the remaining Turkish Sylvaemus in its larger size and grey colour, single characters, which would safely allocate each specimen into the proper group, are lacking. Colour works well, although subadults of A. witherbyi are occasionally as grey as A. mystaci-
nus, while the buffy form of the latter resembles Sylvaemus species. Size overlaps, but in Anatolian material the molar row is distinctly longer in A. mystacinus. Ellerman (1948) distinguished A. mystacinus from the Sylvaemus species by skull length (occipitonasal length of 29 mm as a cut-off point) and by the width of $1^{\text {st }}$ upper molar (cut-off point $=1.4$ mm). Several authors (Corbet, 1978; Niethammer, 1978c; Gromov \& Erbajeva, 1995) report shape of the anterior margin of the masseteric plate to be a taxonomic character (oblique in A. mystacinus, vertical in Sylvaemus mice), but we found it of little use (cf. Figs. 83-86). Bobrinskij et al. (1965) state that $3^{\text {rd }}$ upper molar has two cusps on its labial side in A. mystacinus and a single one in Sylvaemus;
we could not confirm the validity of this character. Miller (1912) keyed out the two groups on the presence of the postero-labial accessory cusp t12, and Niethammer \& Krapp (1978) used presence of t12 cusp on the $2^{\text {nd }}$ upper molar as being diagnostic. Although the cusp t12 is the norm in A. mystacinus and $A$. epimelas, it occurs with varying frequencies also in Sylvaemus species (Tvrtković, 1976, 1979; see also text and figures in this volume). Shape of t12 on the $1^{\text {st }}$ molar is characteristic although not strictly categorical. While t12 is primarily connected to a cusp t9 in $A$. mystacinus, it forms an enamel crest with t8 in great majority of Sylvaemus mice, but also in A. epimelas.


Figure 82. Skins of Apodemus mystacinus in dorsal and ventral view. Based on adult females from Göre, district Nevşehir (a), and Damar, district Artvin (b). Photo: C. Mlinar.

## Description

External characters (Fig. 81). The largest Apodemus species in Turkey with the longest tail, both absolutely and relative to body length. Tail is longer than head and body (range $=90-139 \%$ ) in great majority of specimens, being shorter than head and body only in $2.4 \%$ of individuals we measured ( $\mathrm{N}=$ 134). Tail annulations are distinct and hairs dens; terminal pencil is long ( 4 mm ). Body is slender; ears are longer than in Sylvaemus, both absolutely and relatively; hind foot is longer and also narrower. Front foot with four fingers and hind foot with five fingers; palms and soles are naked with five and six tubercles, respectively. Claws are shorter than in A. sylvaticus (2.3-2.4 mm). Eyes are relatively large (4.9-5.1 mm in diameter). Pelage is silky, summer hairs up to $7-9 \mathrm{~mm}$ long on mid-back (sparse long hairs up to 10 mm ), approximately $3-4.5 \mathrm{~mm}$ long on the belly. Lehmann (1966a) reports hairs to be essentially longer in animals from Borçka which were collected in November. Vibrissae are distinctly long (up to 43 mm ).

Colour (Fig. 82). Dorsal side predominantly grey, but this varies geographically (see below). Dark form differs from Sylvaemus species occurring in Anatolia, but buffy extremes resemble that group. Faint greyish tint of dorsal hairs is darkened by an admixture of blackish hair-tips; blackish zone along the spine is fairly sharply delimited and extends over the posterior half of the back in some specimens. Brown-grey dorsal colouration is not uncommon; in palest extremes buff shades predominate but never entirely replace grey tints. Flanks, snout and region behind the ears are buff in some specimens, grey in others. Belly is either pure white throughout or clouded by the slate grey undercolour; the extent of grey shades varies among localities and within them. Ventral hairs tend to be white throughout in the medial belly, with increasingly wider grey slate belt towards flanks. Delineation line along flanks is sharp. Chest between forelegs is of same colour as the belly; a pale and indistinct buffy spot is extremely rare ( $<1 \%$ of individuals). Ears are grey, feet white and tail distinctly bicoloured, whitish below and dark grey or grey brown above. Detailed description of colour (in terms of the Munsel Soil Colour Charts, 1954) was provided by Felten et al. (1973).

Nipples. There are six nipples, two pairs of inguinal and one pair of pectoral, respectively.

Penis. Glans penis and baculum are figured and described by Çolak et al. (2004). Glans is cylindrical, clubbed-like in lateral view. The distal section has a dorsal and a ventral groove. The wide dorsal groove is restricted to the anterior portion of the section while the ventral groove extends over the entire distal part of the glans. Relatively large epidermal spines cover the entire glans (Çolak et al., 2004). Baculum is composed of two parts. The distal cartilaginous tract is triangular in dorsal view (Harrison \& Bates, 1991), followed by the osseous proximal stalk with tapered tip and expanded base. Shape of the basal part is variable, being club-like (Çolak et al., 2004; Yiğit et al., 2006c) or trilobed (Harrison \& Bates, 1991: Fig. 337 on p. 238). Williams et al. (1980) described the glans and baculum in a closely related A. epimelas. Distal tract of the glans (length $=$ $7.71-8.97 \mathrm{~mm}$ ) and the proximal section of the baculum (4.99-5.38 mm) are categorically longer than in the remaining Apodemus species from the western Balkans.

Skull is essentially as in Sylvaemus (Figs. 8386). It is smoothly rounded and not ridged. Dorsal profile is evenly convex and occipital region is rounded; nasals protrude anterior to praemaxillary bone. Rostrum is relatively long, nasals are long and narrow, tapered anteriorly; they converge towards the frontal bone. In old animals, rostrum tends to be broadened anteriorly. Zygomatic arches are weak, running parallel or diverging posteriorly. Greatest breadth of skull normally exceeds half of condylobasal length (zygomatic breadth equals to 49.0-58.4 \% of condylobasal length; mean = 54.5 \%). Interorbital region is broad, flat and smooth; brain-case is relatively large and rounded. The fronto-parietal suture is either smooth or angled. Interparietal bone is large and broad. Incisive foramens are long (22.3-25.3 \% of condylobasal length; mean $=23.7 \%$ ), their anterior margin is shifted forward. Posterior margin of hard palate is straight, with a medial protuberance in some animals. Pterygoids run parallel or slightly diverge posteriorly; interpterygoid space is broad. Bullae are short relative to condylobasal length (15.720.4 \%), rounded or triangular. Mandible is slender and lower than in Sylvaemus; coronoid process is weak.

Teeth. Incisors match the general pattern seen in Sylvaemus; enamel is orange on the upper incisor's


Figure 83. Skull and mandible of Apodemus mystacinus, based on an adult female from Kaz Dağları, Çanakkale. Scale bar $=5 \mathrm{~mm}$.


Figure 84. Skull and mandible of Apodemus mystacinus, based on an adult male from 2 km north of Aşağigürlek, Bozbel, Muğla, Taurus Mts. Scale bar $=5 \mathrm{~mm}$.


Figure 85. Skull and mandible of Apodemus mystacinus, based on an adult male from Buzluk, Harput, Elazığ. Scale bar $=5 \mathrm{~mm}$.


Figure 86. Skull and mandible of Apodemus mystacinus, based on an adult female from Damar, district Artvin.
Scale bar $=5 \mathrm{~mm}$.


Figure 87. Upper (a) and lower molars (b) in Apodemus mystacinus from Buzluk, Harput, Elazığ. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
anterior surface, light-orange or yellow on the lower ones.

Maxillary molar row is parallel, shorter than diastema. Molars are robust, $2^{\text {nd }}$ and $3^{\text {rd }}$ molars large relative to the $1^{\text {st }}$ one; cusps are robust (Fig. 87). Fusion of cusps is retarded on upper molars, particularly so $\mathrm{t} 1-\mathrm{t} 2, \mathrm{t} 5-\mathrm{t} 6, \mathrm{t} 6-\mathrm{t} 9, \mathrm{t} 7-\mathrm{t} 8$ on the $1^{\text {st }}$ molar; $\mathrm{t} 4-\mathrm{t} 5$, $\mathrm{t} 5-\mathrm{t} 6, \mathrm{t} 6-\mathrm{t} 9, \mathrm{t}-\mathrm{t} 8$ on the $2^{\text {nd }}$ molar. Stephanodonty is lacking, although t 3 on $1^{\text {st }}$ molar frequently bears a well developed spur. Tendency of tubercles towards reduction into a ridge is weak; it is occasionally seen in $\mathrm{t7}$ on the $2^{\text {nd }}$ upper molar. The postero-labial accessory tubercle (t12) is present on $1^{\text {st }}$ and $2^{\text {nd }}$ upper molars in great majority of specimens: $98.0 \%$ on $1^{\text {st }}$ molar (Fig. 88b-f) and $91.2 \%$ on $2^{\text {nd }}$ molar (Fig. 89). On the $2^{\text {nd }}$ molar the cusp t 12 is connected with t 8 (Fig. 89b-e) in $79.9 \%$ of specimens, while it is connected to t9 in the remaining $20.1 \%$. Contrary to this, on the $1^{\text {st }}$ molar t12 connects first to t9 (Fig. 88d; 94.2\% of

a

b

e

C


Figure 88. Variation in postero-labial cusp $t 12$ (shown by arrow) on $1^{\text {st }}$ upper molar in Apodemus mystacinus from Turkey. a - Safranbolu, Zonguldak; b, e - Damar, Artvin; c - Feke, Adana; d - Seyfe, Amasya; f - Kaz Dağları, Çanakkale. Lingual side is to the left, anterior is at the top. Scale bar $=0.5 \mathrm{~mm}$.


Figure 89. Incidence of postero-labial cusp t12 (shown by arrow) on $2^{\text {nd }}$ upper molar in Apodemus mystacinus from Turkey. a-c, e - Seyfe, Amasya; d -Kaz Dağları, Çanakkale; $\mathbf{f}$ - Feke, Adana. Lingual side is to the left, anterior is at the top. Scale bar $=0.5 \mathrm{~mm}$.
specimens with t12 present) while a connection to t8 is established subsequently, either directly (Fig. 88c) or via t 9 , or both (Fig. 88e,f; mystacinus morphotype in the terminology of Storch, 1977). Connection between t8 and t12 (Fig. 88c; epimelas morphotype) is quite rare before t 12 and t 9 are connected ( $5.8 \%$ of specimens showing t12). The pattern becomes obscured with the progressive enamel abrasion. On the other hand, young specimens with unworn teeth occasionally still have t12 as an isolated cusp (Fig. 88b). Third upper molar is relatively large and with a deep labial fold.


Figure 90. Alveolar pattern in Apodemus mystacinus. Based on a specimen from Borçka, Artvin (ZFMK). a - upper, $\mathbf{b}$ - lower row. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

Labial margin of $1^{\text {st }}$ molar bears a narrow enamel ledge with accessory cusplets; cusplets tend to be larger and more numerous than in Sylvaemus. The enamel ledge with accessory cusps is frequently well developed also on the $2^{\text {nd }}$ lower molar.

Number of roots is same as in A. sylvaticus: 4, 4, 3 (upper row), 2, 2, 2 (lower row; Fig. 90). Deviations are rare (reported by Niethammer, 1962, for the upper row in specimens from the Island of Crete and the Near East; sample size is 17 and 18, respectively): additional small medio-labial root on $1^{\text {st }}$ molar ( $2.8 \%$ of individuals); accessory small medial root (14.3\%) or fused lingual roots ( $8.6 \%$ ) on $2^{\text {nd }}$ molar; accessory lingual root (11.4\%) or fused labial roots ( $11.4 \%$ of specimens) on $3^{\text {rd }}$ molar. Deviant numbers of roots are 5 or 3 on $1^{\text {st }}$ and $2^{\text {nd }}$ molars, and 2 or 4 on $3^{\text {rd }}$ molar.

Dimensions are given in Table 16. Felten et al. (1973) did not detect secondary sexual dimorphism in size. The only significant difference we found in
our pooled sample from the Taurus region was in hind foot length (longer in males). For age variation see Felten et al. (1973).

Сhromosomes. The diploid number of chromosomes in A. mystacinus from Asia Minor is $2 \mathrm{~N}=$ 48, and the fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=50$. With the exception of the two smallest pairs of metacentric autosomes, all the remaining chromosomes are acrocentrics (Doğramacı \& Kefelioğlu, 1991a). The same diploid number is reported also from Israel (Zima \& Macholán, 1995) and Jordan (Sözen et al., 2008). Apodemus epimelas from the Balkans has the same conventional karyotype (Zima \& Král, 1984).

## Variation

The eastern broad-toothed field mouse shows higher interpopulation variation in morphological traits than sympatric Sylvaemus species. The darkest animals are from humid mountains in north-eastern Anatolia: back is dark grey, with not many brown tints (if any at all), and belly is heavily clouded by slate grey hair bases (Fig. 82b); flanks and snout are frequently buffy even in this dark morphotype. Slightly paler mice, frequently with an admixture of brown shades on the back and a predominantly grey belly, occupy central and western Black sea Mts. Individuals from arid parts of Anatolia show grey ground colour with a strong admixture of brown and buffy tints; white shades are more expressed on the belly (Fig. 82a). Ventral hairs are white throughout in some places along the Aegean coast, in the Taurus Mts. and in eastern Anatolia. Osborn (1965) linked colour to climatic conditions with deeper pigmentation being developed in regions of greatest rainfall.

Apodemus mystacinus is the largest in eastern Anatolia and the smallest in the Taurus Mts. Specimens from the Taurus are also characterised by long bullae (maximum $=5.6 \mathrm{~mm} ; 5.2 \mathrm{~mm}$ is the highest value in the rest of Anatolia). Tail is the shortest, relative to head and body length, in eastern Anatolia (101 $\%$ on average), and the longest in the western Taurus Mts. (mean = 119 \%). Size varies clinally (Felten et al., 1973) and associates positively in Isreal with mean minimum January temperature, hence in accordance with Bergmann's rule (Yom-Tov \& Geffen, 2006).

Neuhäuser (1936) recognised three subspe-

|  | north-west Black Sea Mts. |  |  | east Black Sea Mts. |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | min - max | N | mean | min - max |
| Head and body | 7 | 118.3 | 113-125 | 46 | 113.0 | 100-125 |
| Tail | 5 | 127.4 | 120-138 | 37 | 123.1 | 106-139 |
| Hind foot | 7 | 25.5 | 24.3-26.7 | 46 | 25.0 | 23.0-27.0 |
| Ear | 7 | 20.3 | 19.7-21.0 | 44 | 18.8 | 17.0-20.0 |
| Weight | 7 | 41.1 | 34-47 | 19 | 36.7 | 27-47 |
| Condylobasal length | 5 | 27.7 | 27.2-28.9 | 13 | 26.4 | 25.8-27.3 |
| Zygomatic breadth | 7 | 15.1 | 14.5-16.5 | 12 | 14.5 | 13.4-15.1 |
| Maxillary tooth-row (alveoli) | 10 | 4.9 | $4.7-5.2$ | 12 | 4.8 | $4.6-5.0$ |
| Maxillary tooth-row (crown) | 13 | 4.7 | 4.6-4.9 | 17 | 4.5 | $4.4-4.7$ |
| Bulla length | 12 | 4.9 | $4.6-5.2$ | 14 | 4.7 | $4.2-5.0$ |
|  | west \& central Anatolia |  |  | east Anatolia |  |  |
|  | N | mean | min - max | N | mean | min - max |
| Head and body | 28 | 112.9 | 102-128 | 8 | 117.5 | 110-132 |
| Tail | 32 | 124.7 | 105-139 | 7 | 119.7 | 111-128 |
| Hind foot | 35 | 25.3 | 23.0-27.5 | 8 | 26.2 | 25.0-28.1 |
| Ear | 36 | 19.4 | 17.0-22.0 | 8 | 19.6 | 18.6-20.0 |
| Weight | 25 | 36.3 | 25-48 | 8 | 48.7 | 31-74 |
| Condylobasal length | 30 | 27.3 | 26.0-28.8 | 3 | 27.6 | 26.7-28.9 |
| Zygomatic breadth | 30 | 14.7 | 12.9-15.9 | 3 | 15.4 | 14.9-16.0 |
| Maxillary tooth-row (alveoli) | 41 | 5.1 | 4.8-5.4 | 3 | 5.0 | $4.8-5.2$ |
| Maxillary tooth-row (crown) | 38 | 4.8 | 4.5-5.1 | 3 | 4.8 | $4.5-4.9$ |
| Bulla length | 33 | 4.8 | $4.4-5.1$ | 3 | 5.0 | $4.9-5.0$ |
|  | Taurus Mts. |  |  | Is. Rhodes |  |  |
|  | N | mean | min - max | N | mean | min - max |
| Head and body | 46 | 110.0 | 100-130 | 7 | 120.9 | 113-132 |
| Tail | 44 | 126.5 | 108-145 | 9 | 126.6 | 114-136 |
| Hind foot | 47 | 25.3 | 23.0-27.0 | 9 | 26.5 | 25.0-27.7 |
| Ear | 42 | 19.8 | 16.0-22.0 | 8 | 19.4 | 17.9-21.0 |
| Weight | 23 | 37.3 | 26-50 | 7 | 42.4 | 35-51 |
| Condylobasal length | 51 | 26.9 | 25.6-29.0 | 7 | 28.0 | 26.9-29.5 |
| Zygomatic breadth | 47 | 14.7 | 13.7-15.9 | 8 | 15.2 | 14.8-16.1 |
| Maxillary tooth-row (alveoli) | 20 | 4.8 | $4.5-5.0$ |  |  |  |
| Maxillary tooth-row (crown) | 29 | 4.6 | $4.3-5.0$ | 9 | 4.9 | 4.6-5.1 |
| Bulla length | 24 | 4.9 | $4.5-5.6$ | 7 | 5.1 | $4.8-5.5$ |

Table 16. External and cranial dimensions of Apodemus mystacinus from Anatolia (according to regions) and from the Greek Island of Rhodes. Based on specimens in BMNH, SMF and ZFMK, in addition to our own material.
cies in Turkey and diagnosed them by size and colour: A. m. mystacinus from the eastern Taurus Mts. (back yellowish brown, belly pale grey to white; maxillary molar row length mainly 4.8 mm ; range $4.8-5.2 \mathrm{~mm}$ ), A. m. smyrnensis from western Anatolia (paler and more yellowish than the nominate race; longer upper molar row, mean $=5 \mathrm{~mm}$ ), and $A$. $m$.
euxinus from wooded regions of the Black Sea Mts. (back dark brown grey, belly grey; maxillary molar row length $4.5-4.8 \mathrm{~mm}$, mean $=4.6 \mathrm{~mm}$ ). Ellerman (1948) synonymised smyrnensis with the nominate race. Division into two subspecies was maintained also by Lehmann (1966a), who did not, however, consider material from western Anatolia. Contrary to
this, Felten et al. (1973) conclude that A. mystacinus (sensu lato) contains only two subspecies, i.e. mystacinus and epimelas. Translated to a current taxonomy, this means that A. mystacinus is a monotypic species. Çolak et al. (2004) recognised two subspecies within Turkey (mystacinus and euxinus), which they found to be of same size.

Multivariate analysis of morphometric data revealed rather low level of interpopulation variation and did not support recognition of conventional subspecies (Vohralík et al., 2002). The only clear exception was an extralimital isolate from the Al-Duruz Mts. in Syria. Contrary to a supposed west-to-east cline in Asia Minor (Lehmann, 1965; Felten et al., 1973), a study by Vohralík et al. (2002) revealed only a gradual decrease in few molar measurements from the Middle Taurus Mts. towards Jordan. Larger molars were found in populations from the Island of Crete, Al-Duruz Mts., Taurus Mts., and western Anatolia (Vohralík et al., 2002).

Nucleotide sequences of the mitochondrial cytochrome $b$ gene and of $D$-loop revealed two well supported clades within $A$. mystacinus. One lineage encompassed samples from northern Turkey, Georgia and Syria, and the other one contained specimens from Antalya and Crete. The divergence time between these two lineages was estimated at 1.0-0.9 million years ago (Michaux et al., 2005). Note however, that the above phylogeographic structuring was not supported by the IRBP nuclear gene (Michaux et al., 2005). Samples from the Taurus and the Black Sea Mts. clustered close to each other also in the electrophoretic study of the esterase enzyme system, while samples from the Aegean coast emerged to be more distant (Çolak et al., 2007).

On the base of molecular evidence, Michaux et al. (2005) ascribed mice from southern Turkey to subspecies A. m. rhodius Festa, 1914 (type loc.: Agios Isidoros, Rhodes Island). Proposed taxonomic and nomenclatural solution involves several difficulties. The eastern broad-toothed field mice from the Island of Rhodes are larger on average than any Anatolian sample (Table 16) but their genetic identity remains unknown. The geographic scope of the Antalya-Crete clade of A. mystacinus, as defined by Michaux et al. (2005), is also not resolved in Anatolia. If this clade encompasses populations from western Anatolia, then smyrnenis holds priority over rhodius; if the
lineage extends eastward across the Taurus Mts., then mystacinus has an absolute priority over both, rhodius and smyrnensis.

## Distribution

The bulk of the range of $A$. mystacinus is in Anatolia, along the eastern Mediterranean coast (Lebanon, Syria, Israel, Jordan), and in the Aegean islands of Greece (Crete, Karpathos, Rhodes, Kos, Cephalonia, Euboea, Samos, Ikaria, Chios, and Lesbos; Ondrias, 1966; Storch, 1977; Musser \& Carleton, 2005). Marginal populations occur in Georgia (Bukhnikashvili, 2004) and northern Iraq (Kock et al., 1972). The eastern broad-toothed mouse is widespread across Asia Minor but is possibly absent from majority of the Central Anatolia and to the east of Lake Van.

Apodemus mystacinus is presumably expanding its range northwards in Georgia. Šidlovskij (1976) found broad-toothed field mice around Poti and Kutaisi in 1939-1943, where they were absent in 1916-1917.

Palaeontology. Apodemus mystacinus presumably evolved from the Early Pliocene A. gorafensis and appeared in the fossil record during the Middle Pliocene (Ruiz Bustos et al., 1984). The evolution of $A$. mystacinus lineage was slow and its range shrank gradually over time (Pasquier, 1974). During the Upper Pleistocene, A. mystacinus (sensu lato) still occurred along the Mediterranean coast of Europe as west as Spain; cf. map in Terzea (1992; Fig. 2 on p. 92).

The broad-toothed field mouse has been known in the Eastern Mediterranean since the Upper Villanyian (Lower Pleistocene) at the latest (Meulen \& Kolfschoten, 1986). Middle Pleistocene records are available from Emirkaya-2 in central Anatolia (Late Biharian; Şen et al., 1991; Montuire et al., 1994) and from the Island of Chios (Storch, 1975). Storch (1988) demonstrated a continuous occurrence of $A$. mystacinus in Karayin near Antalya since the Middle Pleistocene, with intermittency during the Chalcolithic (Early Holocene). In Israel, a continuous presence of A. mystacinus has been documented for the last 250,000 years (Tchernov, 1988). Records of the Palaeolithic age are also known from Lebanon (Turnbull, 1975).

The Levantine populations changed considera-


Figure 91. Distribution of Apodemus mystacinus in Turkey and adjacent countries. For further details on records see Appendix 3.
bly over the last 120,000 years. Ancient populations show a more massive mandible and more developed molar tuberculation (Tchernov, 1968a, 1975). Their largest size was attained during the warm post-Glacial (Tchernov, 1979). Contrary to this, Montuire et al. (1994) detect little change in molar morphology since the Middle Pleistocene in central Anatolia.

No fossils are known from the area of the Caucasus (Vereščagin, 1959).

## Habitat

Apodemus mystacinus is widespread in both arid and humid regions of Anatolia, however, rocks and stones are an essential component of its habitat (Neuhäuser, 1936; Osborn, 1965; Felten et al., 1973). Forests on rocky ground are inhabited all along the Anatolian coasts. This includes deciduous and coniferous forests (Fagus orientalis, Carpinus betulus, Quercus infectoria, Q. cerris, Q. pubescens, Cistus laurifolius, Crataegus monogyna, Cotonaaster nummalaria, Acer sp., Juglans regia, Salix sp., Alnus sp., Platanus sp., Abies nordmanniana, Picea orientalis) in a well wetted northern regions, as well as dry oak (Quercus pedunculata, Q. sessiliflora), pine (Pinus
brutia, Pinus nigra pallasiana) and cedar (Cedrus libani) forests in the south. Forested habitats along the eastern Black Sea coast frequently abound with rich undergrowth but have very few stones (Fig. 92d).

Degraded forests, shrubland, and pastures with scattered bushes (Quercus coccifera, Juniperus excelsia, J. oxycedrus, etc.) ensure suitable habitats, providing there are some rocks (Fig. 92a). In central and in eastern Anatolia, the species is mainly associated with rocky outcrops (Fig. 92b) in pastures and meadows of various grasses and herbs (Hordeum sp., Eryngium sp., Securigeria sp., Peganum sp., Agroshyron sp.). Characteristic habitats are also riverbeds with plenty of rocky cover, regardless of the surrounding vegetation. The eastern broad-toothed field mouse also lives in cultivated areas where it prefers terrace walls in orchards, fields, vineyards, olive groves and gardens, as well as stony walls and piles of stones in fields. It has also been captured in houses (Osborn, 1965).

Similar habitats are populated further south, where $A$. mystacinus is abundant in moister hills and in the mountains along the eastern Mediterranean coast (Harrison \& Bates, 1991). Mesic microcli-


Figure 92. Habitat of Apodemus mystacinus in Turkey. a - Taurus Mts. above Antalya; b - Buzluk, Harput, district Elazığ; c - Meryem Ana, district Trabzon; d - Duroğlu, district Giresun. Photo: A. Kryštufek (a, d); B. Kryštufek (b, c).
mate becomes increasingly important in arid regions; e.g. in Israel (Mendelssohn \& Yom-Tov, 1999) the animal requires a layer of foliage (Abramsky 1981). In Transcaucasia, A. mystacinus is tied to a belt of deciduous and mixed forests (Šidlovskij, 1976).

Altitude occupied by A. mystacinus ranges from sea level up to $2,000 \mathrm{~m}$ on the Taurus Mts. The highest records are at $1,000-1,225 \mathrm{~m}$ a.s.l. in the Marmara and the Black Sea region, $1,960 \mathrm{~m}$ in central Anatolia, and $2,280 \mathrm{~m}$ in eastern Anatolia. The altitudinal range in Lebanon is $100-2,500 \mathrm{~m}$ (Atallah, 1978), and the highest record in southern Syria is from 2,700 m a.s.l. (Mt. Hermon; Shehab et al., 1999a); the only Iraqi record is from $1,200 \mathrm{~m}$ (Hatt, 1959). The highest observation in Transcaucasia is from 2,000 m a.s.l. (Bukhnikashvili \& Kandaurov, 1998).

Associates. The eastern broad-toothed field mouse is quite frequently sympatric with one or
more Sylvaemus mice (A. flavicollis, A. witherbyi, A. uralensis), but is only rarely the most abundant species in such assemblages. In mesic forests along the Black Sea coast $A$. mystacinus typically co-occur with much smaller $A$. uralensis, and in more arid habitats further south, A. witherbyi is its most frequent associate. In open rocky situations, A. mystacinus is occasionally syntopyc with Chionomys nivalis, and in mesic forests in the Black Sea Mts. with C. roberti. A list of other associates includes shrews (Sorex volnuchini, S. raddei, Neomys anomalus, N. teres, Crocidura leucodon, C. suaveolens, C. arispa), Microtus voles (M. subterraneus, M. majori, M. guentheri), and, more rarely also Myodes glareolus, Mus domesticus, Acomys cahirinus, and hamsters (Cricetulus migratorius, Mesocricetus brandti).

Along the eastern Mediterranean coast south of Anatolia, the eastern broad-toothed field mouse co-
occurs also with Eliomys melanurus, Rattus rattus (at low elevations and near villages; Atallah, 1978), and Meriones tristrami (in cultivated areas; Harrison \& Bates, 1991). In Israel, A. mystacinus exclude Sylvaemus mice from preferred mesic habitats to a drier environment (Mendelssohn \& YomTov, 1999).

Density. Despite of its wide range in Anatolia, the Levant broad-toothed field mouse is less abundant than Sylvaemus species. Relative densities in Anatolia are nearly always much less than 10 A. mystacinus per 100 trap nights. The highest relative abundance we came across was at Ayvacık near Behram on the Aegean coast (approximately one third of a total small mammal catch). This contradicts the situation in Israel, where A. mystacinus is found in a wider variety of habitats than A. flavicollis, and is common in most forested or well-vegetated parts of the Levant region (Qumsiyeh, 1996). Populations vary only a little between years in Israel (Mendelssohn \& Yom-Tov, 1999).

## Biology

Activity is nocturnal with two peaks, one after sunset the other between 2-3 a.m.; there is almost no activity after 11 p.m. in Israel (Mendelssohn \& YomTov, 1999). On Mt. Carmel, Yahav \& Haim (1980) noted marked reduction in activity during the colder months (September to January). Apodemus mystacinus readily climb trees in Israel (Abramsky, 1981); a similar observation from Turkey is reported by Osborn (1965). The average radius of activity varies from 8 m (young females) to 15 m (adult males). Home ranges do not overlap during low population density (Mendelssohn \& Yom-Tov, 1999).

Male-male interactions are more agonistic than female-female interactions. Agonistic behaviour is nearly absent during the summer period of sexual inactivity but increases afterwards. Strong association of the sexual period with aggression in males presumably results from competition for mates (Váchová \& Frynta, 2004).

Burrows are under rocks (Atallah, 1978) and tree roots (Šidlovskij, 1976). The species occupy natural burrows or dig own ones (Mendelssohn \& Yom-Tov, 1999). In Transcaucasia nests were found inside rotten fallen logs, in piles of rocks, and in crevices (Šidlovskij, 1976).

Reproduction lasts from August-October to April in Israel. Gestation period is 23-26 days, litter size is $1-5$, and female may give birth up to four times annually; life expectancy is 7-8 months (Mendelssohn \& Yom-Tov, 1999). For the eastern Mediterranean coast, Atallah (1978) suggests continuous breeding from early April through late October with two litters per year. From Transcaucasia, Šidlovskij (1976) reports pregnant females between May and October. Data for Anatolia, based on our field notes and museum specimen tags (BMNH, SMF, ZFMK), suggest continuous breeding throughout the year, regardless of elevation. Lactating females were hence captured in April - July and October - December, pregnant females from May to July, and females with fresh placental scars between June and October. Young animals were obtained also in December, January and March. In a representative BMNH sample from the mountains south of Trabzon, females with clearly visible nipples were trapped in October, November and December. Testes in adult sexually active males measured up to $20 \times 12 \mathrm{~mm}$.

In Anatolia, embryo count is lower in A. mystacinus than in the remaining species of Apodemus: mean $=3.5$, range $=1-5(\mathrm{~N}=25)$. Šidlovskij (1976) reports for Transcaucasia six embryos at most.

Food is basically same as in A. sylvaticus. In the eastern Mediterranean region the diet consists of grains, weeds and pine seeds, acorns, carob (Cerathonia siliqua) seeds (Lewis et al., 1967), land snails and insects (Qumsiyeh, 1996). In Quercus calliprinos stands, where $A$. mystacinus is very common in Israel, oak acorns comprise its main diet (Qumsiyeh, 1996). Bird eggs and nestlings are also preyed upon (Mendelssohn \& Yom-Tov, 1999).

Predation. The eastern broad-toothed field mouse is the dominant mammal prey of the tawny owl Strix aluco, and is also rarely preyed upon by the eagle owl Bubo bubo (Obuch, 1994) and barn owl Tyto alba (Kasparek, 1988; Brinkmann et al., 1990). Corbet \& Morris (1967) found A. mystacinus to be the second most abundant species (next to Microtus hartingi) in a dissolved pellet material at Yalniz, the Taurus Mts. Reports from the Near East and from the Greek Island of Kos suggest the eastern broadtoothed mouse to be only rarely preyed upon by the barn owl Tyto alba (Niethammer, 1989; Rifai et al., 1998; Shehab, 2005). Amr (2000) reports from

Jordan a case of predation by the coined snake (Coluber nummifer).

## Striped field mouse - Apodemus agrarius

Mus agrarius Pallas, 1771. Type loc.: Simbirsk (= Uljanovsk), banks of the Volga, Russia.

## Description

External characters. The striped field mouse differs externally from other Apodemus species occupying Turkey due to its chunkier body, smaller eyes, shorter ear and hind foot, by a shorter tail, and by sharply defined black dorsal line. Tail is always shorter than head and body length ( $65-84 \%$; mean $=78 \%$ ). Feet are more robust than in other members of the genus, but number of fingers is same: four on palm and five on hind foot. Palms and soles are naked, with five and six pads, respectively; pads are smaller than in A. sylvaticus. Claws are strong and curved, up to 3.5 mm long. Tail annulations are coarse and very distinct; caudal hairs are sparser than in A. sylvaticus, and terminal pencil is short (up to 2.5 mm ). Pelage is coarse, $6-7 \mathrm{~mm}$ long on mid-back, shorter on the belly (up to 4 mm ). Vibrissae are short ( 19 mm ).

Colour (Fig. 93). Upper parts are dark reddish brown to hair-brown, more dull along the medial stripe and on front head. Flanks are brighter, ventral side is dull white clouded by the slate undercolour. Demarcation line is fairly sharp. Mid-dorsal black stripe is $2-5 \mathrm{~mm}$ wide, but this varies among specimens. Stripe starts shortly behind ears and extends close to base of tail; base of tail is reached in some specimens or the line terminates up to 15 mm anterior to it. Tail is dark hair-brown throughout, slightly paler ventrally, but not bi-coloured. Ears are dark greybrown, feet are dull whitish.

Nipples. There are four pairs of nipples, two pairs of each, pectoral and inguinal.

Penis and baculum are essentially as in A. sylvaticus. The dorsal ridge is elliptical and restricted to the proximal section. The narrow ventral groove is well defined. Epidermal nodules and spines are present over the entire glans; the spines are smaller and more numerous than in $A$. sylvaticus. In Croatian material of $A$. agarius, the distal glans is $5.63-5.72 \mathrm{~mm}$ long and $2.81-3.21 \mathrm{~mm}$ wide; the proximal part is wider
(3.03-3.51 mm). At the midsection, the glans is 2.733.20 mm wide and $2.41-2.91 \mathrm{~mm}$ deep. For a drawing of specimen from Turkish Thrace see Yiğit et al. (2006c: Fig. 38B). In Croatian mice the entire baculum is $4.85-6.01 \mathrm{~mm}$ long; proximal section measures 3.28-4.43 mm in length, and is $1.10-1.65 \mathrm{~mm}$ wide at base (Williams et al., 1980). In specimens from Turkish Thrace, the proximal baculum is 3.653.75 mm long (mean $=3.72 \mathrm{~mm}$; Kefelioğlu et al., 2003).


Figure 93. Skin of Apodemus agrarius in dorsal and ventral view. Based on an adult female from 7 km north of Sivriler, Istranca Mts. Photo: C. Mlinar.

Skull (Fig. 94) is long and narrow, with relatively long brain-case. Zygomatic breadth narrow relative to condylobasal length (49.8-52.3 \%; mean $=51.3$ \%). Nasals long and slender, not expanded anteriorly. Interorbital constriction clearly defined; posterior to it start supratemporal ridges which extend onto parietals. Interparietal bone is broader than in A. sylvaticus, and does not reach lateral margins of the braincase. Profile is less convex than in A. sylvaticus and zygomasseteric plate is relatively larger. Rostrum is long and narrow, incisive foramens relatively short, only occasionally reaching the level of $1^{\text {st }}$ molar. Interpterygoid region is moderately broad, bullae are small. Mandible is essentially as in A. sylvaticus, but more slender, shallower, and with more reduced coronoid process.

Teeth. Incisors as in A. sylvaticus; enamel orange on the upper incisors, yellow on the lower ones. Molar-row is noticeably smaller and molars narrower. Cuspidation essentially as in other field mice, except that the antero-labial tubercle ( t 3 ) is missing on $2^{\text {nd }}$ upper molar (Fig. 95). Note, however, that
minute cusp t3 is present in a small part of population (Musser et al., 1996). Central row of tubercles (t2, $\mathrm{t} 5, \mathrm{t} 8$ ) is small on the $1^{\text {st }}$ upper molar, postero-labial accessory cusp t12 is exceptionally present. Posterior spur on one of the lateral cusps of the anterior row (t1 or t 3 ) rarely seen on $1^{\text {st }}$ molar. The postero-labial tubercle (t9) on $2^{\text {nd }}$ upper molar varies from cusp-like to a ridge-like.

Number of roots is basically same as in A. sylvaticus. Deviations prevail on $1^{\text {st }}$ upper molar where 4 roots are found only in about a quarter of central European material (= $28.2 \%$; Zejda, 1965); due to the presence of small accessory roots, the total count is 5 (33.4\% of individuals), 6 ( $28.2 \%$ ) or 7 roots (10.2\%). Second molar has 4 roots in majority of specimens (92.6\%); other counts are 2 , 3 , or 5 roots. Three roots are the prevailing condition in $3^{\text {rd }}$ upper molar (65.8\% of animals); due to fusion of roots, their count can be reduced to 2 or 1 (Zejda, 1965).

Dimensions are given in Table 17. Males are heavier than females, but size differences are not significant in cranial dimensions (Böhme, 1978a).


Figure 94. Skull and mandible of Apodemus agrarius, based on an adult male from 7 km N of Sivriler. Scale bar = 5 mm .


Figure 95. Upper (a) and lower molars (b) in Apodemus agrarius from about 5 km south-west of Ĭğneada, Kırklareli. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

|  | N | mean | $\min -\max$ |
| :--- | :---: | :---: | :---: |
| Head and body | 35 | 114.2 | $104-126$ |
| Tail | 35 | 80.1 | $68-93$ |
| Hind foot | 32 | 20.7 | $18.8-22.0$ |
| Ear | 8 | 12.3 | $11.0-13.0$ |
| Weight | 33 | 38.5 | $30-45$ |
| Condylobasal length | 33 | 25.6 | $23.8-26.5$ |
| Zygomatic breadth | 33 | 13.1 | $12.3-13.6$ |
| Maxillary tooth-row | 36 | 4.3 | $3.9-4.6$ |

Table 17. External and cranial dimensions of Apodemus agrarius from Turkish Thrace. Based on Osborn (1961), Kefelioğlu et al. (2003), specimens in BMNH, and our own data.

Chromosomes. The diploid number of chromosomes is $2 \mathrm{~N}=48$ and the fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=54$. Autosomal complement consists of 19 pairs of acrocentrics and four pairs of small bi-armed elements (Zima \& Král, 1984).

Based on Turkish material, Kefelioğlu et al. (2003) reported bi-armed elements to be metacentrics (three pairs) and submetacentrics (one pair). Contrary to this, Yiğit et al. (2000a) report four pairs of small metacentrics in specimens from the Istranca Mts. Heterosomes are acrocentric, the X is large, and the Y is small (Yiğit et al., 2000a; Kefelioğlu et al., 2003). Diploid number $2 \mathrm{~N}=48$ is reported from European Turkey also by Zima \& Macholán (1995).

## Variation

Colour and size vary across Europe; southern populations are the largest, and some of them also the darkest (e.g. A. a. kahmanni Malec \& Storch, 1963; type loc.: Banja Bansko, Macedonia). Morphological differences in linear skull dimensions are best attributed to non-genetic, environmental adaptations (Hille \& Meinig, 1996). Electrophoresis of 44 enzymes encoded by 57 gene loci revealed low interpopulation genetic diversity along a transect from Kaliningrad (north-western Russia) to western Slovenia, thus providing no support for subspecific division (Hille \& Meinig, 1996).

Doğramacı (1974) and Kefelioğlu et al. (2003) ascribed Turkish sample to A. a. kahmanni. We agree that Thracian material matches topotypes of this subspecies in its large size and dark colour, however, as shown by Hille \& Meinig (1996), the phenotype is plastic in A. agrarius and responds promptly to environmental conditions.

## Distribution

Range is in two segments. In western Palaearctic, the striped field mouse ranges from central Europe, the Balkans and southern Finland as far east as Lake Baikal. The other segment is in eastern Palaearctic and in Oriental region, specifically in China, Korea and Taiwan (Musser \& Carleton, 2005). The western distributional border in Europe is dynamic and still has not stabilized (Kratochvíl et al., 1976); for a small scale range dynamics over several decades see e.g. Flousek et al. (2004). There are numerous small isolates along the distributional edge; see Petrov (1992) for the western Balkans and Vohralík \& Sofianidou (1992b) for the southern Balkans. For this reason, any sharp range border of distribution is tentative and arbitrary.

Turkish records are along the Black Sea coast of

Thrace (Doğramacı, 1974; Yiğit et al., 2006c), between the İstanbul area and Turkish - Bulgarian border. Several records are also known from the coastal area of Thrace in Bulgaria further north (Vohralík \& Sofianidou, 1992b). Species is absent along the lower reaches of the Meriç River (Özkan, 1987) despite the existence of suitable habitats. This is even more surprising, considering its presence along the upper flows of the Marica (= Meriç) River in Bulgaria and along its tributary, the Tundža (= Tunca) River (Vohralík \& Sofianidou, 1992b). The striped field mouse also occurs along the lower reaches of the Nestos River in Greek Thrace; this population is possibly an isolate (Vohralík \& Sofianidou, 1992b).

In north-eastern Anatolia, A. agrarius approaches Turkey along the eastern Black Sea coast in Georgia; Mukhura as the most exposed locality (Bukhni-
kashvili, 2004) is only slightly more than 100 km to the north of the Turkish border. In spite of this, the species has not been found in this part of Turkey so far (Kefelioğlu et al., 2003; Yiğit et al., 2006c). The striped field mouse had already reached the Caucasian region from the north in the Upper Pleistocene (Vereščagin, 1959).

Palaeontology. European records of Biharian and Toringian age are dubious and the striped field mouse most likely appeared during the Early Holocene (Kowalski, 2001). There are several securely dated Mesolithic records from the north-western Balkans in Slovenia (the oldest is $9,600-7,800$ years old; Toškan \& Kryštufek, 2006); slightly younger ( 7,000 years before present) is a report from Germany (Böhme, 1978a).


Figure 96. Distribution of Apodemus agrarius in Turkey and adjacent regions. Records: 1 - İğneada, Kırklareli; 2a - Üçgöller (= Sakalongus), east of Demirköy, Kırklareli; 2b - Demirköy, Kırklareli; 2c - 5 km south-west of Iğneada, Kırklareli, ca 50 m a.s.l.; 2d - 7 km north-west of Sivriler, Kırklareli, ca 50 m a.s.l.; 3a - Belgrad Ormani, İstanbul; 3b - Bahçeköy, Tekırdağ; 4 - Çamlıköy, Tekırdağ; 5a - Istranca, İstanbul; 5b - Karamandere, Karacaköy, İstanbul; 5c - Podima, İstanbul; 6a - Gökçeali, Çatalca, İstanbul; 6b - Subaşı, İstanbul; 6c - Akalan, İstanbul; 4 - Çamlıköy, Tekırdağ; 7 - Terkos, İstanbul; 8a-4 km west of Kemerburgaz, İstanbul; $\mathbf{8 b}$ - Kemerburgaz, İstanbul; $\mathbf{9}$ - Halkali, Altinşehir, İstanbul. Corresponding references: Kahmann (1961): 3a. Osborn (1965): 8a. Kurtonur (1972): 1, 3b, 5a, 5b, 5c, 6a, 6b, 6c, 4, 7, 9. Doğramaci (1974): 2a. Kefelioğlu et al. (2003): 2b, 8b. Our own material: 2c, 2d.

## Наbitat

Yiğit et al. (2006c) report A. agrarius to live "in deciduous forests consisting of oak, pine, beech, hazel, and hornbeam trees in the coastal regions of northern Thrace." Kahmann (1961) collected striped field mice in densely shaded places on damp ground, most commonly along streams and rivers. Osborn (1965) provides the following information on the habitat in European Turkey: dense vegetation beside a stream, blackberry thickets in and adjacent to a poplar plantation, and beech and chestnut coppice. In Turkish Thrace the striped field mouse was rarely obtained from parks (Kahmann, 1961) and never from the fields (Kahmann, 1962). Osborn $(1961,1965)$ reports an unusual occurrence within maquis along a stream that lacked water during summer; presence in such an atypical habitat could be due to a mass effect. We collected striped field mice in two habitats on the Black Sea slopes of the Istranca Mts.: dry hardwood deciduous forest (Carpinus betulus, Quercus sp.) near Iğneada and softwood forest (Alnus sp., Populus sp.) on sandy substrate with dense undergrowth


Figure 97. Habitat of Apodemus agrarius in Istranca Mts., Turkish Thrace. Photo: A. Kryštufek.
of stringing nettle (Urtica sp.) and close to a stream (near Sivriler).

Typical habitats in Bulgaria are wet and muddy places, shaded by poplar trees, willows and oaks, frequently in river valleys; A, agrarius also penetrates into fields (Peshev et al., 2004). Wide range of habitats is populated in Georgia: forests and clearings inside them, bushes, fields, orchards and gardens. The striped field mouse also enters farm houses (Šidlovskij, 1976).

Altitude. Striped field mouse is predominantly tied to lowlands, although does ascend into the mountains; the highest record from the Balkans is from an elevation of $1,700 \mathrm{~m}$ (Petrov, 1992). Altitudinal range in eastern Transcaucasia is from sea level up to 850 m a.s.l. (Ejgelis, 1980). Not surprising, and considering the topography of Turkish Thrace, majority of records are from low elevations (below 100 m a.s.l.).

Associates. On the Istranca Mts., we collected striped field mice in habitats dominated by A. flavicollis; Crocidura suaveolens was also captured in the same trap lines.

Density. Although the striped field mouse can be extremely numerous in flooded lowland forests in the northern part of the Balkan Peninsula, nowhere did we find it to be abundant in Turkish Thrace.

## Biology

Activity. Striped field mouse is more diurnal than other Apodemus species (Böhme, 1978a); we collected our specimens during the night.

Burrows. Šidlovskij (1976) reports for Georgia burrows with 3-4 entrances and 1-2 nests. Simple burrows, $30-40 \mathrm{~cm}$ deep, with a nest chamber lined by dry plant material, are reported from Bulgaria (Peshev et al., 2004).

Reproduction. Kahmann (1961) provides data on reproduction from the İstanbul area. Lactating females were collected already in the first week of June and were still found around mid-October. Body mass of reproductively active mice varied between 25 and 40.8 grams. Females with embryos were recorded between June 12 and September 5. Number of embryos was $4-6$ (mean $=5.1 ; \mathrm{N}=10$ ) which is in agreement with data elsewhere in Europe (Böhme, 1978a). Slightly higher values are reported from the western Balkans: mean $=5.9$, range $=4-7, \mathrm{~N}=15$ (Petrov,
1992). At the foothills of the Istranca Mts., we collected a single pregnant female (six embryos) on June 24. Reproductive season in Bulgaria lasts from March till September or early October, but reproduction is most intensive in May and June; number of embryos is 2-9 (mean = 6; Peshev et al., 2004).

Food. Feeding generalist with preference towards animal diet (arthropods, molluscs, annelids; Böhme, 1978a). Diet in Bulgaria consists of seeds, green plants and insects (Peshev et al., 2004). Our macroscopic observations of stomach contents are in agreement with this.

## Genus: Rattus Fischer, 1803

Small to large murins with long tail and no special external modifications (Fig. 98). Of the 66 species currently recognised by Musser \& Carleton (2005), only two are found in Turkey and Cyprus; both are largely commensal. Morphological separation between these two rats does not pose problems; cf. also determination keys in Miller (1912) and Niethammer \& Krapp (1978). For a detailed osteological comparison see Wolff et al. (1980). Musser \& Carleton (2005) divided Rattus into six groups


Figure 98. Rat Rattus. Drawing: J. Hošek.
(but not all species could be allocated to a particular group), placing the two species from the study area into the rattus and the norvegicus group, respectively. In older literature, rats are referred to under the generic name Epimys Trouessart, 1881.

## Key to species:

1 Ear longer (covering half of the eye when laid forward); tail uniformly dark, longer than head and body length; antero-labial cusp (t3) on $1^{\text {st }}$ upper molar well developed and separated from t2 by clearly visible re-entrant angle
R. rattus

1* Ear shorter (hardly reaching eye when laid forward); tail bicoloured, shorter than head and body; antero-labial cusp (t3) on $1^{\text {st }}$ upper molar much reduced, not separated from t 2 by re-entrant angle
R. norvegicus

## House rat - Rattus rattus

Mus rattus Linnaeus, 1758. Type loc.: Uppsala, Sweden.
Mus latipes Bennett,1835. Type loc.: Erzurum, northeast Turkey.

## Taxonomy

Two karyotypes, reported earlier for house rats, the Oceanian (or European; 2N = 38 or 40 ) and the Asiatic ( $2 \mathrm{~N}=42$; Niethammer, 1975a) represent two sibling species (Musser \& Carleton, 1993, 2005), Rattus rattus and R. tanezumi Temminck, 1844 (type loc.: Japan), respectively. Only the former occurs in the western Palaearctic.

## Description

External characters. Form slender, tail usually decidedly longer than head and body. Range for tail length relative to head and body is $99-144 \%$ in material from Turkey and Cyprus; only one specimen of 48 examined had tail shorter than head and body. In half of specimens the relative tail length is 115-130 $\%$. Head is narrow with a pointed muzzle; eyes are
large and ears are long; whiskers are long (up to 4865 mm ). Feet are quite robust, front ones with inner digit reduced to a mere tubercle (four digits); hind foot with five digits, the central three are the longest and subequal. Palm and sole are naked, with large and distinct pads; five pads on the front and six pads on the hind foot. Claws are simple, curved and strong, $3.5-4 \mathrm{~mm}$ long on front digits and $3.8-5.4 \mathrm{~mm}$ on hind ones. Tail has distinct annulations, uniformly but thinly haired throughout, with no clear terminal pencil. Pelage is soft but interspersed with thin bristles on the dorsal side; soft back hairs up to 10 mm long, protruding coarse hairs up to 27 mm in length.

Colour is variable even within the same population. Three colour types can be distinguished tentatively (Osborn, 1965). In one extreme ("rattus"), the back is almost black and belly is dark grey or dark slate; there is no demarcation line along flanks. Another extreme ("frugivorus") has pale (white to light


Figure 99. Skin of Rattus rattus in dorsal and ventral view. Based on an adult female from the district of Nicosia, Cyprus (NMW).
grey, yellowish white or pale buff) and sharply defined belly, and dark back which is blackish brown, dark grey brown, reddish brown or light brown. In the intermediate type ("alexandrinus"), back is dark to light brown or grey and belly is darker than in the previous type, albeit clearly paler than back; flanks are frequently grey and demarcation is faint. All three types co-occur locally and relative frequencies of individual morphotypes vary among localities. All possible intermediate stages connect these colour types.

Ventral side is normally blank, some populations however show pale to dark grey stripe on chest, which occasionally extends into abdomen or forms a more or less regular collar. Spot is rarely whitish and as such contrasts with dark belly.

Ears are dark grey-brown to black. Colour of feet varies from nearly white (occasionally with sharply defined grey metatarsal stripe), to grey or to slate. Tail is uniformly blackish; scales in older animals occasionally with white posterior margin.

Nipples. Miller (1912) and Niethammer \& Krapp (1978) report ten nipples, two pairs of pecto-
ral and three pairs of inguinal, respectively. The same count we found on a skin from Balıkesir (FMNH), however a female from Yalnız near Finike (BMNH 66.190) was found with three pectoral pairs, thus having 12 nipples in total.

Penis. The baculum of a specimen from Turkey was figured by Yiğit et al. (1998a: Fig. 8 on p. 210) and Yiğit et al. (2006c: Fig. 45B on p. 62). Proximal baculum has long stalk and short rhomboid proximal expansion; it is about 4.9 mm long and 1.8 mm wide across the base.

Skull. In comparison to other murins from the region, skull is strong and heavily built, and supraorbital ridges diverge posteriorly along parietals; close to occipital region they are slightly bent. No other peculiarities are evident. Rostrum is strong but narrow; nasals are long, evenly diverging towards blunt tip. Interorbital region is well defined, narrow (5.8-6.4 mm ), and short. Zygomatic arches are strong, moderately wide ( $=48.1-52.8 \%$ of condylobasal length); interparietal bone is triangular. Skull is moderately low (brain-case height across bullae $=12.6-14.7$


Figure 100. Skull and mandible of Rattus rattus, based on an adult male from Dhenia, 25 km west of Nicosia, Cyprus (SMF). Scale bar $=5 \mathrm{~mm}$.
mm ), lightly convex in lateral profile, occasionally slightly depressed in interorbital region; occipital is vertical. Nasals do not protrude forward much. Incisive foramen is relatively long, its anterior margin shifted well behind incisors; diastema is long. Posterior margin of the hard palate terminates behind $3^{\text {rd }}$ molars; it is straight and frequently with a medial protuberance. Interpterygoid region is broad, hamular process does not reach bulla; bulla fairly small. Mandible is robust, with strong processes.

Teeth. Incisors are strong and powerful, but do not deviate from the general murine plan. Enamel on upper incisors is mainly orange, on lower ones paler, yellow in nearly all specimens we saw. Molars are robust relative to skull size, anterior root of $1^{\text {st }}$ upper molar strongly projecting forward beyond the base of the crown. There is no trace of cingulum or accessory cusps on any upper molar; tubercles are connected to transverse laminas. First upper molar is the larg-

a

b

Figure 101. Upper (a) and lower molars (b) in Rattus rattus from Inçekum, 26 km north of Alanya (SMF). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
est, labial and lingual cusps of medial lamina nearly equal in size; cusp $t 7$ clearly smaller than $t 9$ and occasionally absent (cf. Fig. 6 on p. 245 in Kahmann \& Haedrich, 1957). Only two laminae on $2^{\text {nd }}$ upper molar; antero-labial cusp t3 very small or absent. Third upper molar with a single lamina formed by cusps t4-t5-t6. Biserial cusps form clear transverse laminae in lower molars. Mesial lamina on $1^{\text {st }}$ lower molar narrower than central and distal ones. Labial cingulum occasionally bears accessory tubercles on first two lower molars.

Number of roots on upper molars: 5 ( $1^{\text {st }}$ molar), 4 ( $2^{\text {nd }}$ molar), 3 ( $3^{\text {rd }}$ molar); lower row: 4 ( $1^{\text {st }}$ molar), 3 ( $2^{\text {nd }}$ and $3^{\text {rd }}$ molars). Coşkun (1991) reported for a specimen from Diyarbakir five alveoli for $2^{\text {nd }}$ upper molar and four alveoli for $2^{\text {nd }}$ lower molar.

Dimensions are given in Table 18. In central Europe, males are longer and particularly heavier (maximal body mass $=232 \mathrm{~g}$ ) than females ( 210 g ; Wolff


Figure 102. Alveolar pattern of the upper molars in Rattus rattus. Based on SMF specimens from Moni Profitis Elias near Lythrodontas, Troodos, Cyprus. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
et al., 1980). Similarly, in Cyprus, 28.5\% of males were $>200 \mathrm{~g}$ in body mass, as opposed to $12.6 \%$ of females ( $\mathrm{N}=1,358$; Watson, 1951a).

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 63 | 182.7 | $155-234$ |
| Tail | 60 | 216.9 | $180-269$ |
| Hind foot | 40 | 36.2 | $33.0-42.0$ |
| Ear | 30 | 23.7 | $20.0-26.0$ |
| Weight | 35 | 188.4 | $100-279$ |
| Condylobasal length | 60 | 42.5 | $38.0-46.4$ |
| Zygomatic breadth | 45 | 21.2 | $19.4-23.4$ |
| Maxillary tooth-row | 49 | 7.2 | $6.0-7.9$ |

Table 18. External and cranial dimensions of Rattus rattus from Turkey and Cyprus. Based on Neuhäuser (1936), Lehmann (1966a), Spitzenberger (1978a), and specimens in BMNH, FMNH, NMNH, SMF, and ZFMK.

Chromosomes. The diploid number of chromosomes is $2 \mathrm{~N}=38$ and the fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=58$. The autosomal set consists of 9 metacentric, 2 subtelocentric and 7 acrocentric pairs. Heteorosomes are acrocentric; the X is medium sized and the Y is the smallest element (Zima \& Král, 1984). Identical karyotype was found in European Turkey and in Anatolia (Yiğit et al., 1998a). Recently, Kankılıç et al. (2006) reported polymorphic populations from three localities in Turkish Thrace. Polymorphism reportedly affects three chromosomal pairs (nos. 9, 10, and 13) which are either acrocentric or subtelocentric due to pericentric inversions. We are hesitant to accept these results, which are entirely based on conventionally stained karyotypes. Thracian populations are reported also to have supernumerary chromosomes (one or two pairs of small metacentrics; Kankılıç et al., 2006), so far unknown in $R$. rattus.

## Variation

Colour types were frequently given a subspecific rank, which is rarely accepted in recent papers. Miller (1912), who recognised two subspecies (frugivorus and the nominate one) on colour grounds, believed that they have established themselves in Western Europe, "though now so completely intermingled in many localities that exact determination of specimens is often impossible". In the not-so distant past, Felten et al. (1971) still advocated a similar opinion on the basis of colour variation of house rats from western Anatolia. They reported differences in stiff hairs between sspp. frugivorus (hairs narrower and longer) and alexandrinus. Niethammer (1975a) was also supportive of the opinion that co-occurrence of two or more colour morphs results from the secondary admixture due to passive transportation of originally allopatric types. In the opinion of Harrison \& Bates (1991), various colour phases were selected under different environments, they predominate in certain habitats and act as ecological races. Therefore, rattus and alexandrinus colour types are predominantly synanthropic, while frugivorus colouration is typical for field rats on moist subsoil (cf. also Atallah, 1978). Our observations from Turkey and Cyprus (see below) mainly fit with such a distribution of the colour morphs. Yiğit et al. (2008a) proposed that three subspecies, based on colour types, occur in Turkey, but are linked by "intermediate colour stages."

All three colour types occur in Turkish Thrace (Kurtonur, 1972). In a large museum sample from Balıkesir in the Marmara region, all three types were present. Approximately $15 \%$ of specimens were transitional and their classification into one of the three morphotypes would be entirely arbitrary (Table 19). This is a common case one faces when classify-

| Region | N | "rattus" | "alexandrinus" | "frugivorus" | intermediate |
| :--- | :--- | :---: | :---: | :---: | :---: |
| Marmara | 61 | $44.2 \%$ | $32.8 \%$ | $8,2 \%$ | $14.8 \%$ |
| Antalya region | 16 |  | $25.0 \%$ | $75.0 \%$ |  |
| Adana region | 56 |  | $44.6 \%$ | $55.4 \%$ |  |
| Cyprus | 24 |  | $25.0 \%$ | $75.0 \%$ |  |
| Is. Gökçeada | 32 | $13.0 \%$ | $6.0 \%$ | $81.0 \%$ |  |
| Is. Bozcaada | 15 |  | $94.0 \%$ | $6.0 \%$ |  |

Table 19. Incidence of colour types in Rattus rattus according to regions. See text for definition of morphs. Based on Özkan (1995), specimens in BMNH, FMNH, NMNH, SMF, ZFMK, and our own material.
ing house rats according to colour types; e.g. Yiğit et al. (1998a) solved the difficulty by recognising the fourth type. Colour type, which is intermediate between alexandrinus and frugivorus is reported to be common in Lebanon (Lewis et al., 1967).

The darkest type ("rattus") is mainly restricted to the northern parts of Anatolia (including the Island of Gökçeada ; Özkan, 1987) and is largely synanthropic; Yiğit et al. (1998a) report it also for Ankara. On Cyprus, it is occasionally found in ports (Watson, 1951a). The remaining two morphs are widespread, and include a great majority of free living rats. All house rats which we saw from the southern coast and from Cyprus resembled frugivorus or alexandrinus type. Watson (1951a), who examined large samples, concluded that "All the rats seen in Cyprus were the variety of brown back and white belly which is usually given the subspecific name of frugivorus." Colour polymorphism is maintained also in the Arabian region; note that Aharoni (1932) reported the alexandrinus type under the name flaviventris.

Size varies with smallest rats occurring in central Europe (mean condylobasal length in adults from Austria is 38.2 mm ; Wolff et al., 1980), and largest rats in the Mediterranean region, including Turkey and Cyprus (Table 18). The house rats of Iran are possibly even larger, but the material we saw is scarce (mean condylobasal length $=45.5 \mathrm{~mm}$; range $=43.8-47.2 \mathrm{~mm} ; \mathrm{N}=4 ;$ BMNH specimens). Yiğit et al. (1998a) published, but not commented on, measurements (means and standard deviations) for three Turkish samples which deviate from our data. Mean condylobasal lengths for rats from Ankara ( 37.4 mm ; $\mathrm{N}=9$ ) and from Demirköy in Turkish Thrace (37.7 $\mathrm{mm}, \mathrm{N}=4$ ) are clearly less, while those for Antalya ( $42.7 \mathrm{~mm} ; \mathrm{N}=4$ ) match those reported in Table 18. We assume that differences are not genuine but rather result from a bias posed by age criteria applied.

Yiğit et al. (2008) assessed the geographic variation in Turkey on the basis of 16 allozymes coded for 22 presumptive loci. Mean heterozygosity among six geographic regions varied between $H_{e}=0.022$ (Thrace) and $H_{e}=0.059$ (Central Anatolia). Geographic samples were moderately different with $7.3 \%$ of genetic variation found among regions; gene flow between populations was moderate (Wright's F-estimator $F_{S T}=0.595$ ). Main divergence was between the Aegean and the Mediterranean sam-
ples (Kemalpaşa, Bayındır, Akseki, Alanya, Belek, Dalaman, Mersin, Nizip, Pozant, Adana, Nusaybin, Birecik, Ceylanpinar) on the one hand, and the remaining samples on the other. Within the later group, rats from Central Anatolia (Ankara, Düzce, Gerede) and the Black Sea region (Bartin, Zonguldak, Fatsa, Ordu, Trabzon, Artvin) clustered together.

## Distribution

Native to India and introduced worldwide in tropical and temperate regions where they are now common, albeit largely synanthropic, (Musser \& Carleton, 1993). In temperate regions of Europe and western Asia, house rats strongly depend on human settlements. Free living populations are common within the Mediterranean climate, hence rats are frequently the most widespread small mammals in the Mediterranean islands.

Widespread in Turkey but inland and along the northern coast mainly associated with human settlements. Since the house rat is water dependent, it is normally restricted to seashores and to valleys of the Euphrates and Tigris Rivers in Arabia (Harrison \& Bates, 1991). It is common and widespread on the Aegean islands offshore western Anatolian coast, including Gökçeada and Bozcaada (Özkan, 1987). In Cyprus, it is widespread from the sea coast up into the mountainous pine forest belt; the highest reported records are from 1,605 m (Landová et al. 2006) and 1,540 m (BNMH material).

Palaeontology. Fossil history of the genus Rattus is controversial in south-west Asia and the adjacent Balkans, and opinions diverge whether or not the house rat arrived to the Mediterranean basin independently or was passively transported by humans. The genus possibly invaded Europe for short periods during the Pleistocene, but is poorly represented in the fossil material from the south-eastern part of the continent (Kowalski, 2001). Besides, Pleistocene records are frequently considered dubious because of unclear stratigraphy and/or taxonomy; AudoinRouzeau \& Vigne (1994) ignored them entirely.

Two species were described from the Pleistocene (Toringian) of Romania: Rattus casimcensis Radulescu \& Samson, 1973 (Middle Pleistocene), and Rattus dobrogicus Terzea, 1973 (Upper Pleistocene); both are very similar to extant $R$. rattus (Storch, 2004). In the opinion of Kowalski (2001), these two fos-


Figure 103. Distribution of Rattus rattus in Turkey, Cyprus and adjacent countries. For further details on records see Appendix 4.
sil taxa represent a single species and $R$. casimcensis has priority over $R$. dobrogicus. A further fossil species, described from the Early Upper Pleistocene of Israel (R. haasi Tchernov, 1968), shows characteristics intermediate between $R$. rattus and $R$. norvegicus (Tchernov, 1968a).

Santel \& Koenigswald (1998) report R. rattus from the Middle Pleistocene of Yarımburgaz cave on the Istranca Mts. Since the material (left maxilla with all molars in place) was well fossilized, contamination by the recent material was considered improbable. The Middle Pleistocene record from the eastern Aegean Island of Chios and reported as "cf. Rattus sp." (Storch, 1975) actually belongs to the fossil genus Kritimys which might be closely related to African Praomys (Storch, 2004). Rattus kiridus Bate, 1942, from the Pleistocene of Crete is also a member of Kritimys (Storch, 2004). No Middle Pleistocene records of Rattus are known from Asia Minor (cf. Storch, 1988; Montuire et al., 1994).

The house rat appeared in Israel during the Upper Mousterian approximately 40,000 years ago and was continuously present in the region into the Holocene; e.g. a record in Jordan dates to 19,400 years before
present (Belmaker et al., 2001). Earlier colonisation of the region was presumably prevented by other large murids: $R$. haasi, Mastomys batei and Arvicanthis ectos Bate, 1942 (Tchernov, 1968a). When these fossil murins finally disappeared (during the Levalloiso-Mousterian), the black rat suddenly appeared and quickly spread (Tchernov, 1968a). The Upper Palaeolithic-Natufian R. rattus (approximately $10,000-20,000$ years before the present) morphologically differed only slightly from extant populations (Tchernov, 1968a).

Armitage (1994) believes that only extensive trade between the Indus Valley and Mesopotamia brought the species to the Near and Middle East in the $2^{\text {nd }}$ millennium $B C$, from where it reached the Mediterranean during the Roman period in the $2^{\text {nd }}$ century BC (Reumer, 1986). According to Tchernov (1984), the commensal black rat was widespread in the eastern Mediterranean, from Syria to Egypt, already by the start of the Holocene. At any rate, European records of the Neolithic and Bronze age are considered by some authorities to be in need of reconfirmation (Vigne \& Femolant, 1991; Au-doin-Rouzeau \& Vigne, 1994; Ervynck, 2002)
and the only reliable pre-Roman record is believed to be the one from the Swiss site of Hauterive-Champréveyres (1,050-1,030 years BC; Roguin \& Studer, 1991). From the coastal zone of the north-western Balkans, Toškan \& Kryštufek (2006) published a Late Broze/ Early Iron Age record (approximately 1,400-400 years BC). The record was ascribed to the maritime trade, as a presumed main agent of the black rat dispersion in the European Mediterranean (Armitage, 1994), between the Levant and Asia Minor on the one hand and the European Mediterranean (including the northern Adriatic) on the other. Such trade was well established by the Middle Bronze period at the latest (Toškan \& Kryštufek, 2006). Bauer (2001) accepts even earlier evidence from the European Mediterranean (Neolithic of Sardinia and Late Bronze Age of Spain) as being reliable.

Early Holocene records are rare in the region under study. The house rat was found in the Holocene layers of the Island of Kasos, in a typical association of human settlements (Kotsakis, 1990), but not on Chios (Besenecker et al., 1972; Kock, 1974). Records which predate the Hellenistic period are known from Asia Minor (Ervynck, 2002). Vereščagin (1959) reported the house rat from south-western Azerbaijan during the $1^{\text {st }}$ millennium; the earliest Georgian finds are also of the Holocene age (Vereščagin, 1959).

## Habitat

Throughout Turkey and Cyprus, the house rat occupies dwellings (houses, granaries, stables and farm buildings, mills and so forth). Along the Aegean and the Mediterranean coasts of Anatolia and in Cyprus it is abundant and widespread also outside buildings, either in urban and suburban areas (parks, gardens, orchards), in cultivated areas (hedgerows along fields) and in various types of shrubland, but is most common in humid places and in high maquis.

Non-commensal house rats live in a variety of disturbed habitats with dense woody vegetation. Humid and even damp places are preferred within the dry Mediterranean climate. In Marmara, specimens were captured in dense bushes of Rosa sp., Corylus avellana, Ligustrum sp., and Rubus sp. (Felten et al. 1971b). Along the western and southern Anatolian coast, rats were trapped in thickets of Rubus sp. and Rosa sp., along hedgerows, in rows of Arundo don-
$a x$, in eucalyptus stands, and in Liquidambar orientalis forests. Y üzbaş \& Benli (1995) recorded rats in abandoned yards in the provinces of Adana, Hatay, and Içel. Yiğit et al. (2003) report findings of the house rat for all twenty localities they sampled across Turkey; such a postulated widespread occurrence and wide habitat preferences are in sharp contrast with our field experience.

In Cyprus, house rats live wherever there is suitable cover, but dense shrubby maquis and forests are their main habitat (Watson, 1951a). Dominant plants in various shrubby successional stages inhabited by rats are Broteroa corymbosa, Cynara cardunculus, Scolymnus hispanicus, Echinops viscosus, Poterium spinosum, Lithospermum hispidulum, Coridothymus capitatus, Cistus villosus, C. parviflorus, Pistachia lentiscus, P. terebinthus, Calycotome villosa, Bosea cypria, Mytrus communis, Styrax officinalis, Smilax aspera, Acer obtusifolium, Nerium oleander, Cupressus sempervirens, and Pinus brutia (Watson, 1951a). Rats also occupy other types of dense vegetation (e.g. rows of Arundo donax) and plantations, particularly of Ceratonia siliqua. Shrub cover is essential in the Mediterranean and rats avoid clearings (Kutiel et al., 2000).

The dependency of $R$. rattus on water becomes critical in arid regions of Arabia. Lewis et al. (1967) did not collect specimens in the city of Beirut, or in extensive citrus and banana groves along the coast of Lebanon. On the other hand, rats were abundant along drainages with stagnant water, within stands of acacia and eucalyptus trees and in thickets of thorny


Figure 104. Habitat of Rattus rattus near Neo Chorio, Akmaz peninsula, Cyprus. Photo: I. Horáček.
shrubs (Lewis et al., 1967). Rats are very common and widespread in scrub woodland and agricultural areas of the Mediterranean zone in Israel. They are often the only mammal in the Aleppo pine plantations and occur in oases and mangrove areas (Mendelssohn \& Yom-Tov, 1999). In Transcaucasia, the house rat prefers dry places particularly where sympatric with $R$. norvegicus (Šidlovskij, 1976). In eastern Transcaucasia $R$. rattus locally occupies the lowland forest zone and semideserts; it is abundant nowhere (Ejgelis, 1980).

Altitude. Abundant at low elevations and along seashore. The highest reliable record from Anatolia known to us is a BMNH specimen collected in Çosandere (above Trabzon) at 1,200 m a.s.l. Yiğit et al. (2003) reported the black rat from high altitudinal steppe and grain fields at 1,700 m a.s.l. (10 km south of Van) and 1,829 m (between Kars and Ardahan); presence of outdoor rats at such high elevations seems unlikely to us. In Cyprus, the presence of rats is reported up to $1,605 \mathrm{~m}$ a.s.l. (Landová et al., 2006).

Associates. In Cyprus, we captured house rats, similarly as did Watson (1951a), along with Acomys cahirinus and Mus cypriacus. Misonne (1957) collected in Akçakale (south of Şanlıurfa ) rats in a village, and Meriones tristrami in its vicinity. The house rat occasionally co-occurs with the brown rat; see under that species.

Density. On Cyprus, the house rat seems to be by far the most abundant small mammal, particularly so in the maquis and, to a lesser extent, in forests (Watson, 1951a; Landová et al., 2006). A century ago, Bate (1903b) wrote that rats "are excessively common, being found everywhere, both in or near buildings and at distance from any inhabited house." From March 1947 to April 1948 Watson (1951a) executed a Capture-Recapture trapping on two plots near Kyrenia, on the seaward side of the Northern Range. His sampling "Area I" was on a sloping ground falling from ca. 250 m to 130 m with "a succession of vegetation from arable through fallow and heavily grazed ground to slightly grazed land and areas impenetrable to domestic animals"; rocky outcrops were common on one part of the grid and there was also a small perennial spring. The second trapping area (Area II) "included a steep sided gulley with a perennial stream at the bottom, on one side grew car-
ob and olive trees"; the remaining vegetation was the natural climax forest of pine (Pinus brutia) and cypress (Cupressus sempervirens). These two areas encompassed a complete succession from arable land to a forest climax. In total, Watson (1951a) caught 100 rats in Area I (surface area $=12.95 \mathrm{ha}$ ) and 50 rats in Area II (6.9 ha); percentage of the animals recaptured in subsequent periods was low (52.0\% and 62.8\%, respectively), possibly a result of trap shyness. Rat population remained relatively stable and number of animals was the highest in the winter months (December to January), evidently a consequence of a large number of young rats following the late summer breeding season. The population was the lowest in June with no juveniles recruited. During January, 33 rats were presumably present in Area I and 19 rats in Area II, thus giving densities of 2.5 and 2.8 animals per hectare, respectively. Watson (1951a) interpreted these figures as minimal estimates. Rats were not evenly distributed across the habitat mosaic, but concentrated particularly "in the boulder-strewn piece of ground with macchie [= maquis] vegetation $\ldots$, an area of about 3.5 acres [ $=1.4$ ha]"; 19 animals were known to be living there (density of 13.6 rats per ha). Removal trapping in another grid with a surface area of 3.24 ha, resulted in 78 rats killed in the course of the year. Fourteen rats were trapped during the last three weeks of July 1947 alone, i.e. during the summer population bottom. The habitat was a valley bottom with oleander (Nerium oleander) thickets and dense maquis on either side. Populations on cultivated ground with carob and olive trees were much smaller; a density of 2-4 rats per hectare (1-2 per acre) was estimated in plantations where severe damage to carob trees occurred. Watson (1951a) found no evidence of population outbreaks and believes that rat numbers fluctuate slowly over a number of years. Climate fluctuations were unlikely responsible for population changes. Two peaks in damage to carob trees in 1938 and 1945 were possibly indicative of the abundance of rats in Cyprus (Watson, 1951a).

A situation similar to Cyprus can be expected on the Aegean islands offshore of the western Anatolian coast. On the two Turkish islands, Gökçeada and Bozcaada, the proportion of house rats in a small mammal assemblage was $19.5 \%$ and $9.6 \%$ respectively (Özkan \& Kryštufek, 1999), but might be an underestimate due to trapping bias. We found rats
to be very abundant on the islands of Rhodes and Kos, where lines of small museum special traps were invariably disturbed by rats.

The house rat is very abundant locally in human settlements as well; cf. Misonne (1957) who reported for Akçakale, Şanlı Urfa and adjacent Syria, 1947 to be a plague year.

## Biology

Activity. House rats are active at all hours of the day or night (Atallah, 1978). They climb well and also move through the canopy (Šidlovskij, 1976), "often at a considerable height above ground" (Bate, 1903b). Nests are frequently constructed above ground, on trees, palms, in high maquies and in bushes. On Cyprus, Watson (1951a) only rarely collected marked rats more than 90 m (100 yards) from the site of first capture (8.4\% of records); an outlier of 485 m poses doubt as to the correct identification of the recaptured individual. Thus, rats tended to remain in a relatively small area with a radius of 45-90 m (50100 yards; Watson, 1951a). Males tended to move further than females; Watson (1951a) found that a distance $>90 \mathrm{~m}$ was covered by $37 \%$ of males but only by $13 \%$ of females (sample sizes were 35 males and 31 females). Only six animals of a total 66 travelled $>180 \mathrm{~m}$. Reinvasion of an area after the removal of rat population was therefore believed to be a rather slow process on Cyprus (Watson, 1951a).

Burrows and Nests. Bate (1903b) described nests constructed by rats in a dense cover of brambles and bushes on high stream banks in the Papho District of Cyprus. Nests, generally at height of 2.5-3 m, were "loosely made of leaves and coarse herbage, and lined with finer grasses, or else entirely composed of leaves of the tall bamboo-like reeds that edge the streams here and there. The entrance is at one side of the nest, which is flatly domed like a squirrel's drey, and, from casual inspection, would appear to be nothing more than a bunch of rubbish or dead leaves, which the thickness of the vegetation prevented from falling to the ground." In Lebanon, Atallah (1978) found nests on mimosa trees (Acacia cyanophylla) about 2.5 m above the ground; they were made of densely packed mimosa leaves and twigs. Lewis et al. (1967) reported nests to be 1.5 m in diameter, loosely constructed of twigs and dried leaves and grasses. Kahmann \& Haedrich
(1957) found on the Island of Corsica nests on a variety of tree species from 1.8 to 7 m above ground; cf. their paper for a photograph of such a nest (Fig. 7 on p. 251). Nests of twigs and leaves and located in tea bushes and in citrus plantations are reported from Transcaucasia (Šidlovskij, 1976).

Atallah (1978) located burrows under stones, along houses and beneath mimosa trees. Lewis et al. (1967) state that rats maintain burrows in the ground beneath the trees with nests. Watson (1951a) suggested that in Cyprus, dense maquis provides the best cover, while on arable land animals find shelter in terrace walls and in hollow olive and carob trees.

Reproduction. A detailed study from Cyprus was done by Watson (1951a,b) who dissected 1,258 rats collected between March 1947 and April 1948. Sex ratio of the entire sample was slightly skewed towards females (= 53 \%). Males, however, dominated among the youngest animals with body mass <50 g ( $60.6 \%$ ) and again among those with mass $>200$ g (66.7 \%). Their preponderance among the heaviest animals was possibly due to males growing to a larger size than do females (Watson, 1951a). Rats in breeding condition were trapped in every month of the year except for January. All females with a body mass >150 g showed macroscopically visible corpora lutea in the ovaries, indicating that ovulation had taken place. Between late March and early November, 37.5 \% of females with a body mass 7080 g already showed corpora lutea; this size class was shifted to $80-90 \mathrm{~g}$ for the rest of the year. The median body weight at which females reached maturity was 78 g in March and 97 g in November. Watson (1951a) estimated age of maturity to be between three and four months. Among 572 examined females, 12.9 \% were pregnant; the proportion correlated positively with body mass. Breeding activity was greatest in March, April and September, when $30 \%$ of adult females were visibly pregnant. The proportion of young rats ( $<75 \mathrm{~g}$ ) fluctuated widely from month to month and peaked in May - June and November. The chief breeding seasons in Cyprus were spring and late summer, while reproductive activity was lowest in mid winter. A spring peak in breeding activity, however, had little effect on rat population in plots studied by Watson (1951a). Number of embryos varied between 1 and 11 (mean = 6.5; $\mathrm{N}=74$ ). Due to an appreciable intrauterine mortal-
ity, litter size at birth was nearer 5 than 6 (Watson, 1951a).

Very few data are available from the rest of the region. Lactating females were collected in Turkey in nearly all months of the year, indicating a year round reproduction. One female, captured in June near Antalya, had 7 embryos (Felten et al., 1971). In April, two nests in Lebanon contained 4 and 6 juveniles, respectively (Atallah, 1978; Lewis et al., 1967). Reproduction in Armenia is year-round with five litters per female, each litter with 1-8 young (Dahl, 1954). Contrary to this, Šidlovskij (1976) reported reproduction from Transcaucasia only during the warm season; females produce 2-3 litters each, and the maximum litter size is nine.

Food. Omnivorous. Harrison \& Bates (1991) reported diet of human foodstuffs, crops, seeds, fruits, insects and molluscs; rats also prey on fish (Aharoni, 1932), Uca crabs, bird eggs and chicks (Mendelssohn \& Yom-Tov, 1999), beetles, mantis, ants, crickets and freshwater crabs (Kahmann \& Çağlar, 1970). Šidlovskij (1976) reported predominantly vegetarian diet in Transcaucasia. A study of free living rats in the province of Hatay revealed the predominance of vegetable items (Kahmann \& Çağlar, 1970).

Rats occupying forests in Cyprus feed on the seeds of the Aleppo pine (Pinus brutia), but not of Pinus nigra which are consumed by crossbills (Loxia curvirostris). Rats gnaw off scales of the cone close their base (Watson, 1951a) by using exclusively the spiral stripping technique (Landová et al., 2006). Watson (1951a) suggests that rats on Cyprus "take advantage of an ecological niche which is filled elsewhere by the squirrel, an animal which is not found on the island." Rats have developed a special technique for opening pine seeds and young animals have to learn this from their mothers otherwise they usually do not survive in pine plantations in Israel (Mendelssohn \& Yom-Tov, 1999), and at high elevations in Cyprus, where pine seeds are presumably the only available source of food (Landová et al., 2006). The tradition of pinecone opening possibly arouse independently in rats living in Israel and in Cyprus (Landová et al., 2006). The maquis, however, which is seemingly the chief rat habitat on Cyprus, is believed to contain "a continuous and varied food supply throughout the year." (Watson, 1951a).


Figure 105. Cache of pinecones striped by black rats Rattus rattus near Neo Chorio on Akmaz peninsula, Cyprus. Photo: I. Horáček.

On plantations, rats make use of crops growing under the trees and store barley and wheat ears in the hollow branches, particularly so in May, before the harvest (Watson, 1951a). Caches of closed and stripped pinecones were found in caves in Cyprus (Fig. 105); the largest cache contained about $1 \mathrm{~m}^{3}$ of cones, thus suggesting that such places had been in use for years (Landová et al., 2006).

From, Hatay, damage to the fruit of fig (Ficus carica), pomegranate (Punica granatum) and orange (Citrus aurantia) trees were reported; the bark of the cypress (Cupressus sempervirens) and of orange trees were also frequently damaged (Kahmann \& Çağlar, 1970). Similar damage to fruit and bark is also known in mandarin and lemon plantations in Transcaucasia (Šidlovskij, 1976).

The majority of the damage done on Cyprus is to the carob tree (Ceratonia siliqua), with a total loss to the carob crop about 3\% in the 1940s (Watson, 1951a). Rats remove short strips of bark ( ca 2.5-5 cm long and 0.65 cm wide) and eat the cambium layer (Plates 11-14 in Watson, 1951a). This damage is done throughout the year with the exception of winter (November to February) and is at its worst in late summer (August to September). Particularly selected for attack are fresh shoots, however, branches up to 10 cm in diameter are also occasionally stripped.

The proportion of trees attacked is approximately 15 \% and bearing capacity of attacked trees is reduced at 20 \% (Watson, 1951a). In late winter (January to March) rats strip also lemon trees and in spring they attack buds about to open on the shoots of the mulberry trees (cf. Plate 15 in Watson, 1951a). Occasional damage is also reported to ripe pomegranates, oranges, ripening almonds and on fields of beans (Watson, 1951a). Little serious damage is done by house rat in stores and warehouses in Cyprus (Wats on, 1951a).

Predation. Surprisingly few records from owl pellets have been published so far from Turkey (Nadachowski et al., 1999). Obuch (1994) did not record a single incidence in his extensive samples from the country. Our pellet sample from Harran (Şanlıurfa) contained only few house rats and Seçkin \& Coşkun (2006) reported on a single specimen preyed upon by Asio otus. Spitzenberger (1978a) found $R$. rattus to be common in barn owl Tyto alba pellets in Cyprus. Niethammer (1989) report few unidentified rat remnants from barn owl pellets from the Island of Kos, and we recorded house rats in pellets of an unidentified owl from Rhodes. House rats were found in owl pellets in Syria (Nadachowski et al., 1990) and are preyed upon by the barn owl in Israel (Rifai et al., 1998). Watson (1951a) who studied the ecology of the house rat in Cyprus in great detail, assumed that the fox and two snakes (Coluber gemonesis and Vipera libetina) may be important predators, but was unable to provide any evidence in support of this.

Remarks. The house rat is believed to be one of the main carriers of bubonic plague in the Near East (Harrison \& Bates, 1991). Anatolia constantly suffered from the plague. Major epidemics struck until the 1840s while in eastern Anatolia, minor outbreaks lasted into the 1890s. The plague was present in Ottoman cities so often that it was almost a common disease. Between 1701 and 1844 (i.e. during 144 years), the city of İstanbul suffered from plague epidemics in a total of 94 years and İzmir in 78 years. Strikes in 11 years (İstanbul) and 15 years (İzmir) were strong or terrible. During the great epidemic of 1786 an estimated one third of the population of İstanbul died (McCarthy, 1997). Outbreaks in Palestine have been reported until 1947 (Qumsiyeh, 1996).

For control measures in the Mediterranean landscape see Watson (1951a).

## Brown rat - Rattus norvegicus

Mus norvegicus Berkenhout, 1769. Type loc.: Great Britain.

## Description

External characters. Form robust, tail usually decidedly shorter than head and body. Range for tail length relative to head and body is 62-100 \% in Turkey (on average about $85 \%$ ). Head is stronger with blunter muzzle than in $R$. rattus; eyes are smaller and ears are shorter; whiskers are long (up to 48 mm ).


Figure 106. Skin of Rattus norvegicus in dorsal and ventral view. Based on an adult female from Samsun (BMNH). Photo: B. Kryštufek.

Feet are more robust than in the previous species, but other peculiarities remain the same. Claws are simple, curved and strong, 4 mm long on front digits and up to 5.4 mm on hind ones. Tail annulations are less distinct that in $R$. rattus; bristles less numerous and pelage consequently softer.

While adult brown rats differ clearly from $R$. rattus, more slender juveniles with a pointed muzzle and relatively larger ears can be misidentified as house rats. Relative tail length, however, remains constant regardless of age.

Colour on the back is variable mixture of dull ochraceous brown to dark brown and slate grey; it is interspersed by black hair tips. Head, shoulders and spine are the darkest; flanks are more buff or grey; belly is greyish white of varying intensity, occasionally washed with buff; demarcation line is either relatively sharp or entirely faded. Ears are grey brown, feet pale grey to nearly white; tail indistinctly bi-coloured, greyish brown above, pale below.

NippLes. There are twelve nipples, three pairs of
pectoral and three pairs of inguinal, respectively (Fig. 106).

Penis. The baculum of a specimen from Turkey is figured by Yiğit et al. (1998a: Fig. 5 on p. 208; 2006c: Fig. 45A on p. 62). Proximal baculum has long stalk and short triangular proximal expansion; it is of about same size as in $R$. rattus.

Skull is strong and heavily built. Brain-case is narrow and nearly sub-cylindrical, supraorbital ridges ran mainly parallel along parietals. In other respects, the skull closely resembles that of $R$. rattus, except that palate is broader behind, bullae relatively smaller and incisive foramen slightly shorter. Mandibular processes are more robust, particularly the angular and the articular.

Teeth are essentially as in $R$. rattus. Cingulum tends to be better developed at anterior base of $1^{\text {st }}$ molar crown, occasionally with accessory cusplets. Tubercle t 3 is much suppressed on $1^{\text {st }}$ upper molar; antero-labail re-entrant angle is frequently missing due to fusion of t 3 with t2. Labial margin of lower


Figure 107. Skull and mandible of Rattus norvegicus, based on an adult male from Akçakoca, north of Düzce, district Bolu $(S M F)$. Scale bar $=5 \mathrm{~mm}$.


Figure 108. Upper (a) and lower molars (b) in Rattus norvegicus (same specimen as in Fig. 107). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
molars never has accessory tubercles. Alveolar pattern is same as in $R$. rattus.

Dimensions are given in Table 20. Yiğit et al. (1998a) published means and standard deviations for a sample of eight brown rats from Anatolia (in mm, body mass in grams): length of head and body 217.3 $\pm 41.4$; length of tail $187.4 \pm 22.3$; length of hind foot $43.0 \pm 3.1$, ear length $22.3 \pm 0.7$, condylobasal length $45.4 \pm 3.2$, zygomatic breadth $23.8 \pm 2.5$, maxillary molars $7.4 \pm 0.6$; body mass $259 \pm 85.2$.

In central Europe, males are on average heavier, but maximal body mass was recorded in a female (470 g; Wolff et al., 1980). The largest body mass reported by Šidlovskij (1976) from Transcaucasia was 522 grams.

Chromosomes. The diploid number is $2 \mathrm{~N}=42$, and the fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=62$. The autosomal set includes 7 medium to small metacentric, 4 submetacentric and 9 acrocentric pairs. Heterosomes are acrocentric; the X chromosome is of medium size and the Y chromosome is small (Zima \& Král, 1984). Identical karyotype

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 9 | 222.9 | $192-255$ |
| Tail | 9 | 187.9 | $145-216$ |
| Hind foot | 9 | 41.6 | $38.0-44.0$ |
| Ear | 9 | 21.5 | $20.0-23.0$ |
| Weight | 1 | 498 |  |
| Condylobasal length | 10 | 45.5 | $40.8-51.2$ |
| Zygomatic breadth | 9 | 24.2 | $22.5-26.1$ |
| Maxillary tooth-row | 10 | 7.3 | $6.5-8.3$ |

Table 20. External and cranial dimensions of Rattus norvegicus from Turkey; included are also three specimens from Lebanon (Lewis et al., 1967) and a specimen from Syria (Ras al-Ain; SMF). Other sources: Neuhäuser (1936) and specimens in BMNH, FMNH, and SMF.
was found in brown rats from Anatolia (Yiğit et al., 1998a).

## Variation

Contrary to the house rat, the brown rat is surprisingly stable morphologically and no subspecies are recognised from the western Palaearctic (Becker, 1978).

## Distribution

The brown rat is presumably native to south-eastern Siberia and northern China but is now cosmopolitan in boreal and temperate regions. In tropics and subtropics where the brown rat is outnumbered by the house rat, it depends heavily on human dwellings and significantly disturbed habitats. In Turkey, the brown rat is presumably widespread in Thrace, but it is perhaps absent from the eastern and Central Anatolia (cf. map 6 on p. 43 in Sokolov \& Karasjova, 1990); in any case, records are few, regardless of the region. Özkan (1997) reports the brown rat for the Island of Gökçeada. The brown rat is much less widespread on the Aegean islands than R. rattus; Becker (1978) reported the brown rat from the following islands: Rhodes, Karpathos, Crete, Kos, and Ikaria. Presence on Cyprus is dubious. Harrison (1972) and Harrison \& Bates (1991) plot a dot onto the island but, as shown by Spitzenberger (1978), no reliable report is available. Watson (1951a) states for Cyprus that "The brown rat $R$. norvegicus also occasionally turns up in the ports but none were encountered elsewhere."

The brown rat has successfully invaded seaports


Figure 109. Distribution of Rattus norvegicus in Turkey, Cyprus and adjacent regions. Tentative range (shaded) is modified from Sokolov \& Karasjova (1990). Records: 1 - Island of Gökçeada; 2 - Keşan, Edirne; $\mathbf{3}$ - Tekirdağ; $\mathbf{4}$ - European part of İstanbul (localities: Tünel, Aksaray, Kasımpaşa); 5 - Akçakoca, Bolu; 6 - Zonguldak; 7 - Bartin, Zonguldak; 8 - Ankara; 9 - Samsun; 10 - Rize; 11 - Topboğazı Geçidi, Belen, Hatay; 12 - Iskenderun, Hatay; 13 - Ömer Gölü, Yumurtalık, Adana; 14 - Adana; 15 - Berdan river, near Tarsus, Mersin; 16 - Mersin; 17 - Island of Cyprus. Greek islands: $\mathbf{1 8}$ - Crete; 19 - Karpathos; 20 - Rhodes; 21 - Kos; 22 - Ikaria. Corresponding references: Neuhäuser (1936a): 6, 7, 10, 16. Watson (1951a): 17. Felten et al. (1971b): 5. Kurtonur (1975): 3, 4. Becker (1978): 18 - 22. Winden \& Bosman (1988): 13, 15. Obuch (1994): 11. Yiğit et al. (1998b): 8, 9. Özkan \& Kryštufek (1999): 1. Verimli et al. (2000b): 14. FMNH: 12. Our own data: 2.
and major urban centres in the northern part of Arabia, but is absent from the arid inland (Harrison \& Bates, 1991). In Transcaucasia, Šidlovskij (1976) mapped its range only along main rivers; contrary to this, Sokolov \& Karasjova (1990) provide records which cover majority of the region. In 1960s, free-living brown rats were still spreading their range in Transcaucasia, which originally encompassed the Black Sea seashore, the Colchic marshes and tributaries of the River Araks southward to Erevan; the main vector of spreading was supposedly railways and the motor-car traffic (Šidlovskij, 1976).

Palaeontology. No fossil records are known from Europe (Kowalski, 2001), the Near East (Tchernov, 1968a) and Transcaucasia (Vereščagin, 1959). Earliest occurrence of the brown rat in the region is from the $1^{\text {st }}$ to $9^{\text {th }}$ century from Yemen and the Per-
sian Gulf (Sokolov \& Karasjova, 1990). On the northern side of the Caucasus, the brown rat appeared during the $14^{\text {th }}$ centry (Vereščagin, 1959). Although the species was already reported in Palestine by Tristram (1866), it appeared in Tel Aviv only in 1936 (Mendelssohn \& Yom-Tov, 1999).

## Habitat

Mainly commensal throughout Europe, Transcaucasia and the Near East. For the eastern Mediterranean coast, where the brown rat prefers more mesic areas than the house rat (Qumsiyeh, 1996), Harrison \& Bates (1991) reported the former to occupy cities and ports, garbage piles, warehouses, houses, shops, slaughterhouses, lavatories and irrigation canals. Similar habitats are populated also in Transcaucasia: cellars of inhabited buildings, wet places
in stables and store-houses, etc. (Šidlovskij, 1976). Neuhäuser (1936) found the brown rat to be common in Turkey, but restricted to coastal regions. Kurtonur (1975) collected brown rats only in a corpse store and a slaughterhouse in Thrace, but they were far less common than house rats. The FMNH specimens were collected in a house in the town of Iskenderum, Hatay.

Free living brown rats are common along the Meriç River in Thrace (B. Özkan, personal communication) and in small fishery ports along the Black Sea coast (H. Kefelioğlu, personal communication). Felten et al. (1971) collected one specimen in dense bushes at the estuary of a small river not far from inhabited houses of Akçakoca, Bolu. In Transcaucasia, free living populations were found along river banks and lake shores, in marshes and in dense vegetation along fields (Šidlovskij, 1976). In eastern Transcaucasia, free-living populations inhabit the zone of lowland forests and semidesert, isolates were also found in the steppic habitats of the Talyš plateau; in dry habitats they are restricted to lakes and irrigation ditches. The brown rat is more sensitive to winter colds than other rodents living in the same environment. It also occurs on several islands in the Caspian Sea (Ejgelis, 1980).

Altitude. All Turkish records are from low elevations. The same situation is found in Transcaucasia, where the occurrence at high elevations (up to 1,800 m) depends on man's presence (Šidlovskij, 1976). Free-living populations range from sea level up to 300 m a.s.l. in eastern Transcaucasia (Ejgelis, 1980). In Daghestan, commensal rats were found up to 1,0001,700 m high (Sokolov \& Karasjova, 1990).

Associates. The two rat species co-occur on the island of Gökçeada (Özkan, 1997), but the house rat is by far more numerous ( $3 R$. norvegicus : $32 R$. rattus; Özkan \& Kryštufek, 1999). No other data are available from Turkey. In the Balkans, the brown rat was occasionally collected along with $R$. rattus, both in buildings and outside them. Habitats, populated by the brown rat yielded also the following small mammals: Crocidura suaveolens, Mus domesticus, Apodemus sylvaticus, A. agrarius, and Micromys minutus.

Lewis et al. (1967) found brown rats to be extremely common in the city of Beirut whereas house rats have not been collected at all. In Transcaucasia, where both rat species are found in the same build-
ing, brown rats dwell at ground level while house rats exploit attics (Šidlovskij, 1976). Inside buildings, the house rat tends to construct nests at higher places when sympatric with the brown rat (Mendelssohn \& Yom-Tov, 1999). Brown rats attack and kill house rats, consequently they displaced them in many places in the high humidity coastal zone of Israel (Mendelssohn \& Yom-Tov, 1999). In the Colchidic marshes in western Georgia, the brown rat is replacing the water vole Arvicola amphibius (Šidlovskij, 1976).

Density. Locally abundant; see case studies cited above.

## Biology

While the brown rat is considered a significant pest, its albino form is widespread in laboratories worldwide. Not surprisingly, the biology of this species has been studied thoroughly (cf. Sokolov \& Karasjova, 1990; Corbet \& Harris, 1991). Contrary to this, data from the region under study are very scarce.

Activity is predominately nocturnal but rats were observed also during daytime (Atallah, 1978). As already stated, the brown rat is a less active climber than the house rat and is frequently restricted in buildings to cellars and ground floors (Bodenheimer, 1958). Swims and dives well (Mendelssohn \& Yom-Tov, 1999).

Burrows are dug along stream banks and sewage steams (Qumsiyeh, 1996). Nests are underground, only rarely in hidden places above ground, but never high up (Mendelssohn \& Yom-Tov, 1999).

Reproduction. No data are available from Turkey. For Armenia, Dahl (1954) reports sexual maturity of females at the age of three months and up to five litters per year, each with $2-12$ young. Šidlovskij (1976) states for Transcaucasia all year round reproduction with litter size up to 15 young.

Food. The brown rat is an omnivorous and adaptable feeder. Harrison \& Bates (1991) report wide variety of food consumed: carrion, eggs, refuse, grain etc.; it also attacks chickens and even larger animals. Fish carrion is consumed on the Black Sea coast of Turkey.

Predation. Obuch (1994) found brown rat remnants in pellets of Strix aluco from Hatay. Juvenile and subadult rats are preyed upon by the barn owl Tyto alba in Syria (Shehab, 2005).

## Genus: Nesokia Gray, 1842

Rat-like rodents, with high-crowned and laminated molars. Musser \& Carleton (2005) placed Nesokia into Rattus division, with Bandicota Gray, 1873, as its closest relative. The genus of two recent species predominantly occurs in Asia. A long-tailed and amphibious N. bunnii (Khajuria, 1981) is known only in the marshlands at the confluence of the Tigris and Euphrates rivers in south-eastern Iraq; populations are declining and the species is listed as endangered (IUCN, 2008). A short-tailed and fossorial $N$. indica has a wide range which also marginally captures Turkey.

## Short-tailed nesokia - Nesokia indica

Arvicola indica Gray and Hardwicke, 1832. Type loc.: India (uncertain; Ellerman \& MorrisonScott, 1951; Musser \& Carleton, 2005).

## Description

External characters. Rat-like rodent with a robust body and short, thick tail (relative length to head and body length about 55-60 \%). The head is heavy and broad; the muzzle is deep and less pointed than in Rattus. Sparsely haired ears are relatively short; eyes are well developed. The mystacial vibrissae are short (up to 40 mm ). The limbs are robust and scantily haired; hind foot is much longer than forefoot. There are four front and five hind digits with sharp, nearly straight claws (length $5.1-5.6 \mathrm{~mm}$ ). Palm and sole are naked, with six and five pads, respectively; pads are comparatively small (cf. Fig. 208 on p. 435 in Gromov et al., 1963). Pelage is relatively soft and long (up to 15 mm on posterior back), scattered with coarse guard hairs (up to 25 mm long) projecting from the shoulders backward. Ventral hairs are short (up to $7-8 \mathrm{~mm}$ ). Tail is sparsely haired, almost naked and scaly, with no terminal tuft.

Colour is variable. Back is sandy fawn, pale brown, greyish-brown or reddish-brown; front and


Figure 110. Short-tailed nesokia Nesokia indica. Drawing: J. Hošek.
snout are darker. Side is buffy and belly is either buffy grey or greyish white, with a white patch on the throat which varies individually; demarcation line along flanks is faint. Hair bases are slate grey. Whiskers are black or white; ears and paws are grey brown; tail is blackish brown, only slightly darker dorsally.

Nipples. There are two pairs of pectoral and two pairs of inguinal nipples (eight mammae in total).

Skull (Fig. 112) is strong, broad, deep and angular. Rostrum is short and heavy; the nasals do not tip over praemaxillary bone and incisors. The interorbital region is wide and the brain-case is convex and strongly ridged; supratemporal ridges extend from


Figure 111. Skin of Nesokia indica in dorsal and ventral view. Based on a young adult female from Ahwaz, south-west Iran (NM 40,800).
Photo: B. Kryštufek.
the fronto-maxillary suture backward to the lambdoid crests. Zygomatic arches are widely expanded, equalling 61-64.4 \% of condylobasal skull length; masseteric plate is expanded, its anterior edge is usually straight. Lacrimals are minute in size. Incisive foramens are narrow and shorter than half of length of diastema. Hard palate terminates at the posterior alveolar margin of $3^{\text {rd }}$ molars. Interpterygoid region is comparatively wide and bullae are small. Mandible is short, robust and powerful. All processes are short but heavy; the lower incisor root forms a prominent alveolar process on the labial side, which is slightly lower than the articular process (Fig. 113).

Teeth. Upper incisors are slightly proodont, heavy and robust, coated in a yellow to orange enamel. Lower incisors are evidently longer, with paler enamel on their front surface. Molars are high-crowned, broad and transversely laminated. First molar is the longest, with three simple laminas, $2^{\text {nd }}$ and $3^{\text {rd }}$ molar are of descending size, with two laminas each. Cuspidation is seen only in very young animals. Cusps merge into laminas with advanced age and closed dental islets emerge in very old animals.

Dimensions. Although Osborn \& Helmy (1980) reported sexes to be subequal in Egypt, Hussain et al. (2002) found adult males to be significantly larger in Pakistan.

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 12 | 204.5 | $175-240$ |
| Tail | 29 | 130.1 | $95-145$ |
| Hind foot | 29 | 38.9 | $32-45$ |
| Ear | 25 | 18.1 | $13-22$ |
| Weight | 6 | 300.0 | $237-350$ |
| Condylobasal length | 24 | 45.6 | $38.5-52.7$ |
| Zygomatic breadth | 24 | 29.1 | $24.4-33.1$ |
| Maxillary tooth-row | 30 | 9.7 | $7.5-11.2$ |

Table 21. External and cranial dimensions of Nesokia indica from the Near and Middle East, with the exception of $N$. i. buxtoni. Sources: Aharoni (1932), Atallah (1977), Kock \& Nader (1983), Harrison \& Bates (1991), Mendelssohn \& Yom-Tov (1999), Misonne (1975), and specimens in NM.

Chromosomes. Diploid number in specimens from Iran was $2 \mathrm{~N}=42$ (Kamali, 1975). The karyotype of specimens from Tadjikistan was $2 \mathrm{~N}=42$ and $\mathrm{NF}_{\mathrm{a}}=$ 54; there were 7 pairs of metacentric and 13 pairs of


Figure 112. Skull and mandible of Nesokia indica, based on a young adult female from Mosul, Iraq (NMW). Scale bar = 10 mm.
acrocentric chromosomes; the X and Y were the largest metacentrics in the set (Král, 1971). Sex chromosomes are large due to additional constitutive heterochromatin. The X chromosome is polymorphic for


Figure 113. Caudal view of right ramus mandibulae of Nesokia indica from Ahwaz, south-west Iran (NM 40,800). al - alveolar process; an - angular process; ar - articular process; co - coronoid process. Scale bar $=5 \mathrm{~mm}$.
the amount of constitutive heterochromatin (Dubey \& Raman, 1992) which results in only partially synapsed heterochromatic arms in X bivalents (Singh \& Raman, 1993).

## Variation

A substantial geographic variation possibly points to more than one single species, but this still has to be assessed (Gromov \& Erbajeva, 1995; Musser \& Carleton, 2005). Size varies significantly, with adult body mass in Pakistan being 112-177 g (Roberts, 1997) and in Egypt 205-280 g (Osborn \& Helmy, 1980). Distinct colour morphs intergrade (Corbet, 1978), but colour is also affected by moult (Lay, 1967). Ellerman \& Morrison-Scott (1951) tentatively recognized nine subspecies while Corbet (1978) retained only three. Harrison \& Bates (1991) reported three subspecies for the Near and Middle East: N. i. buxtoni Thomas, 1919 (Type loc.: Amara, Iraq), N. i. bacheri Nehring, 1897 (Type loc.: Ghor-el-Safieh [= Ghawr as Safi; Amr et al., 2004], "Palestine"), and N. i. myosura (Wagner, 1845) with Syria as the type locality. The subspecies bacheri is a geographical isolate in the Dead Sea region. The remaining two subspecies differ in size; $N$. i. buxtoni from Iraq and eastern Saudi Arabia is smaller (mean


Figure 114. Upper ( $\mathbf{a}, \mathbf{b}$ ) and lower molars (c, d) in Nesokia indica. a, c - Mosul, Iraq (NMW); b, d - Ahwaz, Iran (NM 60,806). Note differences in enamel abrasion. Lingual side is to the left, anterior is at the top. Scale bar $=2 \mathrm{~mm}$.
condylobasal length $=40.9 \mathrm{~mm}$ ) than $N$. i. myosu$r a$ from the riverine plains in Syria (Harrison \& Bates, 1991); Lay (1967) synonymised N. i. myosura with N. i. indica. Mursaloğlu (1976; quoted from Yiğit et al., 2006c) identified Turkish population as $N$. i. myosura, in line with an earlier classification by Misonne (1957) who studied material from northern Syria. Corbet (1978) synonymised $N$. i. myosura with N. i. indica. We saw no specimens from Turkey.

## Distribution

Range is in three main fragments. Two fragments are in north-western China, and in north-western India and eastern Pakistan, respectively. The main segment covers Afghanistan, Uzbekistan, Turkmenistan, Iran, Iraq, Syria, and marginally Turkey as well. There are three additional small isolates along the western margin: in north-eastern Arabia, in the Dead Sea region, and on the western side of the Nile delta in Egypt. Nesokia populations are scattered and isolated along the western range border (Osborn \& Helmy, 1980; Mendelssohn \& Yom-Tov, 1999).

Past range exceeded the recent one and $N$. indica
has been recovered from the Late Palaeolithic sites in Sudan (Robinson, 1966) and Egypt (Osborn \& Helmy, 1980). Recent shrink was reported in the Nile valley and delta, presumably due to intensification of agriculture (Osborn \& Helmy, 1980). In Asia, nesokia benefited from irrigation, and spread throughout the Indus plain (Roberts, 1997). Similarly, it extended its range for more than 100 km over 30 years in the Karakorum Desert (Gromov \& Erbajeva, 1995). Along the banks of a desiccating Aral Sea, the nesokia is colonizing the sea bottom two to three years following retardation of the seawater (Gromov \& Erbajeva, 1995).

Demirsoy (1996) mapped the presence of $N$. indica in south-eastern Anatolia, but provided no localities. Due to the lack of convincing evidence, we assumed (Kryštufek \& Vohralík, 2001) that the inclusion of nesokia onto the list of Turkish mammal fauna might be based on the nearby records from Syria, i.e. Sheikh Hassan, 60 km south-east of Tell Abiad (Misonne, 1957) and Tell Abu Hurera (Kock \& Nader, 1983). Doğramacı (1989) and Kurtonur et al. (1996) did not report $N$. indica for Turkey. Besides, Yiğit \& Çolak (1998b) and Yiğit et al.


Figure 115. Distribution of Nesokia indica in Turkey and adjacent regions. Records: $\mathbf{1}$ - Şanlı Urfa; 2 - Mardin; 3 - Göbekli Tepe, Şanlı Urfa (a pre-pottery Neolitic site). Syria: 4 - Tell Abu Hurera, 5 km above Tabaqah on west bank of Lake Assad; 5 - Sheikh Hassan, ca 60 km south-east of Tell Abiad; 6 - Qal'a ar-Rahba, 45 km south-east of Dair az-Zur. Corresponding references: Misonne (1957): 5. Kock \& Nader (1983): 4, 6. Peters \& Schmidt (2004): 3. Yiğgit et al. (2006c): 1, 2.
(2003) did not record nesokia in their country-wide rodent survey. Recently Yiğit et al. (2006c) quoted Mursaloğlu (1976) who reported two localities from south-eastern Anatolia: Şanlı Urfa and Mardin. These two records are evidently on the very northern margin of the range of Mesopotamian population. Noteworthy, excavations in the pre-pottery Neolithic site at Göbekli Tepe near Şanlı Urfa showed that $N$. indica was present along the upper flow of the Güllab River, a left tributary of the River Euphrates, already about 9,500 years ago (Peters \& Schmidt, 2004).

Palaeontology. Musser \& Carleton (2005) considered a fossil Nesokia panchkulaensis from early Pleistocene of Siwaliks, northern India, as the earliest record of the genus. Note that Black (1972) reports material from the Neogene Siwalik beds in the sub-Himalayan range as 'Nesokia cf. Nesokia hardwicki’; Mus hardwickei Gray, 1837, is a junior synonym of $N$. indica (Ellerman \& Morrison- Scott, 1951). Nesokia has been known in southern Uzbekistan since the Middle Pleistocene (Gromov \& Baranova, 1981) and in Tadjikistan since the Upper

Pleistocene (Forsten \& Sharapov, 2000). Around 19,400 years before present, nesokia was still present in Jordan (Belmaker et al., 2001) and during the lower Holocene in south-eastern Turkey (see above). It was present in Egypt already during the Upper Palaeolithic period and in Sudanese Nubia around 15,000-20,000 years before the present. Holocene records from Khuzistan province in Iran are at most 8,000 years old (Turnbull, 1975). Fossil or subfossil nesokia were never reported from Israel (Tchernov, 1968a, 1975, 1994).

## Habitat

Nesokia requires firm damp soil to dig in and succulent grass roots or underground bulbs to feed upon (Roberts, 1997). As such, it is found in humid areas in dry steppes, semideserts and deserts, but mainly around permanent water bodies. Densely overgrown edges of streams and irrigation ditches seem to be the main habitat. In Israel and Egypt, nesokia was also collected from salty marshes, the borders of saline lakes, and in desert oases (Osborn \& Helmy,

1980; Mendelssohn \& Yom-Tov, 1999). In the Kuzistan Plain of Iran, Lay (1967) found extensive burrow systems under Tamarisk underbush. Cultivated fields are the main high-density habitat throughout the range, and nesokia is strictly limited to agricultural activity in Jordan (Amr, 2000). Irrigated orchards are populated in Pakistan (Roberts, 1997) and in central Asia (Gromov et al., 1963). The presence of nesokia is tied to the edges of fields and does not penetrate deep inside. In Pakistan, 42 \% of burrows were within 1 m of the field boundaries (a majority of them on the margin), and $65 \%$ were within 5 m into the fields (Brooks et al., 1988).

Altitude. Majority of populations live in the lowlands, and the highest occurrence is at $2,150 \mathrm{~m}$ in Pakistan (Roberts, 1997). In Iran, Lay (1967) collected nesokia from below sea level (-8 m) on the Caspian coastal plain up to $1,280 \mathrm{~m}$ at the Northern fringe of the Great Salt Desert. Nowak (1999) states altitudinal range from about 26 m below to $1,500 \mathrm{~m}$ above sea level.

Associates. In Iran, nesokia lives along with He miechinus auritus, Mus sp., Apodemus sp., Rattus rattus, R. norvegicus, Tatera indica, Meriones crassus, M. lybicus, and Gerbillus nanus (Lay, 1967). Associates in Egypt are Rattus rattus, R. norvegicus, Mus domesticus, Arvicanthis niloticus, Acomys cahirinus, and Gerbillus pyramidum (Osborn \& Helmy, 1980). In the arable land in Pakistan, Bandicota bengalensis is reported to co-occur with nesokia (Brooks et al., 1988). Given that the eastern limit of the range of Arvicola amphibius "virtually corresponds with the western limit of Nesokia indica


Figure 116. Habitat of Nesokia indica along the River Euphrates in northern Syria. Photo: V. Vohralík.
in Iran", Lay (1967) suggests competitive exclusion between the nesokia and the water vole.

Density was not reported. Nesokia is one of the most abundant rodents in cultivated areas in Pakistan (Roberts, 1997), locally abundant in suitable moist habitats in Arabia (Harrison \& Bates, 1991), and common in cultivated areas near Baghdad and Basra in Iraq (Hatt, 1959). In general, the increase of population follows an increase in irrigated agriculture (Mendelssohn \& Yom-Tov, 1999).

## Biology

Nesokia indica is one of the major pests to agriculture and a potential vector of epizootics. In addition, it also undermines water channels through weakening their banks and is the cause of a loss of irrigation water and of much land erosion. Despite all this, the life of nesokia has attracted surprisingly little attention.

Activity of nesokia is predominantly a fossorial one, particularly so during wintertime (Gromov et al., 1963). Animals do not venture far from the burrow entrances (Harrison \& Bates, 1991), and adults in particular only very rarely emerge above the surface (Roberts, 1997). Nesokia is active both day and night (Roberts, 1997), although nocturnal in Israel (Mendelssohn \& Yom-Tov, 1999). Various sources report captive nesokia as being extremely aggressive (Lay, 1967; Osborn \& Helmy, 1980; Roberts, 1997). Adults are solitary and each animal occupies one particular burrow system. Home ranges are regularly shifted to non-overlapping areas at one to two-week intervals (Roberts, 1997).

Burrows. Nesokia is primarily a fossorial rodent, although it is rather poorly adapted morphologically for such a mode of life (cf. Description above). Despite this, its burrows are more extensive than in other fossorial rodents of comparable size (Roberts, 1997). Tunnels are close to the surface, $15-90 \mathrm{~cm}$ (mainly less than 50 cm ) deep, and may ramify up to 24 m in length (Roberts, 1997); network of corridors vary from 2.5 to 9 m in length in Egypt (Osborn \& Helmy, 1980). Harrison \& Bates (1991) reported the main tunnel length of about 4.6 m in Iraq. Surface tunnels are in a function of feeding, while deeper burrows are used as living quarters. Nest chamber (diameter of about 30 cm ) is filled with finely chewed soft grasses. The network of burrows includes periodical side tunnels, an alternative exit, and
ventilation holes leading to the surface (Harrison \& Bates, 1991). During summer in Egypt, at the air temperature of $30-41^{\circ} \mathrm{C}$ and relative humidity of 29.7-47.0 \%, the microclimate within nesokia’s burrows is characterized by a temperature of $29-40^{\circ} \mathrm{C}$ and relative humidity of 54.4-75.0 \% (Osborn \& Helmy, 1980). Nesokia digs into a firm wet or damp soil or clay and mounds of loose substrate are pushed up to the surface. The burrow mounds tend to be clumped, with as many as 20-30 mounds within an area of $25-50 \mathrm{~m}^{2}$ in the fields of Pakistan (Brooks et al., 1988).

Reproduction. The overall sex ratio is significantly female biased in Pakistan (1 male : 2.1 female; Hussain et al., 2002). The proportion of reproductively active animals is about $70-74 \%(n=348)$. The smallest sexually mature males and females are from size class of 70-89 g (Arshad \& Beg, 2004). Scrotal sacs are never very prominent in males.

In Iraq, where pregnant females were collected from March to August, the breeding season possibly extends throughout the year with a peak in the summer months (Harrison \& Bates, 1991). Winter reproduction is reported also from the Amu Darya delta in Central Asia (Gromov et al., 1963). In India, the pregnancy rate peaks in September and October when soil moisture is higher (Greaves et al., 1975), and most of reproductive activity in Pakistan is from July to April (Roberts, 1997). A captive colony in the Pasteur Institute in Tehran reproduced all the year round (Lay, 1967).

Reports on gestation period differ: about 17 days (Roberts, 1997), three weeks (Mendelssohn \& Yom-Tov, 1999), and 26-28 days (Harrison \& Bates, 1991). Litter size in captivity is reported as 1-4 (Giza Zoological Gardens; Osborn \& Helmy, 1980), 2-8 (Pasteur Institute in Tehran; Lay, 1967), and 4-9 (Tel-Aviv University Zoo; Mendelssohn \& Yom-Tov, 1999). Litters in Pakistan were mainly of 3-5 cubs (up to 8; Roberts, 1997) and in Central Asia range was also 3-5 (Gromov et al., 1963). Mean embryo count in Arabia was 4.7 (range $=1-8$; Harrison \& Bates, 1991) and in Pakistan 2.7 (range = 1-5; Arshad \& Beg, 2004). Lay (1967) collected in Iran three females with 2, 4 and 8 swellings in the uterus, respectively, and another one with two embryos. There are at least three litters annually in Central Asia (Gromov et al., 1963).

The young are born naked and blind in an underground nest chamber lined with soft material (Roberts, 1997); females nurse them for 30 days after parturition (Harrison \& Bates, 1991). There is a post-partum oestrus (Mendelssohn \& Yom-Tov, 1999). Longevity is greater in nesokia than in Rattus (Roberts, 1997).

Food. Nesokia is primarily a vegetarian and feeding habits are largely subterranean. Major component in a diet are thus rhizomes, roots, and bulbs, while young shoots, green leaves and seeds provide supplementary food. Insects are an insignificant dietary item (Gromov et al., 1963). In Pakistan, nesokia feed on seeds and the rhizomes of various grasses (Desmostachva bipinnata, Echinochloa colonum, Eragrostis cynosuroides, Cyperus rotundus, and Sorghum halapense; Brooks et al., 1988; Roberts, 1997), in Israel on rhizomes of Phragmites sp. (Mendelssohn \& Yom-Tov, 1999) and in Egypt on fleshy roots of Alhagi mannifera, A. maurorum, Typha elephantine, and T. latifolia (Ali, 1978, Osborn \& Helmy, 1980). Damage to crops are reported throughout nesokia's range, e.g. in Pakistan to grain crops, corn, barley, vegetables, alfalfa and groundnuts Arachis hypogaea (Ali, 1978; Brooks et al., 1988; Roberts, 1997; Khalil Aria et al., 2007), in Central Asia to grain crops, alfalfa, and orchards (Gromov et al., 1963), to date palms in Israel (Mendelssohn \& Yom-Tov, 1999), and to water melons, corn, barley, and vegetables in Egypt (Osborn \& Helmy, 1980). Fleshy parts of vegetation are stored in underground chambers (Ali, 1978; Osborn \& Helmy, 1980) with up to 454 grams of grain per storage chamber (Nowak, 1999). Osborn \& Helmy (1980) maintained captive nesokia on a diet of raw carrots.

Predation. In Arabia, nesokia is preyed upon by the jungle cat (Felis chaus), snakes and owls (Harrison \& Bates, 1991), including the barn owl Tyto alba (Kock \& Nader, 1983). In Pakistan, predators are the barn owl (Mushtaq-ul-Hassan et al., 2004), little owl Athene brama (Ali Shah \& Azhar Beg, 2001) and the jungle cat Felis chaus (Roberts, 1997). The two-headed snake (Eryx johnii) and the sand boa (E. conicus) enter earth mounds excavated by nesokia (Roberts, 1997).

## Genus: Mus Linnaeus, 1758

A genus of cosmopolitan distribution containing about 38 species. The majority of species occur in the tropical and subtropical regions of Africa and south-western Asia. All Palaearctic forms are in the subgenus Mus (Musser \& Carleton, 2005), and were clumped into a single species in the not-so remote past. Such a taxonomy followed a revision by Schwarz \& Schwarz (1943) who concluded that a highly polymorphic Mus musculus complex consists of a single species with four different 'types' (designated by trinomials), three of which were further split into wild and commensal forms. Regardless of the subspecific identity, wild forms were diagnosed by the tail always being shorter than the length of the head and body, white underside and sharp demarcation along the flanks. Characters common to all commensal forms were the tail generally being longer than the head and body, reduced molars (due to the suppression of the last molars) and a shortened
rostrum. The view of Schwarz \& Schwarz (1943) was widely accepted (e.g. Ellerman \& Morri-son-Scott, 1951; Corbet 1978; Niethammer \& Krapp, 1978) and as such further froze taxonomic progress for the several decades that followed. The modern perception on the species richness within the Mus musculus complex emerged from the work by Marshall $(1981,1986)$ and Marshall \& Sage (1981). Following nearly two decades of intensive research, the taxonomy of western Palaearctic taxa largely stabilized (cf. Musser \& Carleton, 2005, and references cited therein).

Starting with Danford \& Alston (1877), the house mice of Turkey were commonly ascribed to a single species M. musculus (Steiner \& Vauk, 1966; Corbet \& Morris, 1967; Felten et al., 1971b; Turan, 1984; Doğramacı, 1989a; Yiğit \& Çolak, 1997). Given that the studied material frequently contained two distinct species, the authors solved the problem of significant within or between sample variation by introducing various sub-


Figure 117. House mouse Mus. Drawing: J. Hošek.
specific names (musculus Linnaeus, 1758, gentilis Brants, 1827, praetextus Brants, 1827, abbotti Waterhouse, 1837, brevirostris Waterhouse, 1837, hortulanus Nordmann, 1840, spicilegus Petenyi, 1882), or designated samples as representing transitional forms (spicilegus $\leftrightarrow$ praetextus, gentilis $\leftrightarrow$ hortulanus) (Neuhäuser, 1936; Ellerman, 1948; Osborn, 1965; Lehmann, 1966a, 1969; Kock et al., 1972). As an exception, Danford \& Alston (1880) recognized in Anatolia three distinct species: Mus abbotti, M. musculus, and M. bactrianus. Taxonomic confusion with Mus was similar also on Cyprus, i.e. only M. musculus was reported (Watson, 1951; Sfikas, 1996); if a subspecific name was applied it was either gentilis (Bate, 1903b) or praetextus (Ellerman, 1948; Spitzenberger, 1978a).

As a matter of fact, three species occur in the region and their existence is well supported by molecular evidence (Gündüz et al., 2000; Bonhomme et al., 2004; Musser \& Carleton, 2005; Macholán et al., 2008). Marshall (1981) was the first to document the presence of two species ( $M$. domesticus and M. macedonicus) for the Near East. The third species (M. cypriacus), which is endemic to the Island of Cyprus, was formally described only in 2006 (Cucchi et al., 2006). Diagnostic morphological traits are listed by Marshall (1981, 1986), Marshall \& Sage (1981), Harrison \& Bates (1990), Macholán (1996b), and Cucchi et al. (2006), and are summarized in a dichotomous key below.

## Identification

Mus domesticus and M. macedonicus are usually separated by the length of the tail relative to head and body length and by width of malar process relative to antero-lateral part of the zygomatic arch (the socalled zygomatic index = width of malar process / width of the antero-lateral part of the zygomatic arch; cf. Fig 118); M. cypriacus reportedly resembles $M$. macedonicus in both character states. In the material


Figure 118. Anterior zygomatic region in Mus domesticus (a) and M. macedonicus (b) (bottom). Based on specimens from Topçam, Ordu (a) and Kürtler, Samsun (b). mp - malar process; az - antero-lateral part of the zygomatic arch. Zygomatic index $=$ A $/ \mathrm{B}$. Scale bar $=2 \mathrm{~mm}$. Frames (upper insert) point on structures which are respectively shown in Figs. 118, 120, 121 and 122.
we saw, the relative tail length overlapped between species (cf. accounts on External characters below for descriptive statistics to individual species) however it is still a useful character in separating $M$. domesticus and M. macedonicus in Turkey. The tail is nearly invariably shorter than head and body in $M$. macedonicus but of approximately the same length or longer in a great majority of M. domesticus. Zygomatic index (ZI) scores also overlap (Table 22) and a significant proportion of individuals fall into the overlapping zone of ZI scores of 0.52-0.62: ten $M$. macedonicus ( $=9.0 \%$ ), three $M$. cypriacus (= 13.6\%) and as many as 45 M . domesticus (= 55.6\%). This character is currently most widely used in determi-

| Species | zygomatic index |  |  | length of $\mathrm{M}^{3}$ |  |  | width of $\mathrm{M}^{3}$ |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ | mean | $\min -\max$ |
| Mus domesticus | 81 | 0.53 | $0.37-0.62$ | 25 | 1.01 | $0.83-1.16$ | 1.02 | $0.88-1.14$ |
| Mus macedonicus | 111 | 0.84 | $0.52-1.42$ | 59 | 1.27 | $1.11-1.44$ | 1.20 | $1.05-1.34$ |
| Mus cypriacus | 22 | 0.78 | $0.53-1.35$ | 22 | 1.34 | $1.23-1.47$ | 1.23 | $1.11-1.37$ |

Table 22. Descriptive statistics for the zygomatic index (in percentages; cf. text for a definition) and dimensions of $3^{\text {rd }}$ upper molar ( $\mathrm{M}^{3}$; in mm) in three house mice (Mus) species occurring in Turkey and Cyprus.


Figure 119. Bivariate plot of width of $3^{\text {rd }}$ upper molar against its length in three Mus species occurring in Turkey and Cyprus. Polygons enclose extreme specimens in $M$. domesticus and M. macedonicus, respectively; diamonds correspond to individuals of M. cypriacus.
nation keys (e.g. Orsini et al., 1983; Macholán, 1996b) but it is not always critically applied. E.g., ranges reported by Yiğit et al. (2006c) for Turkish material show no overlap at all: 0.25-0.46 for $M$. domesticus and 0.63-0.83 for M. macedonicus.

In our results, the dimensions of $3^{\text {rd }}$ upper molar provided better separation among the three house mice (Table 22) particularly in a bivariate plot of width against length (Fig. 119).

Marshall \& Sage (1981) stressed differences between M. macedonicus and M. domesticus in several other cranial and dental traits which were ignored by subsequent students and hence have not been used in recent papers. Despite some overlap (Çolak et al., 2006), we found all of them to be helpful in morphological identification, particularly when samples, rather than single individuals, are available. These characters are (quotations are from Marshall \& Sage, 1981):

1. Shape of the posterior bevel of the upper incisor: clearly notched in M. domesticus, while M. macedonicus "show an angled or serrated posterior bevel, if they are not actually notched." For variability see Fig. 120.
2. Anterior root of the $1^{\text {st }}$ molar: "vertical" in $M$. macedonicus and "slanting" in M. domesticus. For variability see Fig. 121.
3. Ventral wing of the parietal bone: "deep and of tri-

## M. domesticus


a



M. macedonicus

M. cypriacus


Figure 120. Variation in the notch on the posterior bevel of the upper incisor in three Mus species occurring in Turkey and Cyprus. For position of the structure in the skull see Fig. 118. Mus domesticus: a - Island of Bozcaada; b, c - Cayırköy, Zonguldak; d - Niğde; e, f - Topçam, Ordu. Mus macedonicus: a, b - Edirne; c, d - Kürtler, Samsun; $\mathbf{e}$ - Alanya; $\mathbf{f}$ - Island of Gökçeada. Mus cypriacus: a - Kornos; b - Apsiou; c - St. Hilarion; d - Girne; $\mathbf{e}$ - Troodos Mts. Anterior is to the left, dorsal is at the top. Scale bar $=2 \mathrm{~mm}$.
angular outline" in M. macedonicus, "shallow and its suture with the squamosal follows a tortuous course" in M. domesticus. For variability see Fig. 122.

In all these character states M. cypriacus resembles M. macedonicus. Reliable differentiation between these two species on morphological grounds is apparently impossible. Mus cypriacus is, on average, larger and has a relatively longer tail, but ranges overlap.

## M. domesticus


M. macedonicus



C

d

e
M. cypriacus


Figure 121. Shape of the anterior root of $1^{\text {st }}$ molar in three Mus species occurring in Turkey and Cyprus. For position of the structure in the skull see Fig. 118. Mus domesticus: a - Akçakale, Şanlı Urfa; b - Yukarı Karafakılı, Hatay; c - Balkusan, Konya; d, e - Ballı, Mersin. Mus macedonicus: a - Karabulut, Akşehir Gölü, Konya; b, e - 10 km north-east of Bardakçı, Manisa; c - Adana; d - Akçakale, Şanlı Urfa. Mus cypriacus: a-3 km west of Neo Chorio, Polis, Akamas; b - Apsiou, ca 15 km north of Limassol; c - Mt. Olympos, Troodos Mts.; d - Paramytha, ca 12 km north of Limassol; $\mathbf{e}$ - Zeytinlik, Girne (= Kyrenia). Anterior is to the left, dorsal is at the top. Scale bar $=1 \mathrm{~mm}$.

Lavrenchenko (1994) reports differences in the shape of glans penis (Fig. 123; see also accounts on Penis under M. domesticus and M. macedonicus), distal baculum (see species accounts below), and spermatozoa between the two mainland species. The spermatozoa head is relatively broader in M. macedonicus (length 6.70-8.15, breadth $3.00-3.75 \mathrm{~mm}$; based on specimens from Armenia) and narrower in M. domesticus (length 7.55-9.60, breadth 2.95-3.90 mm ; based on specimens from Cuba).

## M. domesticus


a

b

c

d
e

## M. macedonicus


a


C

e

b

d
M. cypriacus


Figure 122. Shape of the ventral wing of the parietal bone in three Mus species occurring in Turkey and Cyprus. For position of the structure in the skull see Fig. 118. Mus domesticus: a - Balkusan, Konya; b, c - Akçakale, Şanlı Urfa; d - Ballı, Mersin; e - 3 km north of Sırbasan, Kars. Mus macedonicus: a, e-10 km north-east of Bardakçı, Manisa c - Karabulut, Akşehir Gölü, Konya; d - Akçakale, Şanlı Urfa. Mus cypriacus: a-3 km west of Neo Chorio, Polis, Akamas; b, d - Paramytha, ca 12 km north of Limassol; c - St. Hilarion Castle, Girne (= Kyrenia); e-Apsiou, ca 15 km north of Limassol. Anterior is to the left, dorsal is at the top. Scale bar $=2 \mathrm{~mm}$.

## Key to species

$13^{\text {rd }}$ upper molar suppressed in size (Fig. 119); posterior bevel of the upper incisor clearly notched in majority of specimens; anterior root of $1^{\text {st }}$ molar slanting; suture of the ventral wing of the parietal bone with squamosal frequently follows a tortuous course; zygomatic index at most 0.62
M. domesticus

1* ${ }^{\text {rd }}$ upper molar of larger size (Fig. 119); posterior bevel of the upper incisor rarely notched; anterior root of the $1^{\text {st }}$ molar more or less ver-
tical; suture of the ventral wing of the parietal bone with squamosal never follows a tortuous course; zygomatic index at least 0.52

2
2 Tail normally shorter than head and body; occurs in Thrace and Anatolia
M. macedonicus

2* Tail frequently longer than head and body; occurs in Cyprus
M. cypriacus

d


Figure 123. Ventral ( $\mathbf{a}, \mathbf{b}$ ) and lateral side ( $\mathbf{c}, \mathbf{d}$ ) of the glans penis in Mus domesticus ( $\mathbf{a}, \mathbf{c}$ ) and Mus macedonicus (b, d). dp - distal protrusion (papilla centralis). Modified from Lavrenchenko (1994).

## Western house mouse - Mus domesticus

Mus musculus domesticus Schwarz \& Schwarz, 1943. Type loc.: Dublin, Ireland.

## Taxonomy

Mus domesticus is parapatric with M. musculus Linnaeus, 1758 , and the two do hybridize in a zone less than 50 km wide in Europe but more than 300 km wide in Transcaucasia. This phenomenon has been the subject of much genetic research, particularly so in Europe (cf. Musser \& Carleton, 2005, and references cited therein). Opinions differ on whether these two parapatric forms should be considered as an independent species (e.g. Macholán, 1996b; Mitch-ell-Jones et al., 1999) or a well-defined subspecies of M. musculus (Musser \& Carleton, 2005). Given the apparent stability of the hybrid zone, we prefer the former view (cf. also Benda \& Sádlová, 1999). Such a taxonomic solution is quite rarely applied by mammalogists dealing with the mammals of Turkey and Cyprus (e.g. Marshall, 1981, 1986; Marshall \& Sage, 1981; Özkan, 1999a; Gözcelioğlu et al., 2005; Çolak et al., 2006; Yiğit et al., 2006a,c), hence M. musculus (or M. m. domesticus) is preferred in recent papers (Niethammer, 1989; Harrison \& Bates, 1991; Chondropoulos et al., 1995; Gündüz et al., 2000; Kryštufek \& Vohralík, 2001; Bonhomme et al., 2004; Cucchi et al., 2005, 2006; Slábová \& Frynta, 2007). Noteworthy, Demirsoy (1996) reported both, M. musculus and $M$. domesticus, to be broadly sympatric in Thrace and Anatolia; a similar view was also advocated by Kurtonur et al. (1996), who, however, listed musculus for the whole of Turkey, and domesticus only for Thrace. Parapatric zone between M. musculus and $M$. domesticus approaches, but does not reach Turkish territory in Thrace (Macholán et al., 2003) and in Transcaucasia (Mezhzherin et al., 1998); a sample from Adjaria is genetically nearly purely $M$. domesticus (Orth et al., 1996). Therefore, there is no evidence of the presence of M. musculus in Turkey.

Mus abbotti Waterhouse, 1837, with Trabzon (north-eastern Anatolia) as its type locality, is currently regarded to be a junior synonym of $M$. domesticus (Musser \& Carleton, 2005). In the past, only Danford \& Alston (1880) and Lehmann (1966a) applied abbotti for long-tailed house mice of Ana-
tolia. The identity of Mus abbotti however, already posed problems in the times by Danford \& Alston: "Under this name Mr. Waterhouse described a Mouse sent many years ago to this Society [Zoological Society, London] from Trebizond [=Trabzon] by Mr. Keith E. Abbott [Proc. Zool. Soc., 1837, p. 77]. His type is not to be found in that portion of the Society's collection which passed to the British Museum; and we can only direct the attention of collectors to his original description. The animal is stated as having been smaller than a harvest mouse (length of head and body 1 inch 3 lines, of tail 1 inch 11 lines) [ 31.8 mm and 48.7 mm , respectively], and of a deeper colour than Mus musculus. Had the description been given by any less trustworthy a writer, we should have had little hesitation in regarding it as having been founded on a young individual of that species." In 1980s, Marshall (1981) and Marshall \& Sage (1981) suggested the use of the name M. abbotti for short-tailed, free living Eastern Mediterra-


Figure 124. Ventral cranium of the type of Mus abbotti (BMNH). Scale bar $=5 \mathrm{~mm}$.
nean mice. Only after the examination of the type of abbotti Marshall (1986) concluded that "the juvenile type specimen (from Turkey) is too small for any member of the house mouse complex. My measurements in millimetres of the type in spirit at the British Museum are 44-50-15.1-9.6 [head and body - tail - hind foot -ear], complete upper molar row 3.0. The two Mus species known to occupy Turkey have larger teeth than these and juveniles larger than the type still lack the third molar. The type must be a mislabelled pygmy mouse from Africa or India." We agree entirely with the above opinion. Dimensions of the type specimen are outside the range of house mice from Turkey; condylobasal length measures 15.2 mm and maxillary tooth-row length equals 3.0 mm (measured on alveoli; 2.8 mm on crowns; cf. Fig. 119). Third molars erupted and the lower ones are already moderately worn (Fig. 125). The smallest M. domesticus at our disposal, with body mass of 6 grams, has the following measurements (in mm ): length of head and


Figure 125. Upper (a) and lower molars (b) in the type of Mus abbotti (BMNH). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
body 68, length of tail 59, hind foot 16.7, ear 11, condylobasal length 18.5, alveolar length of molar-tooth row 3.5. Also the malar process is relatively wide in M. abbotti and score for the zygomatic index is high (= 0.64). The type of M. abbotti is clearly not identical with M. domesticus or any other Turkish murine.

## Description

External characters. A rather small murine rodent. Body is slender with no special peculiarities. Tail shows well defined annulations, and is sparsely haired and with no terminal pencil; it is wider at base and less slender at the tip than in Apodemus. The tail is about same length as head and body (mean $=$ 98.6 \%, range $81.3-121.4 \%$, $\mathrm{n}=88$ ), but this varies individually and geographically. Ears are moderately long. There are four and five toes on fore and hind foot, respectively. Claws are simple, curved and
slightly longer on hind foot. Hind foot is relatively shorter and more robust than in Anatolian Apodemus species. Palm and sole are naked, each with five small and widely spaced tubercules. Pelage is soft, 4-7 mm long on the back.

Colour varies significantly from fairly dark to pale. In dark specimens the back is dusky woodbrown with buff tints along flanks. Belly is buffy-grey with bases of hair slate grey; line of demarcation is obscure. Feet are dusky, ear and tail are dull brownish; tail is slightly paler on its ventral side. The pale form shows buff to light wood-brown back, buffy flanks and white belly. Bases of dorsal hair are slate, white throughout on the belly. Demarcation along flanks varies from obscured to rather sharp. Feet are buffywhite and ears are slightly paler than in the dark form. Tail is also paler, greyish or buff-grey above, slightly paler below, hence indistinctly bicoloured.


Figure 126. Skins of Mus domesticus in dorsal and ventral view. a - Balli, Mersin; b - Balkusan, Konya; c - Akçakale, Şanlı Urfa. Photo: C. Mlinar.

Nipples. There are ten nipples arranged in three pectoral and two inguinal pairs.

Penis (Fig. 123a,c). The glans penis is cylindrical, longer than wide. Distal protrusion (papilla centralis) is sharply pointed in lateral view; its terminal apex is split into two short lobes, which are visible in ventral projection. The surface is densely covered with numerous small spines. The ventral furrow is restricted to the distal $11 / 4$ of the glans. The baculum consists of proximal stalk and elongated triangular distal baculum. The apex of the distal baculum is normally pointed and only exceptionally split terminally (Lavrenchenko, 1994). The proximal stalk (length about 3.3 mm ) is bent dorsally; its expanded base is bi-concave in caudal view (Yiğit et al., 2006c).

Skull is of general murine appearance with no special peculiarities. Rostral portion is relatively short and broad; zygomatic arches are only moderately expanded ( $=50.7-57.8 \%$ of condylobasal length; mean $=54.3 \%, \mathrm{n}=61$ ) and braincase is short-oval and wide. Dorsal profile is slightly convex throughout. Interorbital region is wide and flat, with weak supraorbital ridges. Interparietal is large. Insicive foramens are long, always considerably exceeding the
anterior margin of $1^{\text {st }}$ molars. Pterygoids are weak, more or less parallel; mesopterygoid fossa is narrow. Bullae are fairly small. Mandible shows no peculiarities, and is more robust than in Apodemus. All processes are well developed, and the articular process is fairly robust.

Teeth. Upper incisors are much compressed, with a conspicuous sub-apical notch on outer side of cutting edge immediately behind margin of enamel (Fig. 120). Enamel is yellow to orange, invariably paler on the lower incisors. Molars are brachiodont and cuspidate; they decrease in size from the anterior to the posterior tooth; $3^{\text {rd }}$ molar is more suppressed in size than in the remaining two Mus species of the region. Cusps are large. Lingual row of cusps is shifted posteriorly on $1^{\text {st }}$ upper molar; cusp t7 is reduced to enamel ridge; distal cusps t8 and 9 leave no space for posterior cingulum or postero-labial cusp t12. Second upper molar lacks cusp t3; t7 is suppressed to a mere enamel ridge; t9 is small. Dental fields of mesial and central cusps on $1^{\text {st }}$ lower molars fuse early; mesio-labial cusp is small.

In Europe and Anatolia, upper molars normally have three roots each, one lingual and two labi-


Figure 127. Skull and mandible of Mus domesticus, based on an adult male from Topçam, Ordu. Scale bar = 5 mm .


Figure 128. Upper (a) and lower molars (b) in Mus domesticus from Akçakale, Şanlı Urfa. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
al; lower molars are two-rooted, each with anterior and posterior root (Niethammer \& Krapp, 1978; Coşkun, 1991). In a large sample from Cyprus ( $\mathrm{N}=$ 350-361) which contained M. domesticus and/or M. cypriacus, the three-rooted condition strongly prevailed only in $2^{\text {nd }}$ upper molar ( $82.6 \%$ ). The majority of $1^{\text {st }}$ molars had four roots ( $76.2 \%$ ) and the majority of $3^{\text {rd }}$ molars were two-rooted (63.3\%). Other morphotypes were a single root ( $0.3 \%$ of $2^{\text {nd }}$ molars and $14.8 \%$ of $3^{\text {rd }}$ molars), two roots ( $3.7 \%$ of $2^{\text {nd }}$ molars), three roots ( $23.5 \%$ of $1^{\text {st }}$ molars and $21.9 \%$ of $3^{\text {rd }}$ molars), four roots ( $13.1 \%$ of $2^{\text {nd }}$ molars), and five roots ( $0.3 \%$ of molars $1^{\text {st }}$ and $2^{\text {nd }}$ ) (Spitzenberger, 1978a).

Dimensions. Sexes are subequal. For dimensions see Table 23.

Chromosomes. Mus domesticus displays variation in chromosome number. The standard diploid number is $2 \mathrm{~N}=40$ and all the chromosomes are acrocentric (fundamental number of autosomal arms $\mathrm{FN}_{\mathrm{a}}$

|  | N | mean | $\min -\max$ |
| :--- | :---: | :---: | :---: |
| Head and body | 80 | 86.6 | $70-100$ |
| Tail | 77 | 83.5 | $67-104$ |
| Hind foot | 78 | 17.9 | $14.0-20.0$ |
| Ear | 76 | 14.4 | $11.0-17.0$ |
| Weight | 75 | 22.7 | $13-39$ |
| Condylobasal length | 66 | 21.1 | $19.0-23.0$ |
| Zygomatic breadth | 66 | 11.5 | $10.1-13.2$ |
| Maxillary tooth-row | 83 | 3.7 | $3.2-4.1$ |

Table 23. External and cranial dimensions of Mus domesticus from Turkey and Cyprus. Sources: BMNH, ZFMK, and our own material.
= 38). Karyotypic variation involves only Robertsonian (or centric) fusions, hence chromosomal races differ in arm combination and diploid number ( $2 \mathrm{~N}=$ 22-38). About 35 different cytotypes have been hitherto described (Macholán, 1999a). Centric fusions originated very recently and have not modified either the level or the nature of genetic variability (Brit-ton-Davidian et al. 1989). Robertsonian populations are known only from Europe (Britton-Davidian et al. 1989), including the Balkans (Tichy \& Vucak, 1987); the eastern-most Robertsonian population was reported from Amoudia (Greek Macedonia; Bauchau, 1990).

Only the standard all-acrocentric karyotype $(2 n=$ 40) was reported from Turkey (Yiggit et al., 2006c) and Cyprus (Cucchi et al., 2006). Mice were karyotyped from Zonguldak (Gözcelioğlu et al., 2005), Doğubayazıt (Yiğit et al., 2006a), Kayseri and Samsun (Gündüz et al., 2000). The all-acrocentric cytotype also occurs in Iran (Gündüz et al., 2000; Yiğit et al., 2006a) and in Levant (Qumsiyeh, 1996).

## Variation

The most striking variation in morphology relates to colour. Western house mice from the Black Sea coast are invariably dark, and those from Central Anatolia are paler (Ç olak et al., 2006). Free-living house mice from south-eastern Anatolia belong to the pale morphotype, but their sympatric commensal counterparts are darker. The dark form has not been found in Israel (Mendelssohn \& Yom-Tov, 1999). Commensal populations also have longer tails when compared to sympatric non-commensal populations (Slábová \& Frynta, 2007).

Pale house mice of Turkey and the eastern Mediterranean coast are commonly reported as a subspecies praetextus Brants, 1827 (type locality: Sakhara, Syria; Qumsiyeh, 1996) (e.g. Lehmann, 1957; Hatt 1959; Atallah, 1978; Mendelssohn \& Yom-Tov, 1999; Shehab et al., 2004). Auffray (1988; quoted from Harrison \& Bates, 1991) assigned house mice from Iraq to ssp. bactrianus Blyth, 1846 (type loc.: Kandahar, Afghanistan). In the opinion of Harrison \& Bates (1991) "The subspecific variation in Mus in Arabia is clearly a complex subject and one which requires more study." Qumsiyeh (1996) states that considerable size and colour variation in the Levant region does not warrant subspecific recognition. Benda \& Sádlová (1999) showed that pale and small house mice from Jordan, which they reported as M. d. gentilulus Brants, 1827 (type locality: southern Egypt) did not change in captivity.

Occasionally, dark commensal animals show irregular white spots or patches of variable size. We found such individuals only in northern Anatolia (Topçam, Erzurum, and Sarikamiş) however Çolak et al. (2006) also reported white-spotted house mice for Ankara.

House mice from Turkey and Iran, which are believed to represent the ancestral stock for commensal forms of Europe, are characterized by standard allacrocentric karyotype and a high D-loop nucleotide diversity (Gündüz et al., 2000).

Social behaviour of the western house mouse is pliable rather than rigid. Females from commensal populations are tolerant of each other while those from non-commensal populations are highly agonistic. This phenomenon has been attributed to an increased competition for food in non-commensal populations (Frynta et al., 2005).

## Distribution

Mus domesticus putatively originates from southwestern Asia but is now nearly cosmopolitan (Kucheruk, 1994; Musser \& Carleton, 2005). In Turkey and Cyprus, the species is widespread; it also occurs in the Islands of Bozcaada and Gökçeada (Fig. 129), and in numerous Aegean islands (Macholán 1999a).

Palaeontology of Mus is confusing, a legacy of the fact that taxonomy in south-western Palaearctic stabilized only quite recently. Also, a great mor-


Figure 129. Distribution of Mus domesticus in Turkey, Cyprus and adjacent regions. For further details on records see Appendix 5.
phological similarity of various southwest Palaearctic species contributed to uncertain identification in taphonomically altered material. Besides, fossil remains are scarce and were only rarely studied in detail (Kowalski, 2001). Considerable progress in recent years has benefited from the availability of new methods in morphometrics, particularly those where analyses of landmark data are concerned, which incorporate strong elements of quantification and hypothesis testing.

The earliest fossil record of Mus is from Siwaliks, Pakistan and is of late Miocene age (Musser \& Carleton, 2005). Although Asia, rather than Africa, was the source of species that now occur in the western Palaearctic, the African subgenus Leggada Gray, 1837, reached Israel during the Upper Pleistocene (Bate, 1942). The earliest Mus records from the region represent Mus aegaeus Kuss \& Storch, 1978, known from the Upper Villanyan (late Pliocene) to Early Pleistocene from the Aegean Island of Kalymnos (Kuss \& Storch, 1978; van der Meulen \& van Kolfschoten, 1986), and from the late Middle Pleistocene from the Island of Chios (Kotsakis, 1990). A further two endemic species evolved on Crete: Mus bateae Mayhew, 1977, during the late Middle Pleistocene, and Mus minotaurus Bate, 1942, in the Late Pleistocene (Kotsakis, 1990; Kowalski, 2001). Kotsakis (1990) announced another endemic Mus species from the Middle or Late Pleistocene of the Karpathos Island. Since the Middle Pleistocene, the genus Mus was also present in the Caucasus (Vereščagin, 1959), the Balkans and the Carpathian basin (Kowalski, 2001).

Mus domesticus appeared in the Levant region about 17,000-14,000 years ago which corresponds to the beginning of human sedentism and the earliest human dwellings in caves. Cyprus was already colonized in the pre-pottery Neolithic about 12,500 years ago and subsequent records from the island are dated to the $9^{\text {th }}$ millennium before the present. The first appearance of $M$. domesticus in Syria is documented for about 12,000 years before present (Cucchi et al., 2005). Earliest evidence from Anatolia is from Cafer Hüyük (9,500-10,000 years B.P.) and Çatal Hüyük near Burdur (7,500-8,500 years B.P.; Auffray et al., 1990c; Cucchi et al., 2005). Remnants from Finike near Antalya, which were not assigned taxonomically, are less than 7,000 years old (Corbet \&

Morris, 1967), but 3,300 year old evidence regarding $M$. domesticus is again available from the Uluburun shipwreck found offshore the southern Turkish coast, near Kaş, Antalya (Cucchi et al., 2005). Another site, however, which escaped attention in recent reviews on the western house mouse progress in the Near East (cf. Auffray et al., 1990c; Cucchi et al., 2005) is Norşun Tepe in Central Anatolia. Among zooarchaeological material from the Chalkolithic and Bronze Age strata Kock et al. (1972) distinguished two Mus morphotypes: M. musculus brevirostris Waterhouse, 1837, and M. m. spicilegus Petenyi, 1882 $\leftrightarrow$ M. m. praetextus Brants, 1827; these names might be indicative on the co-occurrence of $M$. domesticus (brevirostris) and M. macedonicus (spicilegus $\leftrightarrow$ praetextus).

The further spread westward of $M$. domesticus was postponed into the $1^{\text {st }}$ millennium B.C. (Cucchi et al., 2005).

## Habitat

The western house mouse is primarily known as a commensal animal. Commensalism evidently evolved in the Fertile Crescent (e.g. Slábová \& Frynta, 2007) where the earliest human dwellings provided a new ecological niche. Cohabitation with man allowed the western house mouse to progress further westward into the zone occupied by M. macedonicus by avoiding competition with this congeneric species (Auffray et al., 1990a). Mus domesticus is now found in almost all populated areas in Turkey and Cyprus. We also collected animals in isolated buildings, far away from settlements (Fig. 130a).

The western house mouse is ecologically highly opportunistic but a weak competitor (Macholán, 1999a). As such it is "partly competitively excluded" from natural environments by M. macedonicus, therefore free-living populations are mainly restricted to areas which lack this congeneric competitor (Auffray et al., 1990a). With the exception of south-eastern Anatolia, we never captured western house mice any great distance from human dwellings. While $M$. macedonicus is a mesic rodent in the Levant region (Haim et al., 1999), M. domesticus can cope with aridity (Auffray et al., 1990a) and is expanding into the desert, e.g. in Jordan (Amr, 2000). Feral populations are therefore largely restricted to pronouncedly arid habitats in Turkey, along the border with

Syria and Iraq. In a desert landscape, we collected house mice in agricultural areas. Across the TurkishSyrian border we found M. domesticus to be abundant in reeds along the Euphrates River; it is also numerous in reed thickets and in agricultural areas along rivers in Iraq (Harrison \& Bates, 1991). The western house mouse was also reported from camel thorn scrub and from desert habitats 1.6-2 km from the nearest human habitation (Harrison \& Bates, 1991).

On Cyprus, we collected the western house mice in disturbed Mediterranean shrubby vegetation (Fig. 130d). According to Cucchi et al. (2006), M. domesticus dominates only in areas under intensive agriculture. In Israel, shrub cover is essential for the western house mouse under the Mediterranean climate (Kutiel et al., 2000).

Altitude. In Anatolia, the western house mouse was collected from the sea level up to $1,950 \mathrm{~m}$ (Erzurum), ca 2,200 m (Sırbasan) and 2,400 m of elevation
(Sarikamiş; specimens in ZFMK and our own data). The highest records outside human dwellings were from a small cultivation in otherwise bare landscape near Niğde (1,800 m a.s.l.; Fig. 130b) and from dry pasture with sparse shrubs ca 3 km north of Sirbasan (ca 2,200 m). Elevations above 2,000 m are not populated in the Caucasus but mice go up to 3,800 m high in Central Asia (Kucheruk, 1994).

Associates are little known in Turkey, clearly a reminiscence of predominantly commensal habits of the western house mouse in the country. In Akçakale (cultivations) and Adana (shrubby habitats) we collected both house mice species in same trap lines. Near Niğde the western house mouse shared habitat with Crocidura suaveolens, Apodemus witherbyi and A. mystacinus, and along the River Euphrates in north Syria the only other mammals we recorded besides M. domesticus were Crocidura suaveolens and Nesokia indica.

On the Island of Bozcaada, the western house


Figure 130. Habitat of Mus domesticus in Turkey and Cyprus. a - an isolated mill near Çayirköy, Zonguldak; b - an isolated garden below Tepeköy, Niğde, (1,800 m a.s.l.); c - Ballı, Mersin, 1,450 m a.s.l.; d - Cyprus. Photo: B. Kryštufek (a, b), V. Vohralík (c), A. Kryštufek (d).
mouse is syntopic with Apodemus witherbyi and Rattus rattus (Özkan, 1999a) and in Cyprus with M. cypriacus, Rattus rattus and Acomys cahirinus. House rats, which are the most abundant rodent species on Cyprus, presumably compete with house mice (Landová et al., 2006). For sympatric occurrence of $M$. domesticus and $M$. macedonicus on the islands see under the latter.

In Arabia, western house mice were found sharing the same burrows as a strictly desert-dwelling Meriones crassus (Harrison \& Bates, 1991).

Density is unknown in Turkey. On the Island of Bozcaada, Özkan (1999a) collected only 18 M. domesticus but 144 Apodemus witherbyi (ratio about 1 : 8) and 15 Rattus rattus. Contrary to this, we found house mice to be by far the most abundant small mammal in reeds along the River Euphrates in north Syria. Mus domesticus is abundant in Arabia, both in commensal and in outdoor situations (Harrison \& Bates, 1991).

## Biology

Literature on the biology of the western house mouse is very extensive (for compilations cf. Berry, 1981; Kotenkova \& Bulatova, 1994) but this aspect attracted no research interest in Turkey (Yiğit et al., 2006c). Besides, older publications are frequently of little use due to taxonomic uncertainties.

Reproduction. Gestation period is 20-25 days (Nowak, 1999). Number of embryos per female in Turkish material is $1-11$ (mean $=5.8, \mathrm{~N}=10$ ); mean in four females from Bozcaada is 5.3 (Özkan, 1999a). Body mass in seven lactating females from a commensal stock was $16-39 \mathrm{~g}$ (mean $=30.4 \mathrm{~g}$ ) and eight scrotal males (testes $5.4-8.4 \times 3-5 \mathrm{~mm}$ ) weight $11-23 \mathrm{~g}$ (mean $=18.0 \mathrm{~g}$ ). Commensal mice breed throughout the year in Armenia with peaks in spring and autumn (Harrison \& Bates, 1991).

Food. Diet "is very varied and includes dates, grain, grass, leguminous and root vegetables, fruits, berries, nuts, seeds and human refuse." (Harrison \& Bates, 1991).

Predation. House mice of undefined species were reported to be the main prey item in the barn owl (Tyto alba) diet in Turkey: 42.2 \% in Hatay (Hoppe, 1986), and 58.6 \% in Lake Bafra in Aegean Anatolia (Kasparek, 1988). A similar situation is also known further south in Syria (Shehab et al., 2004; Shehab,
2005), Iraq (Harrison \& Bates, 1991) and Israel (Tores et al., 2006). In Turkey, the proportion of Mus among preyed upon mammals was lower in the pellets of the tawny owl Strix aluco ( 3.6 \% in Karadut and 11.0 \% in Hatay; Obuch, 1994) and eagle owl Bubo bubo ( 1.3 \% in Central and Eastern Anatolia; Obuch, 1994). Shehab (2004) reports a similar figure for the eagle owl diet in Syria with 1.0 \% of prey items being house mice. A surprisingly high percentage ( $34.4 \%$ ) of western house mice in Jordan, however, were preyed upon by the eagle owl (Amr et al. 1997).

Remarks. Commensal house mice cause "considerable damage in warehouses, agricultural stores and dwellings" and are a potential carrier of human diseases (Harrison \& Bates, 1991).

## Macedonian house mouse - Mus macedonicus

Mus hortulanus macedonicus Petrov \& Ružić, 1983. Type loc.: near Valandovo, Macedonia.

## Taxonomy

Mus macedonicus was first recognised as a distinct species under the name M. abbotti (Marshall, 1981; Marshall \& Sage, 1981). The name abbotti was applied for Turkish house mice already by Danford \& Alston (1880) and Lehmann (1966a; as a subspecies of $M$. musculus) but was used to denominate $M$. domesticus as it is currently known. Using material from the Balkans and Armenia, Kratochvíl (1986) provided a detailed description and comparison of $M$. macedonicus (as M. abbotti) with other Mus species. Mus abbotti remained in use for M. macedonicus for approximately one decade (Storch, 1988; Niethammer, 1989; Brinkmann et al., 1990; Nadachowski et al., 1990). Already by 1980s, abbotti had been replaced by several other names which were not always binominals: Mus spicilegus "South" Orsini et al. (1983), Biochemical group Mus 4A (Bonhomme et al., 1984), and Mus spretoides (Bonhomme et al., 1984). Marshall (1986) replaced abbotti with Mus tataricus. Any of these names, however, proved appropriate: Mus spicilegus is currently a species in its own right whose range covers south-eastern Europe (Mus spicilegus "North" sensu Orsini et
al., 1983); Mus tataricus is a junior synonym of $M$. domesticus, while Mus spretoides should be abandoned as a nomen nudum (Musser \& Carleton, 2005).

Reasons for adopting the name abbotti for shorttailed, free-living house mice from the Balkans and the Near East were never explained and Marshall (1986) abandoned it for reasons we discuss under $M$. domesticus. Auffray et al. (1990b) proposed a replacement of abbotti by macedonicus on the basis of "the clear description". Mus macedonicus was originally described as a subspecies of $M$. hortulanus. Mus hortulanus is a junior synonym of $M$. musculus (Ellerman \& Morrison-Scott, 1951; Musser \& Carleton, 2005) however Petrov \& Ružić (1983) clumped three distinct species under this name (musculus, spicilegus, and macedonicus; cf. also Petrov \& Ružić, 1985). Nevertheless, M. macedonicus was established as a valid name in mid-1990s and was used nearly consistently afterwards (Demirsoy 1996; Kurtonur et al., 1996; Özkan, 1999a; Harrison \& Bates, 1999; Yiğit et al., 2006c; Kryštufek \& Vohralík, 2001; Bonhomme et al., 2004; Gözcelioğlu et al., 2005; Cucchi et al., 2006; Macholán et al., 2007, 2008).

Tchernov (1996) suggested that Mus camini Bate, 1942, described from Late Pleistocene deposits of Tabun Cave (Israel), likely represents M. macedonicus. If so, camini holds absolute priority over macedonicus. Conspecificity of macedonicus and camini is highly probable, given its long record of continuous presence of the former in the Levant on the one hand, and a postponed arrival of M. domesticus on the other (cf. Palaeontology accounts under these two species and discussion in Musser \& Carleton, 2005).

Orth et al. (2002) adopted spretoides as a valid taxonomic name to denote the subspecific level of the phylogeographic lineage of the Macedonian house mouse from Israel. Their step was followed in several recent papers (Bonhomme et al., 2004; Cucchi et al., 2006; Macholán et al., 2007, 2008) Again, and as stated above, spretoides has no taxonomic validity and should be abandoned. Nomenclatural issue of the Israeli subspecies of $M$. macedonicus thus requires proper solution. Given that M. camini is putatively synonymous with $M$. macedonicus, we use this name as a trinomial, but only as a temporary solution until the identity of the type specimen is assessed indisputably. If camini would prove conspecific with


Figure 131. Macedonian house mouse Mus macedonicus from the Balkans. Photo: E. Grimmberger.
M. domesticus, a new subspecific name would be required for the Israeli Macedonian house mice. Considering the great recent interest about the history of Mus in the Near East (e.g. Cucchi et al., 2005), it is surprising that the type of camini, which is deposited in BMNH, remains unstudied.

## Description

External characters are essentially as in Mus domesticus. Tail is not as wide at its base, and is shorter relative to head and body ( $81.4 \%$ of head and body length on average; range $=66.7-100.0 \%, \mathrm{n}=157$ ).

Colour is variable but belly is never pure white, a condition seen in the pale form of Mus domesticus. Upper parts range from dusky wood-brown to buff-


Figure 132. Skin of Mus macedonicus in dorsal and ventral view. Based on an adult male from 10 km northeast of Bardakçi, district Manisa. Photo: C. Mlinar.
brown; flanks are slightly paler, washed with buff in some individuals. Belly is whitish, cream, buffygrey or grey; throat is frequently more whitish than the rest of underside. Hair bases are invariably slate. Some animals have an indistinct buff stripe along the throat and chest or a cream white stripe on the belly. Feet are cream white and ears are greyish brown; tail is indistinctly bicoloured, greyish or buff-grey above, pale grey below.

Nipples are ten, as in Mus domesticus.
Penis (Fig. 123b,d). In general, the glans penis and baculum resemble condition in $M$. domesticus, but there are also some differences between the two species. The distal protrusion (papilla centralis) has a rounded tip in lateral view; in ventral projection the protrusion is split into two lobes throughout its length. The ventral furrow extends all along the glans nearly reaching its base. The apex of a short and wide distal baculum is either concave or with a deep notch, but it is never pointed (Lavrenchenko, 1994). The proximal stalk is straight in lateral view; expanded base is convex dorsally and concave ventrally (Yiğit et al., 2006c).

Skull is essentially as in M. domesticus; for differences see diagnostic characters listed in the determination key above. Zygomatic width accounts for 50.5-59.1\% of condylobasal length (mean $=55.2 \%$, $\mathrm{N}=68$ ).

Teeth are as in M. domesticus although there are some minor differences. Sub-apical notch on outer side of cutting edge immediately behind the margin of enamel of the upper incisors is less conspicuous or absent (Fig. 120). Third molar is less suppressed in size and cusps tend to be smaller. On $1^{\text {st }}$ lower molar, the mesio-labial cusp is large. Second upper molar occasionally bears antero-labial cusp t3. Alveolar pattern in not known.

Dimensions. Females are significantly heavier than males in Turkey (Table 24) and in the Balkans (mean body mass $=14.4 \mathrm{~g}$ in males and 15.5 g in females; Vohralík et al., 1996).

Chromosomes. Standard karyotype is indistinguishable from $M$. domesticus: diploid number of chromosomes is $2 \mathrm{~N}=40$ and fundamental number of autosomal arms is $\mathrm{FN}_{\mathrm{a}}=38$. Therefore, all chromosomes are acrocentrics. The karyotype was reported from Ankara (Gözcelioğlu et al., 2005), Kayseri and Samsun (Gündüz et al., 2000).


Figure 133. Skull and mandible of Mus macedonicus, based on an adult female from Kürtler, Samsun. Scale bar $=5 \mathrm{~mm}$.

## Variation

Mus macedonicus consists of two subspecies, well supported by molecular (Orth et al., 2002; Cucchi et al., 2006; Macholán et al., 2007) and morphometric evidence (Macholán et al., 2008). TamuraNei genetic distance between these two subspecies is 2.19 \%, compared to 0.24 \% between the European and Asiatic samples of M. m. macedonicus and 4.52 \% between M. macedonicus and M. cypriacus.

Therefore, the two subspecies putatively diverged about 200,000-300,000 years ago. Mice in two subspecies are of approximately same size and morphological differences can be assessed only by multivariate methods. Distributional borders of the two subspecies remain unresolved but hybrid zone is expected along the north-western edge of the Lebanon Mts. and/or in the Bekaa Valey (Macholán et al., 2007).

|  | males |  |  | females |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | $\operatorname{mean}$ | $\min -\max$ |
| Head and body | 82 | 81.2 | $65-97$ | 54 | 84.5 | $71-100$ |
| Tail | 80 | 66.7 | $56-81$ | 53 | 66.9 | $57-78$ |
| Hind foot | 84 | 16.7 | $12.0-18.2$ | 55 | 16.6 | $15.0-18.1$ |
| Ear | 80 | 13.0 | $10.5-16.0$ | 52 | 13.0 | $11.0-15.0$ |
| Weight | 72 | 16.1 | $10.5-30.0$ | 47 | 17.6 | $11.5-32.0$ |
| Condylobasal length | 44 | 20.9 | $19.5-22.6$ | 30 | 20.8 | $18.3-22.3$ |
| Zygomatic breadth | 44 | 11.5 | $10.7-12.3$ | 31 | 11.7 | $10.7-12.6$ |
| Maxillary tooth-row | 56 | 3.8 | $3.4-4.1$ | 42 | 3.8 | $3.4-4.1$ |

Table 24. External and cranial dimensions of Mus macedonicus from Turkey according to sex. Sources: BMNH, ZFMK, and our own material.


Figure 134. Upper (a) and lower molars (b) in Mus macedonicus from Adana. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

## Mus macedonicus macedonicus Petrov \& Ružić, 1983

The nominal subspecies occupies the European range of the Macedonian house mouse in addition to Anatolia, Transcaucasia, Syria, and Iran, but is probably also present in Iraq. Kratochvíl (1986) has already remarked that interpopulation variation across the range is low, a view fully confirmed in recent molecular (Gündüz et al., 2000; Cucchi et al., 2006; Macholán et al., 2007) and morphometric studies (Cucchi et al., 2006; Macholán et al., 2008). Coalescent time for Asiatic and European populations is about 23,000-33,000 years (Macholán et al., 2007). Gündüz et al. (2000) postulated recent expansion from a rather small source but the refugial area has so far not been identified.

Mus macedonicus camini Bate, 1942
Mus camini Bate, 1942. Type loc.: Tabun Cave, Israel (Auchelian segment of the Palaeolithic).

Mus spretoides Bonhomme, Catalan, Britton-Davidian, Chapman, Moriwaki, Nevo \& Thaler, 1984. Type locality not specified. Nomen nudum.

For nomenclature, see our discussion on taxonomic issues in M. macedonicus. The subspecies occupies Israel and Lebanon (Ma cholán et al., 2007), and might also be present in Jordan. Measurements in millimetres $(\mathrm{N}=15)$ : length of head and body: 6994 (mean = 79.9), length of tail: 54-71 (mean = 62.5; Cucchi et al., 2006).

## Distribution

Range is in two fragments, separated by the Bosporus and Marmara straits. In Europe, M. macedonicus occupies southern and south-eastern Balkans in Macedonia (Petrov \& Ružić, 1985), Albania (Bego et al., 2008), Greece (Vohralík \& Sofianidou, 1987, 1992a), Bulgaria (Peshev et al., 2004), and Turkish Thrace. Asiatic portion covers Anatolia (cf. below), Transcaucasia in Georgia, Armenia and Azerbaijan (Kotenkova et al., 1994; Macholán et al., 2007), northwestern Iran, Syria, Lebanon, Jordan, and Israel (Musser \& Carleton, 2005; Macholán et al., 2007), and probably Iraq as well. The Macedonian house mouse also occupies several eastern Aegean islands in Turkey: Gökçeada (Özkan, 1999a), Bozcaada (our own data) and Greece: Samothraki, Chios, Lesbos, Samos (Macholán, 1999b), and Rhodes (Kryštufek \& Mozetič-Francky, 2005).

In Turkey, the Macedonian house mouse is widespread both in Thrace and Anatolia (Fig. 135).

Palaeontology. The genus Mus occupied Israel for at least 500,000 years (Tchernov, 1975), while Mus macedonicus has been continuously present there for the last approximately 160,000 years (Tchernov, 1992). In the Qumm-Qatafa layers (late Pleistocene) Mus was the most common animal after Microtus (Tchernov, 1968). Contrary to a long fossil record in Israel, M. macedonicus evidently appeared fairly late in Anatolia. Noteworthy, it is not present in a rich middle Pleistocene small mammal assemblage from Emirkaya 2 in Central Anatolia (Montuire et al., 1994). The earliest record seems to be a report of Mus abbotti from the upper-most Epipalaeolithic (terminal Pleistocene) layers in Karain near Antalya (Storch, 1988). Around 19,400 years B.P., M. macedonicus was also present in Jordan (Belmaker et al.,


Figure 135. Distribution of Mus macedonicus in Turkey and adjacent regions. For further details on records see Appendix 6.
2001). In European Turkey, Mus was not represented in Middle Pleistocene strata of Yarimburgaz (S antel, 1994), although the genus was present around that time in Greece (Kowalski, 2001).

## Habitat

Auffray et al. (1990a) defined the range of M. macedonicus as being confined to the Mediterranean climate zone and only slightly exceeding it in Bulgaria and Greece. These authors evidently based their conclusion on their field experience from Israel, where the species' southern range does coincide with the 400 mm rainfall curve and mice were not captured above 500 m of elevation. The opinion has persisted in the literature until now, no matter how incomplete it is. In the Near and Middle East, M. macedonicus penetrates deep inland and is a common species in areas with mean temperatures of the coldest month far below the freezing point (e.g. highlands of Central and East Anatolia, high Iranian plateau).

Throughout the Balkans and Anatolia, we captured Macedonian house mice in open places with tall and dense vegetation (grasses, sagebrush, reeds, and/ or bushes). Strips of such vegetation were frequently associated with arable land and/or water (streams,
irrigation ditches, lakes in Central Anatolia). Less frequently, we found M. macedonicus in cultivated fields and only rarely in gardens. Not a single specimen among the several hundred individuals sampled, was collected from a house or other type of building. Avoidance of human settlements is also reported from other parts of the range (Harrison \& Bates, 1991; Macholán, 1999b). Similar to the situation elsewhere, the species was never captured in a forest in Turkey.

In Israel, M. macedonicus was also collected in sandy dunes and among Pistacia lentiscus bushes (Harrison \& Bates, 1991). The species typically invades post-fire zones in the first stages of habitat recovery (Haim et al., 1999).

Altitude. The Macedonian house mouse ranges from sea level up to about 1,600 m of elevation. In the western Balkans, it goes as high as 860 m a.s.l. (our unpublished data), in Greek Macedonia up to 620 m (but 24 records of total 25 were $<180 \mathrm{~m}$ a.s.l.; (Vohralík \& Sofianidou, 1987), and in Greek Thrace the altitudinal range is $0-230 \mathrm{~m}$ (Vohralík \& Sofianidou, 1992a). All records from Turkish Thrace known to us are from the lowlands. The highest altitudes in Anatolia are at 1,200 m on the Aegean coast


Figure 136. Habitat of Mus macedonicus in Turkey. a - 2 km south-east of Karakasım, district Edirne, 40 m a.s.l.; b - Doğanköy, Eber Golü, Afyon, 995 m a.s.l.; c - Kızkalesi, Korykos, district Mersin; d - south of Gaziantep. Photo: B. Kryštufek (a, b), A. Kryštufek (c, d).
(based on owl pellets; Niethammer, 1989), 1,400 m in Central Anatolia (near Sivas) and $1,600 \mathrm{~m}$ in the Taurus Mts. (Çığlıkara); in Eastern Anatolia, the species was recorded near Horasan and Erzurum, i. e. at about $1,500 \mathrm{~m}$.

Associates. In Thrace and Anatolia, Macedonian house mice occupy habitats also populated by ground squirrels (Spermophilus citellus and S. xanthoprymnus) and mole rats (Spalax leucodon, S. xanthognath$u s$, and S. ehrenbergi). A wide range of small mammals was collected in traps lines along with M. macedonicus: Crocidura suaveolens, C. leucodon, Neomys anomalus, Arvicola amphibius, Microtus subterraneus, M. socialis, M. hartingi, M. dogramacii, M. levis, Cricetulus migratorius, Mesocricetus brandti, Meriones tristrami, Apodemus mystacinus, A. flavi-
collis, A. sylvaticus, A. witherbyi, Rattus rattus, Acomys cahirinus, Dryomys nitedula, and Myomimus roachi. Syntopic occurrence with Mus domesticus was exceptional and restricted to south-eastern Anatolia but is also known further south in Israel and Jordan (Harrison \& Bates, 1991). Mus macedonicus was the only outdoor house mouse we captured in Thrace. The two house mice are sympatric on the Turkish islands of Bozcaada and Gökçeada (Özkan, 1999a, and our own data). In the eastern Aegean islands of Greece, they are sympatric on Samothraki, Rhodes, Samos, Chios, and Lesbos, while M. macedonicus is probably missing on Kos (Niethammer, 1989; Vohralík \& Sofianidou, 1992a; Macholán, 1999b; Kryštufek \& Mozetič-Francky, 2005).

Density. This species is locally abundant both in Thrace and Anatolia (see also account on predation). On the Island of Gökçeada, M. macedonicus (57 animals collected) was less common than Apodemus flavicollis (96 individuals) but more common than Rattus rattus (32 individuals; Özkan, 1999a).

## Biology

Activity is nocturnal. Macedonian house mice acclimate to photoperiod by modifying thermoregulatory mechanisms and body mass (Haim et al., 1999).

Reproduction. Overall sex ratio is approximately balanced but males are underrepresented in the upper classes of weight (above 20 g ) and body length (above 90 mm ; Vohralík et al., 1996). Females attain reproductive maturity at body mass of 10 g , and males at 12 g . The reproductive season in the Balkans starts in mid-February and first cubs are born at the beginning of March. The last pregnant females were collected in October. The proportion of sexually active males is highest in May (87\%) and June (91\%) and very low in October and November ( $<10 \%$ ). Similarly, the proportion of mature females was highest in May (95\%), June (64\%), July (70\%), and August (75\%), but dropped in September (42\%) and October (40\%), and was very low in November (22\%) and December ( $21 \%$ ). Steady decrease in the proportion of mature mice is due to recruitment of young animals, decreased intensity of maturation, and possibly also to the selective mortality of mature animals at the end of the breeding season. The proportion of pregnant females is highest between May (38\%) and August (50\%; Vohralík et al., 1998).

Number of embryos in the Balkans is 4-10 (mean $=6.73, \mathrm{~N}=45$ ). Resorption rate is low ( $3.63 \%$, N $=303$ embryos). Embryos counts decrease steadily from May and June (mean $=7.73, \mathrm{~N}=11$ ), across July and August (mean $=6.17, \mathrm{~N}=24$ ) to September and October (mean = 5.90, N = 10; Vohralík et al., 1998). Count of embryos is similar in Anatolia (mean $=6.57$, range $=5-9, \mathrm{~N}=7$ ), but it is lower in the Island of Gökçeada (5.33, N = 6; Özkan, 1999a).

Food habits in Mus macedonicus are not known. Captive specimens accept a wide variety of food (mouse and rat breeder diet, wheat, etc.).

Predation. Two studies of the barn owl (Tyto alba) diet in the Menderes delta uncovered M. macedonicus to be by far the most abundant prey item,
representing 53.9\% (Brinkmann et al., 1990) and 64.3\% of all individuals (Niethammer, 1989). In Syria, where M. domesticus is a common component in the owl diet, the Macedonian house mouse is only rarely preyed upon (Shehab et al., 2004).

## Cyprus house mouse - Mus cypriacus

Mus cypriacus Cucchi, Orth, Auffray, Renaud, Fabre, Catalan, Hadjisterkotis, Bonhomme \& Vigne, 2006. Type loc.: Alassa village, Lemassol, Cyprus.

## Taxonomy

House mice of Cyprus were long reported under M. domesticus (e.g. Bate, 1903a). Before being recognized as a species in its own right, the Cyprus house mouse was reported as Mus spicilegus "South" (Orsini et al., 1983), M. spretoides (Bonhomme et al., 1984; Auffray et al., 1990a), M. abbotti (Cheylan, 1991), and M. macedonicus (Harrison \& Bates, 1991; Kryštufek \& Vohralík, 2001; Musser \& Carleton, 2005). Bonhomme et al. (2004) showed that mice from Cyprus, although closely related to M. macedonicus, actually belong to an independent phylogenetic lineage which was formally described in 2006 (Cucchi et al., 2006). Based on the molecular clock, the divergence between M. macedonicus and M. cypricacus is estimated to be 430,000-610,000 years ago (Macholán et al., 2007). Macholán et al. (2008) provided detailed morphometric comparison between the two closely related species.

## Description

External characters. The Cyprus house mouse resembles externally the Central-European Apodemus sylvaticus. Compared to Mus macedonicus, M. cypriacus has, on average, a longer tail relative to head and body length (mean $=98.6 \%$, range $=85.1-117.1$ $\%, n=34$ ).

Colour in adult M. cypriacus is similar to colouration in the Central-European Apodemus sylvaticus. Upper parts are wood brown, rarely dusky woodbrown, darker along the spine in some individuals. Flanks are buff and demarcation line is more distinct in comparison to the two previous Mus species. Bel-
ly is greyish-cream or greyish-buff. Hair bases are invariably slate. Feet are cream white and ears are greyish brown; tail is indistinctly bicoloured, gray brown, greyish or buff-grey above, pale grey to grey-ish-white below.

Nipples are ten, as in Mus domesticus (Cucchi et al., 2006).

Penis and baculum were not studied.
Skull. Apart from its larger size, the skull is essentially as in M. macedonicus. Comparatively great cranial size is ascribed to island gigantism (Macholán et al., 2008). Width across zygomatic arches is on average $55.3 \%$ of condylobasal length (range = 53.9-56.8 \%, $\mathrm{N}=18$ ).

Teeth are as in M. macedonicus but differ by be-
ing larger in size. Alveolar pattern of house mice from Cyprus is described under M. domesticus. It is possible that the prevalence of four roots on $1^{\text {st }}$ upper molar and of two roots on $3^{\text {rd }}$ upper molar is typical of $M$. cypriacus (M. domesticus normally shows three-rooted $1^{\text {st }}$ and $3^{\text {rd }}$ molars).

Dimensions. Sexes are subequal (Cucchi et al., 2006).

Chromosomes. Karyotype is same is in the other two Mus species from the region: diploid number of chromosomes $2 \mathrm{~N}=40$, fundamental number of autosomal arms $\mathrm{FN}_{\mathrm{a}}=38$ (Cucchi et al., 2006).

## Variation

Cyprus house mouse is a monotypic species.


Figure 137. Skins of Mus cypriacus from Paramytha, Limassol, in dorsal and ventral view. Note differences in ventral colouration and tail length. Not to scale. Photo: C. Mlinar.


Figure 138. Skull and mandible of Mus cypriacus, based on an adult female from Apsiou, Limassol, Cyprus.

Scale bar $=5 \mathrm{~mm}$.

## Distribution

Cyprus house mouse is endemic to Cyprus. It is widespread across the island (Fig. 140) from sea level to at least 1,605 m of elevation (Macholán et al., 2007, and in verb.).

Palaeontology. Since the Messinian salinity crisis 5.3-6 million years ago, Cyprus was isolated from the mainland. Therefore, the ancestor of the Cyprus house mouse had to colonize the island by passive immigration. As estimated by the molecular clock

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 51 | 80.2 | $70-95$ |
| Tail | 51 | 76.5 | $63-92$ |
| Hind foot | 30 | 17.2 | $15.1-19.0$ |
| Ear | 25 | 15.1 | $13.6-16.8$ |
| Weight | 27 | 17.4 | $11.5-24.0$ |
| Condylobasal length | 18 | 21.8 | $20.6-22.8$ |
| Zygomatic breadth | 20 | 12.1 | $11.5-14.0$ |
| Maxillary tooth-row | 25 | 4.0 | $3.7-4.3$ |

Table 25. External and cranial dimensions of Mus cypriacus. Sources: Cucchi et al. (2006), specimens in BMNH, and our own material.


Figure 139. Upper (a) and lower molars (b) in Mus cypriacus from Apsiou, Limassol, Cyprus. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.


Figure 140. Records of Mus cypriacus: $\mathbf{1}$ - St. Hilarion Castle, Girne (= Kyrenia), 570 m a.s.l.; 2 - Zeytinlik, Girne (= Kyrenia), 160 m a.s.l.; 3 - 4 mi east of Kyrenia; 4 - Agios Dometios (western border of Lefkosia-Nicosia); 5 - Lakkia (=Latisia); 6 - Kornos, 305 m a.s.l.; 7 - Kophinou (=Kofinou); $\mathbf{8}$ - Skarinou, Limassol; 9 - Pyrgos; 10 - Apsiou, ca 10 km north of Limassol, ca 400 m a.s.l.; 11 - Paramytha, ca 12 km north of Limassol, ca 300 m a.s.l.; $\mathbf{1 2}$ - Alassa; $\mathbf{1 3}$ - Kourio, Episkopi, Limassol; 14 - Pachna; 15 - Potamiou; 16 - Pera Pedi; 17 - Mt. Olympos, Troodos Mts, 1,605 m a.s.l.; 18 - Mandria (ca 4 km west of Kouklia); 19 - Kissonerga (ca 5 km north of Pafos); 20 - Petratis Gorge, Polis, Akamas, 210 m a.s.l.; 21 - Neo Chorio, Polis, Akamas, ca 300 m a.s.l.; 22 - Pelathousa (ca 2 km south-east of Polis), 150 m a.s.l. Corresponding references: Bonhomme et al. (2004): 4, 7, 18, 19. Cucchi et al. (2006): 5, 9, 12, 14, 15, 16. Macholán et al. (2007): 1, 2, 6, 10, 11, 17, 20, 21, 22. BMNH: 3. Our own data: 8, 13.
(Macholán et al., 2007), this happened about 0.5 million years ago. Fossil evidence from the island on this mouse is still weak. "Four Cypriot Pleistocene sites have produced unspecified murid remains ..., although it is possible that some of these remains are Holocene intrusions." (Reese, 1999). Subfossil mice from Aetokremnos are morphologically closer to M. macedonicus than M. domesticus (Reese, 1999). Mus domesticus was introduced into Cyprus during the Neolithic period by the very first agro-pastoral settlers coming from the mainland (Cucchi et al., 2002).

## Habitat

Cyprus house mice were collected from Mediterra-
nean habitat mosaic and from abandoned cultivation terraces. Although vegetation cover is dense and tall, house mice do not penetrate the thick macchie scrub (Watson, 1951a). Cucchi et al. (2006) provided list of common grasses (Avena sp.), shrubs (Calycotome villosa, Genista sphacelata, Cistus creticus, C. salviifolius, Asphodelus aestivus,Pistacia lentiscus,P. terebinthus, Vitis vinifera, Sarcopoterium spinosum, Crataegus azarolus) and trees (Prunus dulcis and Pyrus syriaca) in M. cypriacus habitat. Watson (1951a) suggested that typical habitat of house mice (reported as M. musculus, but possibly representing M. cypriacus) are "gullies and terrace walls covered with small thick bushes of Poterium spinosum and Cistus salvifolia."


Figure 141. Habitat of Mus cypriacus. Photo: A. Kryštufek (top) and I. Horáček (bottom).

Altitude. From sea level (our own observations) up to $1,605 \mathrm{~m}$ on Mt. Troodos (Macholán et al., 2007 and in verb.).

Associates. The Cyprus house mouse co-occurs with Crocidura suaveolens (or C. cypria), Mus domesticus, Acomys cahirinus, and Rattus rattus. There is some evidence on niche segregation between the three murids. Syntopic occurrence between the two Mus species is rare; M. domesticus dominates lowland areas heavily affected by man, while M. cypriacus frequents abundant agricultural areas and is increasingly more common with an increase in elevation (Cucchi et al., 2006).

Relations between house mice (reported as $M$. musculus, but possibly representing M. cypriacus) and spiny mice on Cyprus are quoted from Watson (1951a). Acomys cahirinus "frequently inhabits ground where rats are also living; but its range does not appear to overlap with the house mouse." In habitats suitable for both species but inhabited only intermittently by Acomys, Mus "may be found there when spiny mice are not present" (Watson, 1951a).

House rats are the most abundant rodent species on Cyprus, and presumably compete with Cyprus house mice (Landová et al., 2006).

Density not known. In any case, M. cypriacus is by far more abundant than Acomys cahirinus, but is probably outnumbered by rats.

Biology of M. cypriacus is virtually unknown.
Activity. We collected Cyprus house mice only during the night.

Reproduction. Five females collected in April had 5-7 embryos (mean =5.80).

Food. Captive specimens accept wide variety of food (mouse and rat breeder diet, wheat, etc.; D. Frynta, personal communication).

## Subfamily: Deomyinae Thomas, 1888

Spiny mice, genus Acomys, are currently in the subfamily Deomyinae, which contains a further three African genera: Deomys Thomas, 1888, Lophuromys Peters, 1874, and Uranomys Dollman, 1909 (Musser \& Carleton, 2005). Group names Acomyinae Dubois, Catzeflis \& Beintema, 1999 (containing Acomys and Uranomys) and Acomyinae Michaux \& Catzeflis, 2000 (same scope as for Deomyinae) do not satisfy the requirements set by the International Code of Zoological Nomenclature (ICZN, 1999) and are thus not valid (nomina nuda; Musser \& Carleton, 2005). Earlier, Acomys was frequently placed in Murinae (Musser \& Carleton, 1993) and also reported as such in our checklist of regional mammals (Kryštufek \& Vohralík, 2001). DNADNA hybridization placed spiny mice, together with Uranomys and Lophuromys, closer to Gerbillinae than to Murinae (Chevret et al., 1993). As such, Deomyinae are possibly a sister group to Gerbillinae (Michaux et al., 2001; Chevret et al., 2002). Fraguedakis-Tsolis et al. (1993) found Murinae (Muridae) to be immunologically closer to Arvicolinae (Cricetidae) than to Acomys.

The monophyly of Deomyinae received support from cladistic analysis based on several nuclear and mitochondrial fragments (Steppan et al., 2005). Contrary to this, a cladistic reconstruction based on cranial and dental morphology placed Acomys into a monophyletic clade together with two extinct genera,

Malpaisomys Hutterer, López-Martínez \& Michaux, 1988, and Stephanomys Schaub, 1938 (López-Martínez et al., 1998); Canariomys Crusafont-Pairo \& Petter, 1964, another extinct genus, is possibly also closely related to this clade (Musser \& Carleton, 2005). Noteworthy, morphological evidence does not support close affinities of the Acomys-MalpaisomysStephanomys clade to Deomys and Lophuromys, and Musser \& Carleton (2005) allocated Malpaisomys into Murinae. As stressed by several authors (López-Martínez et al., 1998; Denys et al. 2002), Acomys is cranially and dentally a murine.

## Genus: Асомys I. Geoffroy, 1838

The number of species in Acomys has changed significantly over time and still has not stabilized; e.g. 14 species were recognized by Musser \& Carleton (1993) vs. 19 species in Musser \& Carleton (2005). The genus probably originated in the tropical savannah in southern or in eastern Africa (Barome et al., 2000). The oldest fossils are from southern Africa, while extant $A$. wilsoni Thomas, 1892, which is
presumably the closest to a hypothetical ancestor of Acomys (Denys et al., 1994), occurs in eastern Africa. Spreading from a hypothetical centre of origin possibly started during the Middle Miocene some 9.7-13.7 million years ago (Barome et al., 2000). Fraguedakis-Tsolis et al. (1993) estimated for the Acomys evolutionary lineage, a split from Murinae and Cricetidae some 22-27 million years ago. Denys et al. (1994) estimated the age of Acomys to be 14 million years, while the molecular-clock analysis by Michaux et al. (2001) gives results of 17.9-20.8 million years ago. The earliest fossil from southern Africa, date back to the Early Pliocene (about 5 million years ago; Denys, 1990) or possibly to the Upper Miocene (8-7 million years; Denys et al., 1994). Main speciation events in Acomys did happen in Africa (Barome et al., 2000), were the highest number of species still occurs (Bates, 1994; Barome et al., 2000; Musser \& Carleton, 2005). The cahirinusdimidiatus group putatively radiated at the end of Pleistocene (2-2.8 million years ago). Subsequently, A. dimidiatus (Cretzschmar, 1826) (type locality: Egypt, Sinai) presumably migrated northwards and penetrated the Near East and afterwards dispersed as


Figure 142. Northeast African spiny mouse Acomys cahirinus. Drawing: J. Hošek.
far east as Pakistan (Barome et al., 2000); cf. a map in Bates (1994), where this species is reported as $A$. cahirinus. The first appearance in Israel is from the Upper Palaeolithic about 20,000-30,000 years before the present (Tchernov, 1968a). The Acomys fossil record in northern Africa (Egypt) dates back 120,000 years while the divergence time between A. cahirinus and A. dimidiatus has been estimated at 40,000 years before the present (Denys et al., 1994). The last phase in Acomys evolution was the man-aided dispersion of A. cahirinus across the Mediterranean to the islands of Crete and Cyprus, and to the southern coast of Anatolia (Barome et al., 2000).

Spiny mice translocated into the northeastern corner of the Mediterranean Sea during historic times, founded three populations which diverged in isolation and are recognised either as junior synonyms of A. cahirinus (Corbet, 1978), distinct subspecies of A. cahirinus (Ellerman \& Morrison-Scott, 1951), or a species in their own right (Bates, 1994; Musser \& Carleton, 2005): A minous Bate, 1906, in Crete (type locality is Kanea), A. nesiotes in Cyprus, and A. cilicicus in the vicinity of Silifke, Turkey. Hereafter, we address two questions: (1) the ancestor(s) of the northeastern Mediterranean taxa, and (2) their taxonomic status.

Two Acomys species are the putative ancestors of a small range taxa occurring in the northeastern Mediterranean (subsequently NE Mediterranean taxa): A. cahirinus from northeast Africa and A. dimidiatus from the Near and Middle East. Based on morphology, A. minous, A. nesiotes and A. cilicicus are believed to share their ancestor with A. dimidiatus (Spitzenberger, 1978a,b; Denys et al., 1994). Although Denys et al. (1994) also considered dental traits, size is perhaps the most important single morphological character to distinguish between $A$.

| Taxon | Locality | N | CbL | N | MxT |
| :--- | :---: | :---: | :---: | :---: | :---: |
| A. dimidiatus | Israel | 16 | 29.1 | 16 | 5.03 |
| A. cahirinus | Cairo, Giza | 17 | 25.7 | 18 | 4.34 |
| A. c. minous | Is. of Crete | 13 | 28.9 | 16 | 4.94 |

Table 26. Mean condylobasal length of skull (CbL) and length of maxillary molars (MxT) in various Acomys taxa occurring in the Eastern Mediterranean; for A. c. nesiotes and A. c. cilicicus see Tables 29 and 32, respectively. Based on specimens in BMNH, SMF, ZFMK and NM, and our own material.
dimidiatus (larger) and A. cahirinus (smaller; Table 26). Both island taxa are of same size as A. dimidiatus, while A. cilicicus appears smaller, albeit still bigger than A. cahirinus from Egypt. We failed to detect a phylogenetic signal in a set of size-free cranial variables between $A$. dimidiatus and $A$. cahirinus (our unpublished data) and therefore doubt whether traditional skull morphometrics has the potential to untangle the evolutionary history in the cahiri-nus-dimidiatus group. Contrary to morphology, cytochrome $b$ phylogenetic reconstructions strongly support a monophyly of $A$. cahirinus and the three NE Mediterranean taxa. Acomys airensis Thomas \& Hinton, 1921, from Mali, Niger and Chad, is possibly in a sister position to the A. cahirinus clade ( $c a-$ hirinus + minous + cilicicucs + nesiotes), while $A$. dimidiatus appeared closer to $A$. johannis Thomas, 1912, from Niger, Nigeria and Cameroon (Barome et al., 2000). Barome et al. (2001) reported very low cytochrome $b$ divergences ( $\leq 1.6 \%$ ) in the A. cahirinus clade, which are within intraspecific diversity observed in other Acomys species. Interspecific hybridisation experiments offer, despite slightly contradictory results, an interesting insight into speciation within the cahirinus-dimidiatus group. Frynta \& Sádlová (1998) produced fertile and viable offspring between A. cilicicus and A. cahirinus from Egypt. On the other hand, attempts to hybridize A. cilicicus or A. cahirinus with laboratory lineages of $A$. dimidiatus and $A$. minous produced negative results. Acomys cahirinus successfully hybridized with $A$. nesiotes (Zahavi \& Wahrman, 1956) and A. minous (Matthey, 1963). Eisentraut \& Dieterlen (1969) obtained offspring between A. minous and A. dimidiatus. Hybrid offspring of $A$. minous females were of normal size, but were bigger in $A$. dimidiatus females, which caused difficulties during birth. Backcrossing was successful only between F1 male hybrids (A. dimidiatus mothers) with $A$. dimidiatus females; F2 hybrids were sterile. Cross-breeding trials between Acomys dimidiatus and $A$. cahirinus yielded sterile offspring which exhibited substantial hybrid vigour in offspring which were twice the weight of either parental species (Jordan, 2000). Based on the above evidence, we conclude that NE Mediterranean taxa evidently originate from A. cahirinus.

Several authors (Spitzenberger, 1978a,b; Denys et al., 1994) suggested that morphological dif-
ferences between the three NE Mediterranean taxa suggest that they are distinct species. Differences are certainly impressive however morphology is plastic in Acomys and responds to environmental conditions. Nevo (1989) demonstrated for A. dimidiatus in Israel and Sinai a significant variation between localities in body characters, e.g. a decrease in body mass and length with aridity. Morphology also correlated with allozymic variation. Yom-Tov \& Geffen (2006) confirmed the existence of geographic variation in cranial traits of $A$. dimidiatus; size factor correlated with seasonality, temperature and precipitation. Cyochrome $b$ sequences clustered NE Mediterranean taxa together with A. cahirinus and, as stated above, distances were within intraspecific diversity in other Acomys species (Barome et al., 2000). Furthermore, $A$. minous is paraphyletic with respect to $A$. nesiotes and A. cilicicus, either a consequence of its origin from distinct stock populations (presumably Cyprus and the Anatolian coast), or from a single highly diversified ancestral population. The molecular clock gives $A$. minous a coalescent time of 0.4 million years before the present which predates historic times. However, polymorphism observed among A. minous possibly, reflects the polymorphism of the stock population(s) rather than the diversification following introduction by man (Barome et al., 2001).

Karyologically, the NE Mediterranean taxa belong to the cahirinus-dimidiatus group, which is characterized by a low diploid number of mainly biarmed chromosomes. The three NE Mediterranean taxa display unique chromosome counts (Table 27). Karyotoypes are composed of the same acrocentric chromosomes which differ in their combination into biarmed chromosomes. As a consequence, the biarmed elements are not homologous between NE Mediterranean taxa (Denys et al., 1994). In any case, A. cahirinus, A. cilicicus, and A. nesiotes represent a separate group of karyologically closely related taxa (Zima et al., 1999). The predominant mechanism in their karyotypic evolution was presumably centric fusions (Robertsonian translocations) from a hypothetical ancestor with the acrocentric karyotype. Rapid chromosomal evolution was putatively facilitated by a change in the molecular organization of the chromosomes (Robertsonian fusion is strongly related to the level of amplification of repeated sequences in centromeric regions) and by a change in the pop-
ulation structure in small isolated populations (Denys et al., 1994). Several authors expressed doubt as to whether the minor chromosomal differences are sufficient to cause reproductive isolation between $A$. cahirinus and NE Mediterranean taxa (e.g. Volobouev et al., 2002), a concern which was fully corroborated in hybridization trials (cf. above). Putative specific status of NE Mediterranean taxa is thus supported only by morphological evidence, but not by other data sets (molecular, chromosomal, hybridization experiments). Contrary to our earlier opinion (Kryštufek \& Vohralík, 2001) we have since decided to report the two taxa occurring in Turkey and Cyprus as distinct subspecies of $A$. cahirinus.

| Taxon | 2 N | $\mathrm{NF}_{\mathrm{a}}$ |
| :--- | :---: | :---: |
| A. dimidiatus | 36 | 68 |
|  | 38 | 68 |
| A. cahirinus | 36 | 66 |
| A. c. cilicicus | 36 | 66 |
| A. c. nesiotes | 38 | 66 |
| A. c. minous | 38 | 64 |
|  | 40 | 66 |

Table 27. Karyotypes in various Acomys taxa occurring in the Eastern Mediterranean. Given are diploid number (2N) and fundamental number of autosomal arms $\left(\mathrm{NF}_{\mathrm{a}}\right)$. Source: Macholán et al. (1995).

## Northeast African Spiny Mouse - Acomys CAHIRINUS

Mus cahirinus É. Geoffroy, 1803. Type loc.: Cairo, Egypt.

Note that Mus cahirinus É. Geoffroy, 1803, predates Mus cahirinus Desmarest, 1819; both descriptions were based on material from Cairo (Musser \& Carleton, 2005).

## Taxonomy

As argued in the previous chapter, we consider the two spiny mice taxa occurring in the region, as conspecifics of $A$. cahirinus. For the sake of convenience, we designated them by subspecific names.

## Description

External Characters. Medium-sized and mouse-
like murid rodent, with spiny pelage extending from behind shoulders onto rump. Posterior dorsum consists entirely of flattened spiny bristles which are up to 15 mm long. In A. c. nesiotes, the spines are cylindrical at the base, then suddenly expand and became laminate and taper to a point. "Seen in section the edges are found to be folded downwards and inwards; thus the ventral aspect of the spine is deeply grooved, whilst the upper surface is very slightly rounded" (Bate, 1903a). Intermixed with and projecting beyond spines are a few long fine hairs. Hair on head, the flanks and belly is coarse. Tail is normally longer than head and body, although its relative length varies geographically. Annulation is distinct and coarse. Niethammer (1975b) described dermal bones in the tail of A. c. nesiotes, "forming an armour of overlapping bony rings. Each bony platelet underlies one horny epidermal scale." Skin of tail separates easily from the underlying muscles and vertebrate column in Acomys (Shargal et al., 1999). Tail is sparsely covered with short bristles which slightly exceed length of each ring; longer hairs among the bristles are pale and the terminal tuft is indistinct. Whiskers are relatively long (up to 45 mm ), ei-
ther black or white. Skin is delicate and breaks readily. Ears are about same length as hind foot; feet are broad with naked soles and palms. There are five palmar and six plantar pads; the spaces between main pads are occupied by numerous secondary tubercles.

Colour varies enormously, depending on the environment: desert forms are pale and commensal populations are darker, even melanistic (Osborn \& Helmy, 1980). Free-living populations have pale brownish, dark brown, blackish brown or grey dorsum which is speckled; flanks are pale or dark cinnamon, grayish, or brownish; belly is greyish or white, feet are creamy white to white; ears are grey; tail is indistinctly to distinctly bicoloured, brownish above and white below in pale forms. Ears are with white basal and posterior patches (Figs. 143 and 152). Dark commensal spiny mice display slate to blackish brown back, brownish or greyish flanks and greyish to white belly; feet are white, grey or blackish.

Nipples. In A. c. minous there are six nipples, two pairs of inguinal and one pair of pectoral (Niethammer 1978e).

Penis and baculum are described under A. c. cilicicus.


Figure 143. Northeast African spiny mouse Acomys cahirinus hunteri from Abu Simbel, Egypt. Photo: J. Vogeltanz.


Figure 144. Upper (a) and lower molars (b) in Acomys cahirinus (type of hunteri) from Tokar, Kassala, Sudan (BMNH). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

SkuLl is ridged in the interorbital region and along the sides of brain-case, and as such resembles that of Rattus. Rostrum is long and slender, nasals are elongate and narrow. Incisive foramens are long, extending backward to about the middle of $1^{\text {st }}$ molars. Anterior half of interpterygoid fossa is closed by a platelike outgrowth from the hard palate; the open part of fossa, formed chiefly by the hamular processes, is in a shape of small triangle. Bullae are of moderate size. Interorbital region is wide and interparietal bone is
large, the braincase is depressed posteriorly. Zygomatic arches are strong and parallel. Masseteric plate is long. Coronoid process of the mandible is reduced to a mere protuberance; angular process is blunt.

Teeth. Upper incisors are orthodont and strongly compressed. Molars are essentially of murine type; $1^{\text {st }}$ molar is the largest and $3^{\text {rd }}$ molar is the smallest. Antero-lingual cusp (t1) is shifted backward and isolated from t2 in unworn teeth. Tubercle $t 4$ is separated from t5. There is no trace of supplementary pos-tero-labial cusp $t 12$ on $1^{\text {st }}$ and $2^{\text {nd }}$ molars. Cusps on $3^{\text {rd }}$ upper molar fuse early during life. Lower molars show two parallel rows of cusps with a small distal cusp on first two teeth; $2^{\text {nd }}$ molar has an antero-labial enamel ridge.

Dimensions. Sexes are sub-equal. Dimensions vary geographically (Tables 28, 29, 32).

Chromosomes. Diploid number of chromosomes ( 2 N ) varies between 36 and 40 , and fundamental number of chromosomal arms $\left(\mathrm{NF}_{\mathrm{a}}\right)$ is 66 in all cytotypes with one exception in A. c. minous where $\mathrm{NF}_{\mathrm{a}}$ $=64$ (cf. Table 27). As stated above, karyotoypes are composed of the same acrocentric chromosomes which differ in their combination into biarmed elements. Heterosomes are acrocentric in all cytotypes (Denys et al., 1994). The only exception is subtelocentric X chromosome in A. c. cilicicus; its wholly heterochromatic short arm probably resulted from the amplification of a centromeric heterochromatin segment (Macholán et al., 1995).

## Variability

Great interpopulation variability was reported in colour, size and relative tail length with intergradations in intermediate populations; for dimensions cf. Table 28. On these grounds, Osborny \& Helmy (1980) recognized four subspecies in Egypt to the west of Sinai, not considering megalodus, which we sub-

| Location | N | Head and body | N | Relative tail length |
| :--- | :---: | :---: | :---: | :---: |
| Farafara \& Dakhala Deserts | 18 | 118.0 | 18 | 96.1 |
| Northern Red Sea Mts. | 12 | 113.5 | 8 | 110.3 |
| Nile Valley and Delta | 34 | 111.3 | 27 | 102.0 |
| Southern Eastern Desert | 90 | 107.7 | 76 | 108.5 |
| Bahariya Oasis | 10 | 98.5 | 8 | 106.9 |
| Gebel Uweinat | 8 | 89.5 | 7 | 115.4 |

Table 28. Variation of head and body length (in mm ) and tail length relative to head and body (in \%) in six geographic samples of A. cahirinus from Egypt. Sample are arranged according to descending size. Source: Osborn \& Helmy (1980).
sequently suggest to perhaps be part of A. dimidiatus. Karyotype is polymorphic; cf. Table 27 and text above. Genetic differences among cytotypes are shallow and cytochrome $b$ sequences of spiny mice from Crete suggest NE Mediterranean taxa to be paraphyletic (cf. above).

Of the two forms occurring in the region, A. c. nesiotes is larger (cf. Tables 29 and 32) and with a relatively shorter tail. Acomys c. nesiotes also differs from A. c. cilicus in grey back (predominantly drab to brown in A. c. cilicicus), blackish dorsal side of the tail (dark brown in cilicicus), dark grey ears (dull grey-brown in cilicicus), pure white belly (greyish white in cilicicus), sharp demarcation line along flanks (obscured in cilicicus), and paler feet. Acomys cahirinus cilicicus is reported to have a shorter $3^{\text {rd }}$ upper molar relative to a combined length of $1^{\text {st }}$ and $2^{\text {nd }}$ molars than A. c. nesiotes (Spitzenberger, 1978b; Denys et al., 1994). The difference is genuine and statistically significant, however, A. c. cilicicus does not differ in this respect from the Egyptian A. cahirinus (Fig. 145). Therefore, the $3^{\text {rd }}$ upper mo-


Figure 145. Box and whiskers plot of length of $3^{\text {rd }}$ upper molar relative to a combined length of $1^{\text {st }}$ and $2^{\text {nd }}$ molars (in \%) in A. cahirinus from Egypt (Cairo, Giza, and Eastern Desert), A. cahirinus nesiotes, and A. cahirinus cilicicus. Given are median (square), central quartiles (box), and range (whiskers). Based on specimens in BMNH, ZFMK, NM, and our own material.


Figure 146. Plot of the upper incisor width against condylobasal length of skull (as a single measure describing overall size) in A. cahirinus from Egypt, A. c. nesiotes, and A. c. cilicicus. Based on specimens in BMNH, ZFMK, SMF, NM, and our own material.
lar is relatively the longest in A. c. nesiotes. Small antero-labial cusp ( t 3 ) is occasionally present in A. c. cilicicus (Denys et al., 1994), but occurs also in A. c. minous (Miller, 1912) and in A. cahirinus from Egypt (Fig. 144). Spitzenberger (1978b) reports more delicate upper incisors in A. c. cilicicus in comparison to A. c. nesiotes and our results concur with this. The upper incisor is the broadest in A. c. nesiotes (mean $=2.15 \mathrm{~mm}$, range $=1.80-2.35 \mathrm{~mm}, \mathrm{~N}=62$ ), the narrowest in Egyptian A. cahirinus (mean $=1.78$ mm , range $=1.60-1.90 \mathrm{~mm}, \mathrm{~N}=21$ ) and intermediate in A. c. cilicicus (mean $=1.89 \mathrm{~mm}$, range $=1.65-$ $2.10 \mathrm{~mm}, \mathrm{~N}=17$ ). This might be due to allometry, since width of the incisor evidently follows a general increase in size, which is represented in Fig. 146 by the condylobasal length of skull.

## Key to subspecies

1 Diploid number of chromosomes $2 \mathrm{~N}=38$; on average larger: mean condylobasal length about 29 mm ; tail always shorter than head and body; back in majority of individuals predominantly grey; occurs in Cyprus
A. c. nesiotes

1* Diploid number of chromosomes $2 \mathrm{~N}=36$; on average smaller: mean condylobasal length of
27.5 mm ; tail longer than head and body in about one third of individuals; back in majority of individuals predominantly drab or brown; occurs near Silifke in southern Anatolia
A. c. cilicicus

## Distribution

Acomys cahirinus populates northeast Africa in Egypt, Libya, Sudan and Ethiopia; cf. map in Bates (1994) who reported under cahirinus also taxa which are now regarded as a distinct species (e.g. A. seurati Heim de Balsac, 1936, A. dimidiatus, etc.; cf. Musser \& Carleton, 2005). The northernmost records are in Cyprus, Crete and the southeastern coast of Anatolia; these isolates are also mapped by Bates (1994) under names different from A. cahirinus. Musser \& Carleton (2005) stressed that western and southern distributional limits remain unresolved. We briefly comment on the geographical delimitation of A. cahirinus against A. dimidiatus. Musser \& Carleton (2005) reported Sinai as the easternmost extension of $A$. cahirinus and the westward occurrence of $A$. dimidiatus. The only animal from Sinai we saw (BMNH specimen without exact locality) matches $A$. dimidiatus in size (condylobasal length of skull $=29.4 \mathrm{~mm}$ ) and Osborn \& Helmy (1980) reported for Sinai only dimidiatus (as a subspecies of A. cahirinus). Musser \& Carleton (2005) included Sinai into the range of $A$. dimidiatus on the basis of a report on A. c. dimidiatus by Saleh \& Basuony (1998). A sample from Suez (ZFMK) contains only large spiny mice (condylobasal length $=29.5 \mathrm{~mm}$, range $=28.0-31.3 \mathrm{~mm}, \mathrm{~N}=20$ ) and fits perfectly $A$. dimidiatus megalodus Setzer, 1959 (Type loc.: Bir Abu Seyala, Suez, Egypt). Hence, we suggest that $A$. cahirinus megalodus of Osborn \& Helmy (1980) possibly represents $A$. dimidiatus, as it was originally also classified by Setzer (1959). Osborn \& Helmy (1980) reported that "... dimidiatus is paler and slightly smaller than A. c. megalodus from which it is barely distinguishable" and retained the two as distinct taxa "on the basis of geographical separation."

If our interpretation is correct, then the range borders of A. cahirinus and A. dimidiatus in Africa and Sinai require corrections. In line with the above arguments, the westward extension of A. dimidiatus encompasses the northern part of Eastern Desert
in Egypt south to Bir Qiseib ( $29^{\circ} 24^{\prime}$ north, $32^{\circ} 29^{\prime}$ east) and west to Wadi Hof (also Hoaf, $29^{\circ} 53^{\prime}$ north, $31^{\circ} 18^{\prime}$ east) on the eastern bank of the River Nile; the westernmost documented occurrence on Sinai is Bir Thal ( $29^{\circ} 10^{\prime}$ north, $33^{\circ} 04^{\prime}$ east). The most eastern indisputable record of A. cahirinus is probably Qena (also Kenah, Kina, Qina, $26^{\circ} 10^{\prime}$ north, $32^{\circ} 43^{\prime}$ east). For further details refer to Osborn \& Helmy (1980).

Palaeontology. Tchernov (1968a, 1975) reported continuous presence of A. cahirinus (i.e. A. dimidiatus) in Israel for the last 20,000 years. Acomys carmeliensis Haas, 1952, from the Natufian-Neolithic of the Abu-Usba cave in Mt. Carmel, Israel (Tchernov, 1968a), is conspecific with the extant Acomys dimidiatus.

## Наbitat

In Turkey and Cyprus, spiny mice live in Mediterranean habitats (see under subspecies). The majority of A. cahirinus range however is in deserts and similar arid environments where spiny mice "inhabit rocky hillsides, cliffs, and boulder-strewn canyons" (Osborn \& Helmy, 1980). In the Nile Valley and Delta, A. cahirinus is almost completely commensal and outnumbers Mus domesticus in buildings and houses. Commensalism is not known in Libya. In Egypt, A. cahirinus also inhabits gardens and is concentrated in the vicinity of date palms (Osborn \& Helmy, 1980).

Altitude has no effect on distribution of A. cahirinus in Egypt (Osborn \& Helmy, 1980); for northern Mediterranean see under subspecies.

Associates. In Egypt, A. cahirinus was found with Acomys russatus, Dipodillus dasyurus, Gerbillus gerbillus, Sekeetamys calurus, and locally also with Dipodillus campestris. Commensal populations share their habitat with Mus domesticus and Rattus rattus (Osborn \& Helmy, 1980). For associates in the northern Mediterranean, see under subspecies.

Density. Locally common, but populations fluctuate. Osborn \& Helmy (1980) reported relative density in Gebel Elba (Egypt) as 41 spiny mice per 100 trap nights in spring 1954 and 13 per 100 trap nights in spring 1967; differences were evidently not due to some obvious environmental factor (e.g. drought or food availability). For densities in the Northern Mediterranean see under subspecies.

## Biology

The bulk of biological information available for $A$. dimidiatus, was in the past frequently reported under A. cahirinus; for a summary of the former cf. Mendelssohn \& Yom-Tov (1999). We summarized relevant information on A. cahirinus for Egypt; if not otherwise noted, the source was Osborn \& Helmy (1980). For information related to Turkey and Cyprus, see under subspecies.

Activity is at all hours of the day, but mostly in early morning and late afternoon. Acomys cahirinus is an extremely agile animal.

Burrows were found in sand and in hard gravel terrace; the only reported length is 0.5 m for a simple burrow.

Reproduction. Pregnant females were collected between February and October and litter size (based on embryos and placental scars) was 1-6 (mean $=3$ ). Part of this material possibly involves also A. dimidiatus from northeastern Egypt. Watson (1951a) reports mean number of embryos per female to be 2.5 in a commensal population from Egypt.

The spiny mice are pronouncedly precocial rodents. Gestation period in A. c. minous from Crete is 36 days; in $A$. dimidiatus it is about 38 days ( $\mathrm{Di}-$ eterlen, 1961, 1963). Neonates of A. c. minous are covered with hair but have their eyes and ears closed; eyes open in two days (Dieterlen, 1963). In A. dimidiatus, the longevity is up to five years (Harrison \& Bates, 1991).

Food. Broad spectrum of vegetable (green algae, plants, seeds and fruits) and animal (spiders, insects, desert snails Eremica desertorum) food is utilized. Spiny mice are also known to feed on the dried flesh and bone marrow of mummified humans in the tombs, and to scavenge the faeces of fruit bats (Rousettus aegyptiacus), and possibly also of humans.

Predation. Capability of shedding the tail (caudal autotomy) is a typical predator-avoidance mechanism in the genus Acomys, although inter- and intraspecific aggression may also account for this pattern. The skin of the tail separates easily from the underlying vertebrae with little bleeding. The remainding stump is later chewed off and eaten by the mouse. Tail loss ranges from partial to full and vertebrae do not regenerate. In Israel, where spiny mice are exposed to predation from Blanford’s fox (Vulpes cana), Jume's tawny owls (Strix butleri), snakes, and possibly kes-
trels (Falco tinnunculus), a 25-month field study revealed that percentage of tail-loss was 63 \% in male and $44 \%$ in female A. russatus and $12 \%$ in male and 25 \% in female A. dimidiatus. Tail-less spiny mice may have an advantage over tailed specimens; e.g. mean body mass of tail-less $A$. dimidiatus females was significantly higher and a greater proportion of tail-less male A. russatus were found in reproductive condition (Shargal et al., 1999).

## Cyprus spiny mouse - Acomys cahirinus NESIOTES

Acomys nesiotes Bate, 1903. Type loc.: Kerynia Hills, near Dikomo, Cyprus.

## Taxonomy

Taxonomic status of the Cyprus spiny mouse varied since its formal recognition as a species by Bate (1903a), who considered it to be closely related to $A$. dimidiatus (Bate, 1903b). Mitchell (1903), Matthey \& Baccar (1967), Spitzenberger (1978a), Zima et al. (1999), Bates (1994), Denys et al. (1994), Sfikas (1996), Barome et al. (2000, 2001), Kryštufek \& Vohralík (2002) and Musser \& Carleton (2005) continued to regard nesiotes as a species on its own right, although doubt was expressed by several authors. Other authors considered it to be a subspecies of $A$. cahirinus (Ellerman, 1948; Ellerman \& Morrison-Scott, 1951, 1966), its junior synonym (Corbet, 1978; Harrison \& Bates, 1991), or a subspecies of A. dimidiatus (Watson, 1951a; Niethammer, 1975b).

## Description

External Characters. The Cyprus spiny mouse is a large insular race of $A$. cahirinus. It is peculiar by a relatively short tail which averages $84.1 \%$ of the head and body length (range $=71.5-94.2 \%, \mathrm{~N}=31$ ).

Colour was described in detail by Bate (1903a). The back, which is a mixture of wood-brown and grey, is speckled by the colour of the hairs and spines. The latter "are pale grey or almost colourless for the greater part of their length, and tipped with dark grey or wood-brown" (Bate, 1903a). Grey specimens predominate, but shade varies from pale grey to blackish grey. The flanks are drab-grey to wood-brown; the un-


Figure 147. Skin of Acomys cahirinus nesiotes in dorsal and ventral view. Based on a female from Germasogeia near Limassol, Cyprus. Photo: C. Mlinar.
derparts and the upper surface of the hand and feet are pure white. The tail is mouse-grey above, pale below.

Juveniles are mouse-grey, with the exception of white underside, hands and feet. The development of the speckled appearance of the mature animal is retarded in A. c. nesiotes (Bate, 1903a).

Skull. Apart from its large size, the skull of A. c. nesiotes is essentially as in A. cahirinus from Egypt (Fig. 148). Zygomatic breadth is 49.9-54.8 \% of the condylobasal length (mean $=52.2 \%, \mathrm{~N}=63$ ).

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 63 | 120.4 | $97-135$ |
| Tail | 42 | 102.3 | $91-118$ |
| Hind foot | 62 | 20.4 | $18.8-22.0$ |
| Ear | 17 | 19.3 | $17.0-21.8$ |
| Weight | 47 | 48.3 | $31-70$ |
| Condylobasal length | 72 | 29.2 | $27.0-31.5$ |
| Zygomatic breadth | 76 | 15.2 | $14.2-16.5$ |
| Maxillary tooth-row | 76 | 4.8 | $4.4-5.3$ |

Table 29. External and cranial dimensions of Acomys cahirinus nesiotes from Cyprus. Based on Spitzenberger (1978a), specimens in BMNH, ZFMK, SMF, and own material.

| Age group | Juvenile <br> $(\mathrm{N}=3-5)$ | Subadult <br> $(\mathrm{N}=2-4)$ | Adult <br> $(\mathrm{N}=6-12)$ |
| :--- | :---: | :---: | :---: |
| Head and body | $80-97$ | $92-120$ | $106-132$ |
| Tail | $60-76$ | $71-92$ | $92-118$ |
| Hind foot | $17.6-18.9$ | $19.0-20.0$ | $18.4-21.3$ |
| Ear | $14.4-17.4$ | $20.0-21.0$ | $17.5-21.8$ |
| Weight | $12.6-21.5$ | $23.5-45.2$ | $41.8-64.2$ |
| Condylobasal length | $21.2-22.9$ | $25.6-27.9$ | $28.4-30.0$ |
| Zygomatic breadth | $12.0-13.5$ | $13.0-15.0$ | $15.2-16.4$ |
| Maxillary tooth-row | $4.3-5.2$ | $4.8-5.0$ | $4.4-4.8$ |

Table 30. Range for external and cranial dimensions of Acomys cahirinus nesiotes according to age. Modified from Spitzenberger (1978a).

| Age (months) | $>18$ | ca 12 | $8-9$ | ca 7 |
| :--- | :---: | :---: | :---: | :---: |
| Head and body | 120 | 128 | 125 | 97 |
| Tail |  | 100 |  |  |
| Hind foot | 21 | 20.5 | 21 | 20.5 |
| Weight | 43 | 54 | 49 | 31 |
| Condylobasal length |  | 29.1 | 29.5 | 28.2 |
| Zygomatic breadth |  | 15.3 | 15.1 | 14.8 |
| Maxillary tooth-row |  | 5.0 | 4.9 | 5.0 |

Table 31. External and cranial dimensions of Acomys cahirinus nesiotes with known age (in months). Based on specimens in BMNH.

Teeth.Upper incisor is wider and $3^{\text {rd }}$ upper molar is absolutely and relatively longer than in A. cahirinus from Egypt and in A. c. cilicicus (see Fig. 146, and text above). Enamel on front surface of incisors is yellow. There are traces of stephanodonty, particularly on $2^{\text {nd }}$ lower molar (Fig. 149).

Dimensions (Table 29). Sexes are sub-equal; males are insignificantly larger (mean condyloba-


Figure 148. Skull and mandible of Acomys cahirinus nesiotes, based on an adult male from Ağırdağ, Cyprus. Scale = 5 mm .
sal length of skull $=29.2 \mathrm{~mm}, \mathrm{~N}=18$ ) than females (mean $=28.9 \mathrm{~mm}, \mathrm{~N}=22$ ). Spitzenberger (1978a) gives data on age variation among six age groups based on molar abrasion; this is recapitulated in Table 30, by a tentative pooling of classes into three groups: juveniles (groups 1 and 2 of Spitzenberger, 1978a), subadults (group 3), and adults (groups 4-6). In a BMNH sample of four juveniles, head and body length is between 69 and 75 mm . Four specimens in BMNH from Watson's (1951a) CaptureRecapture study are of known age; cf. Table 31 for dimensions. Noteworthy is the animal with a body mass of 31 g and head and body length of 97 mm , which is about 7 months old. Tail is relatively longer in juveniles (Bate, 1903a).

Chromosomes. The karyotype contains 38 chromosomes and fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=66$. The automosomal complement consists of 30 biarmed elements (meta- and submetacentric) and six acrocentrics; the X chromosome is large acrocentric and the Y chromosome is the smallest acrocentric. The G-banding pattern reveals high similarity between A. c. nesiotes and A. c. cilicicus (Zima et al., 1999).


Figure 149. Upper (a) and lower molars (b) in Acomys cahirinus nesiotes (same specimen as in Fig. 148). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

## Variability

No interlocality variation is reported from the island.

## Distribution

At the time of describing the Cyprus spiny mouse as a new species, B ate (1903a) was familiar with its occurrence only on the type locality. Despite this, she assumed that this spiny mouse "probably occurs at any rate over the whole of the Mesoroea, or central plain, and the southern slopes of the Kerynia Hills." Her presumption was confirmed shortly afterwards by Mitchell (1903) who reported specimens from Ayios (=Agios) Konstantinos and Limassol, and concluded that the range is "probably extending to the whole of the island." Hitherto records confirm the above hypothesis. The spiny mouse inhabits both the northern and southern part of Cyprus, and a lack of
records in the western part of the island is most probably a bias due to insufficient sampling (Fig. 150).

## Habitat

Cyprus spiny mouse lives only on ground with "much rock cover, rocky outcrops or boulder-strewn ground." (Watson, 1951a). Such places are either bare, or covered by poor shrubby trees (Cistus villosus, C. parviflorus, Pistacia lentiscus, P. terebinthus, Styrax officinalis, Calycotome villosa, Bosea cypria, Smilax aspera; Watson, 1951a), maquis and woodland (Ceratonia siliqua, Pistacia lentiscus, Pinus brutia, Cupressus sempervivens, Juniperus phoenicea; Spitzenberger, 1978a). Spiny mice also occur in forests with plenty of rock cover, e.g. on top of the Northern Range at St. Hilarion and Halevga. They live "in small somewhat isolated communities


Figure 150. Records of Acomys cahirinus nesiotes: 1 - 8 km south of Vasilis (= Vasilia), Kyrenia; 2 - Ağırdağ (= ca 5 km south-west of Kyrenia/Girne), 440 m a.s.l.; 3 - Dikomo (= Dikmen), Kerynia Hills; 4 - Buffavento Castle, Kyrenia; 5 - 5 km east of Buffavento, Kyrenia; 6 - Armenian Monastery, Kyrenia; 7 - Syngrasi (= Sygkrasis) Reservoir, west of Trikomo (= İskele); $\mathbf{8}$ - Kantara Castle; $\mathbf{9}$ - Zafer Burnu, 4 km south-west of Apostolos Andreas Monastery; $\mathbf{1 0}$ - Cap Greco (= Akrotirio Greco); 11 - Agios Konstantinos, Kalo Chorio, over 4000 feet a.s.l.; 12 - Yermasoyia (= Germasogeia) Reservoir, Limassol; 13 - 2 km south-west of Apsiou, Limassol; 14 - Near Limassol. Corresponding referrences: Bate (1903b): 3, 14. Mitchell (1903): 11. Spitzenberger (1978a): 1, 4, 5, 6, 7, 8, 10, 12, 13. Zima et al. (1999): 9. Our own data: 2.


Figure 151. Habitat of Acomys cahirinus nesiotes at Ağırdağ near Kyrenia (440 m a.s.l.). Photo: I. Horáček.
and there is much apparently suitable ground unoccupied" (Watson, 1951a). The Cyprus spiny mouse is not known to be commensal (Mitchell, 1903).

Altitude range for the Cyprus spiny mouse is from "a belt of low fragmented cliffs on the sea shore above the tide line" (Watson, 1951a), up to approximately $1,200 \mathrm{~m}$ ("over 4,000 feet") at Agios Konstantinos in the Southern Range (Mitchel, 1903).

Associates. Watson (1951a) found the Cyprus spiny mouse to frequently inhabit grounds where the house rat (Rattus rattus) is also living. On the other hand, ranges of A. c. nesiotes and house mice (Mus sp.) did not overlap in his study, presumably a result of competitive exclusion. Habitats suitable for both species were only occupied intermittently and house mice established when spiny mice were not present. House rats are the most abundant rodent species on Cyprus, and presumably compete with spiny mice (Landová et al., 2006).

Density. The Cyprus spiny mouse lives at low densities. In 19 samplings executed by Watson (1951a) between March 1947 and April 1948, densities varied from $\ll 1$ individual per ha before start of reproductive season in March, and 3.4 per ha at its end in October. Median density was only 0.6 mice per ha. Sfikas (1996) also reports A. c. nesiotes to be a rare animal and we collected only two specimens during three visits to the island between 1999 and 2005.

## Biology

This section largely follows Watson (1951a) who
studied various biological aspects of $A$. nesiotes by Capture-Recapture trapping from March 1947 to April 1948 on two plots in Cyprus.

Activity is presumably nocturnal (Watson, 1951a). Adult females are apparently sedentary and Watson (1951a) repeatedly trapped the same individuals throughout their adult lives in one and the same locality. During 13 months of his study, maximum distance between points of recapture was $\leq 230$ m in 29 animals of total 30 , and $<100 \mathrm{~m}$ in more than half of them. Males ranged much further than females.

Reproduction. Watson (1951a) found the overall sex ratio to be slightly male biased ( $52 \%, \mathrm{~N}=335$ ), but this varied among weight classes. Percentage of males was $47 \%$ in mice $<40 \mathrm{~g}, 49 \%$ in $40-50 \mathrm{~g}$ class, $51 \%$ in $50-60 \mathrm{~g}$ class, and $58 \%$ in specimens $>60$ g. Breeding season started at the beginning of April, peaked in June, continued at a high rate throughout July and August, fell in September and ended in October; a single pregnant female was found also in February and a juvenile with a body mass about 20 g was captured in January. Between May and early September, the percentage of females with macroscopically visible pregnancies varied between $42 \%$ and $74 \%$. Watson (1951a) assumed that some of the pregnancies resulted from a post-partum oestrus and thus concurred with lactation. Number of embryos is reported to be $1-4$ (mean $=2.1, \mathrm{~N}=55$; Watson, 1951a) and 2-4 (mean $=2.9, \mathrm{~N}=9$; Spitzenberger, 1978a). Heavier females tend to have more embryos. Therefore, the mean number of embryos was 1.6 in females $<50 \mathrm{~g}, 2.1$ in females with body mass 50-60 g , and 2.3 in females $>60 \mathrm{~g}$ (Watson, 1951a). Intrauterine mortality is present, and Watson (1951a) found three females in the process of resorbing one of their two embryos. A female with a body mass of 85 g had embryos weighing 10 g (Watson, 1951a) and length of the longest embryo reported by Spitzenberger (1978a) was 30.2 mm . The smallest animal trapped (11 g) had just left the nest. Despite the very high breeding rate Watson (1951a) captured very few young animals in the sampled population. Annual mortality among adults was approximately 70 \% (Watson, 1951a). Adult males collected in late May had 10.0-12.4 mm long testes (Spitzenberger, 1978a).

Food. The Cyprus spiny mouse does little, if
any, damage to the carob trees (Ceratonia siliqua) (Watson, 1951a). Our observations suggest that snails are part of its diet, similar to the case with $A$. cahirinus in Egypt (see Osborn \& Helmy, 1980).

Predation. Watson (1951a) provided a list of potential predators which includes fox (Vulpes vulpes), the little owl (Athene noctua) and two snakes: Vipera lebetina and Zamenis gemonensis. He further reports two anecdotal observations on Zamenis numifer. In one case, the snake chased a spiny mouse, and in another, the predator swallowed a live trapped spiny mouse. Among remnants of ca 550 small mammals found in pellets of the barn owl (Tyto alba) collected in three Cypriot localities, five individuals ( $=0.9$ $\%$ ) were spiny mice (Spitzenberger, 1978a). Remnants of spiny mice were not found in the pellets of the kestrel (Falco tinnunculus) (Watson, 1951a).

Among 63 adult museum specimens, 32 (= $50 \%$ ) were tail-less while all nine specimens collected in Cyprus by Niethammer (1975b) had an intact tail.

## Cilician spiny mouse - Acomys cahirinus cILICICUS

Acomys cilicicus Spitzenberger, 1978. Type loc.: 17 km E Silifke, Vil. Mersin, Turkey.

## Taxonomy

The Cilician spiny mouse was reported under Acomys cahirinus (Lehmann, 1966b; Corbet, 1978), A. dimidiatus (Atallah, 1978; Morlok, 1978; Turan, 1984), or as a member of cahirinus-dimidiatus group (Kumerloeve, 1975). Following its recognition as an independent species (Spitzenberger, 1978b), majority of authors accepted such a taxonomic status (Bates, 1994; Denys et al., 1994; Macholán et al., 1995 Demirsoy, 1996; Kurtonur et al., 1996; Kıvanç et al., 1997; Barome et al., 2000, 2001; Kryštufek \& Vohralík, 2002; Musser \& Carleton, 2005; Yiğit et al., 2006c). Doğramacı (1989a) and Harrison \& Bates (1991) continued to report


Figure 152. Cilician spiny mouse Acomys cahirinus cilicicus. Photo: J. Vogeltanz.
it as A. cahirinus, and Lehmann (1969) suggested it might be part of $A$. nesiotes.

## Description

External Characters. Resembles A. c. nesiotes except for being smaller on average and with a relatively longer tail (on average 96.7 \% of head and body length; range $=80.5-111.0 \%, \mathrm{~N}=18$ ).

Colour. Back is greyish to drab in its anterior part and predominately grey brown posteriorly, speckled


Figure 153. Skin of Acomys cahirinus cilicicus in dorsal and ventral view. Based on a male from Korykos near Kızkalezi, Mersin. Photo: C. Mlinar.
by grey and blackish spine tips. Front and neck are of the same colour as the proximal back. Flanks are drab with grey hues, and ventral side is greyish white; demarcation is less sharp than in A. c. nesiotes. Dorsal side of hand and feet is greyish white. Tail is quite distinctly bicoloured, greyish brown above, cream white below.

Penis and baculum were figured by Kıvanç et al. (1997). The glans penis is cylindrical with a terminal crater and four grooves. The ventral groove is the longest and the dorsal groove is the shortest; dorsally oriented lateral grooves are of medium length. The entire glans is covered with spines which are the shortest at the apex and the longest at the base. Glans is $6-7 \mathrm{~mm}$ long and $3.5-4 \mathrm{~mm}$ wide. Baculum consists of a proximal shaft with expanded base and blunt apex, and a cartilaginous distal process. Proximal baculum is $2.8-4.2 \mathrm{~mm}$ long and $0.6-1.7 \mathrm{~mm}$ wide across the basal expansion. Shaft is bent dorsally (Kıvanç et al., 1997).

SkULL is on average smaller than in A. c. nesiotes, but of same relative zygomatic breadth $=51.2 \%$ of condylobasal length, range $=49.2-53.2 \%, \mathrm{~N}=16$ ).

Teeth. Upper incisor is on average narrower than in A. c. nesiotes but wider than in A. cahirinus from Egypt (Fig. 146). Enamel on front surface is yellow, paler on lower incisors. Molar-row is on average shorter than in A. c. nesiotes and $3^{\text {rd }}$ upper molar is relatively smaller (Fig. 145). Second upper molar has anteromedial crest (Fig. 155).

Dimensions. See Table 32. Sexes are apparently sub-equal.

Chromosomes. The diploid number is $2 \mathrm{~N}=36$ and fundamental number of chromosomal arms is $\mathrm{NF}_{\mathrm{a}}=$

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 22 | 107.2 | $91-121$ |
| Tail | 21 | 103.3 | $91-117$ |
| Hind foot | 22 | 18.5 | $16.2-20.0$ |
| Ear | 17 | 18.7 | $16.2-20.2$ |
| Weight | 20 | 40.2 | $29-63$ |
| Condylobasal length | 19 | 27.5 | $25.8-29.5$ |
| Zygomatic breadth | 20 | 14.1 | $13.1-15.1$ |
| Maxillary tooth-row | 20 | 4.1 | $4.1-4.9$ |

Table 32. External and cranial dimensions of Acomys cahirinus cilicicus from the vicinity of Silifke. Based on Spitzenberger (1978a), specimens in ZFMK, NM, and our own material.
66. The autosomal complement consists of 16 pairs of biarmed (meta- and submetacentrics) and one pair of acrocentric chromosomes. Most autosomes display small centromeric blocks of heterochromatin. The X chromosome is large subtelocentric and the Y is small acrocentric (Macholán et al., 1995; Kıvanç et al., 1997; Arslan et al., 2008a).

## Variability

Considering very small range of A. c. cilicicus, no geographic variability can be expected.

## Distribution

Only three localities can be identified precisely, which are confined to a very small area to the east of the town of Silifke (Fig. 156). Available evidence implies that the range extends about 15 km along the sea shore, but it remains unknown how deep inland this spiny mouse penetrates.

## Habitat

Cilician spiny mice were collected in a mosaic of rocky habitat and Mediterranean brushy vegeta-


Figure 155. Upper (a) and lower molars (b) of Acomys cahirinus cilicicus from Korykos. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.


Figure 154. Skull and mandible of Acomys cahirinus cilicicus, based on an adult female from Kızkalezi. Scale bar = 5 mm .


Figure 156. Distribution of Acomys cahirinus cilicicus. Records: 1a - Kumkuğu, Silifke, Mersin; 1b-20 km east of Silifke; $\mathbf{1 c}-17 \mathrm{~km}$ east of Silifke; $\mathbf{1 d}$ - ca 30 km north-east of Silifke; $\mathbf{1 e}$ - Narlıkuyu Canyon, Mersin; $\mathbf{1 f}$ - Kızkalezi, Mersin. Corresponding references: Lehmann (1966a): 1a. Lehmann (1969): 1b. Spitzenberger (1978b): 1c. Morlok (1978): 1d. Macholán et al. (1995): 1e, 1f.
tion (particularly Quercus coccifera and Rubus sp.). Given that presumably suitable habitats are available along the Mediterranean coast of Anatolia, it is hard to figure why the Cilician spiny mouse is so restricted in its distribution. A single specimen was trapped in a house in a village of Kumkuğu (Lehmann, 1966b).


Altitude. All records are from close to sea level (about 10 m a.s.l.) and within January isotherms of $7.5-10^{\circ} \mathrm{C}$ (Spitzenberger, 1978b).

Associates. Apodemus mystacinus, Mus macedonicus and M. domesticus were also collected along A. c. cilicicus.

Density. Within its restricted range, the Cilician


Figure 157. Habitat of Acomys cahirinus cilicicus near Narlıkuyu, Silifke. Photo: A. Kryštufek.
spiny mouse is the dominant small mammal. A pooled sample from two collecting trips, one by Spitzenberger (1978b) in 1970, the other by us in 1993, contains 22 small mammal specimens, 16 (= 73 \%) of which were spiny mice. The entire population is reportedly less than 250 specimens (Nowak, 1999), which is probably an underestimate. E.g. Kıvanç et al., (1997) collected in 1995 as many as 30 spiny mice from a single locality 20 km east of Silifke, and we got 10 from a small area in a single night.

## Biology

Two pregnant females were collected on 24 July, 1968 (2 and 3 embryos, respectively; SFMK), one in 16 July 1970 (3 embryos; Spitzenberger, 1978b), and one in 20 October 1991 (2 embryos; NM). Body mass of pregnant females was 50 and 55 g (ZFMK), and 63 g (NM). Yiğit et al. (2006c) reported litter size to be 2 or 3 cubs. Analysis of stomach content revealed insects (Yiğit et al., 2006c). The Cilician spiny mouse was found in owl pellets (Morlok, 1978). Among 22 adult museum specimens, only one was tail-less.

## Conservation

During our visit to the site of the Cilician spiny mouse in 2004, we found the habitat partly destroyed due to road reconstruction work; the entire area is under the rapid expansion of urbanization. Yiğit et al. (2006c) classify the Cilician spiny mice as being endangered (EN).

## Subfamily: Gerbillinae Gray, 1825

Muridae rodents of mouse-like to rat-like size, adapted for life in open arid regions of Africa and Asia. Hind limbs are frequently lengthened; tail is long and fully haired with a terminal brush. Gerbils tend towards saltatorial locomotion and are largely also fossorial. Braincase of the skull is broadened; mastoids and auditory bullae are frequently inflated. Rostrum is narrow and weak, zygoma slender, infraorbital foramen significantly narrowed. Mandible is characterised by vestigial coronoid process, high articular process and narrow angular portion. Molars are hypsodont; enamel pattern is simple, of transverse plates separated by inner and outer re-entrant


Figure 158. Front of rostrum in Tatera indica. Arrow points on a groove on the front surface of the incisor. Based on a young specimen from Ceylanpınar, Turkey (ZFMK). Scale bar $=2 \mathrm{~mm}$.
angles. Upper incisors are opistodont and grooved (Fig. 158) in the majority of genera.

Gerbils were mainly considered in the past to be a subfamily of either Cricetidae or Muridae, or a separate family Gerbillidae; see Table 30 in Kryštufek \& Vohralík (2005: p. 123) for various taxonomic systems used. Currently the subfamily Gerbillinae is placed within Muridae(Musser \& Carleton, 2005). Gerbils appeared in the late Miocene (Wessels, 1998) but the molecular clock predates this timing, suggesting their origins date back to the early Miocene (20.8-17.9 million years ago; Michaux et al., 2001). Gerbils were a dominant rodent group in Central Anatolia (Çalta; 57.0 \%) during the Late Pliocene (Şen \& de Bruijn, 1977), when the environment was predominantly a steppic one (Şen, 1978).

Gerbils are the core species in rodent assemblages of the Great Palaearctic desert belt and dominate both in relative abundance and in relative biomass. In two deserts of Israel, the Gerbillinae fraction represented $>80$ \% of all rodent individuals and 88.5-95.8 \% of all rodent biomass (Shenbrot \& Krasnov, 2001). Turkey, however, is on the very border of the Ger-billinae-dominated realm and only a single species (i.e. Meriones tristrami) is widely distributed.

Musser \& Carleton (2005) recognised 103 species in 16 genera which range in arid regions of Asia and Africa. Taxonomy of Palaearctic species
is largely based on Corbet (1978) and Pavlinov et al. (1990). Eight species in three genera were reported for Turkey. First regional review is by Neuhäuser (1936) who recognised three Meriones species (M. blackleri [= M. tristrami], M. vinogradovi and M. persicus). The remaining species, which are all of very marginal occurrence in the country, were subsequently added by Misonne (1957; Tatera indica, Meriones libycus and Meriones sacramenti $[=M$. crassus]), Kurtonur et al. (1996; Meriones meridianus [= M. dahli]) and Yiğit et al. (1997b; Gerbillus dasyurus [= Dipodillus dasyurus]).

## Key to genera

1 Size large (condylobasal length $>43 \mathrm{~mm}$ ); masseteric plate strongly projected forward; coronoid process well developed (Fig. 161);

Tatera
1* Size smaller (condylobasal length <41 mm); masseteric plate not greatly projected forward; coronoid process rudimentary

2 Size smaller (condylobasal length <26 mm); molars cuspidate in juveniles

Dipodillus
2* Size larger (condylobasal length $>28 \mathrm{~mm}$ ); molars without traces of cusps

Meriones

## Genus: Tatera Lataste, 1882

Tatera traditionally encompassed 12 species (e.g. Nowak, 1999) but in its current scope includes only T. indica (Pavlinov et al., 1990; Musser \& Carleton, 2005). The remaining species, which were previously reported under Tatera and all occur in Africa, are now in Gerbilliscus Thomas, 1897.

## Indian gerbil - Tatera indica

Dipus indicus Hardwicke, 1807. Type loc.: between Benares and Hardwar, United Provinces, India.

## Description

External characters. The largest gerbil species in the region. Appearance is rat-like, body heavily-built, tail long (92.9-105.4 \% of head and body length; mean $=97.9 \%$ ). Eyes are large. Ears are moderately long, oval; the snout is elongated and mystacial vibrissae are fairly soft (length up to 41 mm ). Front feet short, with four fingers; hind feet lengthened and narrow, with five toes; soles are naked. Claws are robust, up to 2.8 mm long on front feet, 4.4 mm on hind legs. Pelage is long (up to 15 mm in mid-back) and soft. Tail is densely covered with short hairs; terminal pencil is $>10 \mathrm{~mm}$ long.

Colour. Back is buff brown to tawny greyish brown, lightly speckled with black. Flanks are buff, in some specimens grey washed; ventral side and cheeks are white. Demarcation line is clear but not


Figure 159. Indian gerbil Tatera indica. Drawing: J. Hošek.


Figure 160. Indian gerbil Tatera indica taeniura from Syria Photo: A. Shehab.
sharp. Hairs have slate grey base, those on ventral side are white throughout. Ears are dark grey brown; eyes are encircled with blackish ring. Claws are pale amber. The tail is blackish, darkest on the distal onethird; its ventral side is either buff along proximal two-thirds or is covered with blackish hairs throughout; lateral stripe is pale.

Nipples. Females have eight nipples (Roberts, 1997).

Penis. Glans penis in Turkish material was described and figured by Yiğit et al. (2001); it is oval and elongate, about 12.5 mm long, 6.0 mm wide and 4.8 mm deep. Dorsal side bears a triangular protrusion with a proximally directed apex which comprises over one-half of the glans length. Ventral side has a pronounced globular bump at its base. Glans is covered with epidermal denticles throughout. Terminal crater is evaginated. Proximal baculum has a spadelike base and globular apex; it is about 8 mm long and 3.8 mm wide across base (estimated from Fig. 3 in Yiğit et al., 2001),

Skull is robust and deep, convex in dorsal profile. Nasals do not protrude much anterior to premaxillary. In comparison with other Turkish gerbils, the rostrum is relatively short and heavy. Zygmatic arches are not pronouncedly expanded (56.9-60.5 \% of condylobasal length, mean $=58.3 \%$ ); the anterior root is heavily built. Interorbital region is wider than the rostrum; supraorbital ridges are not very heavy; lacrimal bone is relatively small and triangular. Braincase is strongly angular, narrower than zy-


Figure 161. Skull and mandible of Tatera indica. Based on the type specimen of T. i. pitmani (adult animal from Baiji, Tigris, Iraq; BMNH); mandible is partly reconstructed. Scale bar $=10 \mathrm{~mm}$.
gomatic region (braincase breadth equals 45.9-50.4 \% of condylobasal length; mean $=48.5 \%$ ), parietals are relatively smaller than in Meriones; interparietal is elongate. Masseteric (zygomatic) plate strongly projects forward and curved round in front; its lower border bends backward. Infraorbital foramen is narrow and ventrally compressed to a mere slit. Diastema is approximately twice as long as molar row. Incisive foramens are long and narrow, slightly expanded in their proximal part, and reaching level of molars posteriorly. Posterior palatal foramina are slit-like. Auditory bullae of moderate size for a gerbil, less than one-third of condylobasal length (27.0-31.4 \%; mean $=29.4 \%)$. Paroccipital process is large. Mandible is fairly low, with well expanded alveolar process; a sickle-like coronoid process is long.

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 6 | 195.7 | $185-210$ |
| Tail | 6 | 191.3 | $181-198$ |
| Hind foot | 6 | 48.6 | $41.3-59.0$ |
| Ear | 6 | 28.9 | $27.0-30.0$ |
| Weight | 5 | 246.6 | $200-270$ |
| Condylobasal length | 6 | 45.1 | $43.3-47.0$ |
| Zygomatic breadth | 6 | 26.2 | $25.0-27.2$ |
| Maxillary tooth-row | 8 | 8.0 | $7.6-8.7$ |

Table 33. External and cranial dimensions of Tatera indica from Turkey and Syria. Based on Yiğit et al. (2001), and specimens in BMNH and NMW.

Teeth. Upper incisors are opistodont with a single clearly defined longitudinal groove (Fig. 158); enamel on front surface is orange-yellow on upper incisors, yellow on lower ones. Molars are hypsodont, but to a lesser degree than in Meriones. Young animals show traces of cuspidation (Fig. 162a,c). Adult molars consist of a series of plain straight plates,
with three transverse plates on first molars and two plates on second molars. Third lower molar is a simple transverse plate (Fig. 162b,d).

Dimensions are given in Table 33. Although males tend towards larger size (Table 34) secondary sexual dimorphism is not significant (Bates, 1988).

Chromosomes. Turkish animals have a diploid number $2 \mathrm{~N}=68$ and fundamental number of autosomal arms $\mathrm{NF}_{\mathrm{a}}=80$. The autosomal set consists of seven pairs of bi-armed chromosomes and 26 pairs of acrocentrics of diminishing size. The X chromosome is the largest metacentic in the set and the Y chromosome is the smallest acrocentric (Yiğit et al., 2001). The Indian gerbil is polymorphic chromosomally, with diploid number varying from $2 \mathrm{~N}=68$ to 72 (Bates, 1988; Pavlinov et al., 1990).

## Variation

Infraspecific variation was revised by Bates (1988), who recognised three subspecies. Tatera indica taeniura (Wagner, 1843) (for type locality see Kock, 1998) of northern Arabia and western Iran is the largest subspecies (Table 34) with a relatively short tail and also occurs in Turkey. The nominate subspecies from eastern Iran, Afghanistan, Pakistan and northern India is smaller (mean condylobasal length in males $=39.3 \mathrm{~mm}$; females $=39.1 \mathrm{~mm}$ ). Transitional populations between these two subspecies are expected to occur in central and eastern Iran (Bates, 1988). Colour is variable, even within T. i. taeniura (Harrison \& Bates, 1991).

## Distribution

Range was mapped by Bates (1988). The Indian gerbil occurs from Mesopotamia (where it is known in Turkey, Syria, Iraq and Kuwait) across Iran, Afghanistan and Pakistan to India and Sri Lanka. The

|  | males |  |  |  | females |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |  |
| Head and body | 9 | 186.0 | $155-205$ | 13 | 177.7 | $160-205$ |  |
| Tail | 9 | 185.8 | $167-220$ | 13 | 183.5 | $167-220$ |  |
| Hind foot | 9 | 43.6 | $38-50$ | 13 | 41.9 | $39-45$ |  |
| Ear | 8 | 26.3 | $20-30$ | 13 | 26.6 | $19-28$ |  |
| Condylobasal length | 11 | 44.2 | $40.2-46.7$ | 11 | 42.3 | $40.0-44.8$ |  |
| Zygomatic breadth | 11 | 25.7 | $22.5-27.7$ | 14 | 24.4 | $21.6-26.0$ |  |
| Maxillary tooth-row | 10 | 7.4 | $7.0-8.1$ | 14 | 7.2 | $6.9-7.7$ |  |

Table 34. External and cranial dimensions of Tatera indica taeniura according to sex. From Bates (1988).


Figure 162. Upper ( $\mathbf{a}, \mathbf{b}$ ) and lower molars ( $\mathbf{c}, \mathbf{d}$ ) of Tatera indica, based on a juvenile male from Ceylanpınar, Turkey (a, c; ZFMK), and an adult female from Tell Sheikh Hamad, Syria (b, d; BMNH). Note that $3^{\text {rd }}$ molars still did not erupt in the juvenile animal. Lingual side is to the left, anterior is at the top. Scale bar $=2 \mathrm{~mm}$.

Euphrates River defines the western border and very few records are known from its right bank. The northern border is determined by frosts (Petter, 1961). The species is known in Turkey only from two regions: between Akçakale and Şanli Urfa (no exact locality) and Ceylanpınar, both close to the Syrian border (Fig. 163).

Palaeontology. Tatera pinjoricus from late Pliocene of northwestern India is possibly an ancestor of the recent T. indica (Musser \& Carleton, 2005). The Indian gerbil is largely absent from fossil sites in the Near and Middle East (e.g. Kadhim et al., 1977; Tchernov, 1988, 1994) and possibly colonised the region as late as the Upper Pleistocene. The earliest record we are aware of is from the Mousterian layers from Iranian Kurdestan and predates the remnants from the Deh Luran sequence (8,000-3,460 years before present) and about 7,000 years old find from Jarmo in Iraq (Turnbull, 1975). The species was also recovered from a pre-pottery Neolithic (about 9,500 years before present) faunal assemblage of Göbekli Tepe near Şanli Urfa (Peters \& Schmidt, 2004).

## Habitat

The Indian gerbil is a highly adaptable animal and was found in various habitats throughout its wide
tropical and subtropical range: dry overgrazed landscape, deserts oases, cultivated land, orchards, wet thickset, palm plantations, humid forests, irrigation chanels etc. The species is less adapted to desert life than other gerbils and cannot tolerate frosts. Tatera indica is burrowing inside Indian towns (Nowak, 1999) and is hemisynanthropic in Afghanistan where it does not invade continuous human habitations (Gaisler et al., 1967). In Iran T. indica "resides in man-made shelters, such as fodder piles and stone fences or even dwellings" (Lay, 1967).

In the dry landscape of northern Syria and southeastern Turkey, the Indian gerbil is localised and mostly restricted to proximity of villages and to dam foil in river valleys (Misonne, 1957). Yiğit et al. (2001) did not find this gerbil in cultivated areas during their small mammal survey in south-eastern Turkey. In the flatlands of Iraq, the species mostly dwells near irrigation and drainage canals, sugar cane plantations, natural cane and reed plants, and the edges of crop and vegetable fields with maize, rice, wheat, barley, tomato, cucumber and watermelon. The dominant wild plant species in such areas are Phragmites australis, Typha angustata, Prosopis faricta, Alhaji mannitera and Imperata cylindrica (Kadhim, 1998).

Altitude. From close to sea level up to 1,000 m
a.s.l. in India and 1,370 m in Iran (Pavlinov et al., 1990).

Associates. Misonne (1957) lists seven rodent species in addition to the Indian gerbil which were destroyed during rodent control measures in northern Syria: Allactaga euphratica, Meriones tristrami, M. crassus, M. vinogradovi, Nesokia indica, Mus "musculus" and Microtus guentheri. All except for Nesokia indica were also collected on the Turkish side of the border. In the Near East, T. indica forms mixed colonies with Gerbillus nanus and Meriones crassus (Petter, 1961); the former was also reported using burrows of Indian gerbil in Iran (Lay, 1967).

Density. In India, 10 per ha in rural grasslands, 175-460 per ha in towns (Nowak, 1999); relative abundance in rodent assemblages was 15 \% in the foothills and $44 \%$ in the flatland sandy habitats (Pavlinov et al., 1990). Densities not reported from Turkey and adjacent regions but the Indian gerbil is abundant enough in Iraq to be a common pest in cultivated fields (Kadhim et al., 1977; Kadhim, 1998). Its overall abundance, however, is low in the arid landscape at the northwestern margin of its range and Misonne (1957) captured 45 specimens in Syria
(= $7.7 \%$ of all rodents trapped; $\mathrm{N}=584$ ) and five in Turkey (= 0.4 \%; N = 1,295).

Kadhim (1998) reports an abnormal increase in the population density in 1993, which was the first such case recorded in Iraq. Indications of the outbreak in May and June were followed by a peak during October and November. The outbreak ended in January of the next year, following control measures. Populations of Mus "musculus" increased simultaneously (Kadhim, 1998). Hussain et al. (2003) found a population to be stable in Pakistan during a 16-month study.

## Biology

Activity. Nocturnal, but at high densities active also during early morning and early evening (Kadhim, 1998). Home ranges in Rajasthan Desert, India, measured $1,875 \mathrm{~m}^{2}$ for males and $1,912 \mathrm{~m}^{2}$ for females (Nowak, 1999). Area of activity was estimated to cover 1,200 $\mathrm{m}^{2}$ in Iraq (Petter, 1961) and $250 \mathrm{~m}^{2}$ in Iran (Lay, 1967). The Indian gerbil is an aggressive and territorial animal. Couples frequently live together and juveniles stay together with their parents for extended period (Pavlinov et al., 1990).


Figure 163. Distribution of Tatera indica in Turkey and adjacent regions. Records: 1 - Akçakale-Şanlı Urfa region, no exact locality; 2 - Ceylanpınar, Şanlı Urfa. Corresponding references: Misonne (1957): 1. Lehmann (1969): 2.

Lay (1967) in Iran and Hassinger (1973) in Afghanistan usually found Indian gerbils in colonies occupying large burrow systems. Although this gerbil is gregarious, associations in colonies are loose and individuals occupy separate burrows (Roberts, 1997).

Burrows are typically excavated in embankments or hillocks surrounding bushes in Pakistan (Roberts, 1997). Underground labyrinths have numerous entrances and an enlarged nest chamber (diameter 20 cm ) located in the centre of the tunnel system and 1.2 m below the surface; nest is lined with cut dried vegetable material. Tunnels (diameter $8-10 \mathrm{~cm}$ ) are at various levels, some of them with dead ends. The entrances are usually blocked with loose earth. Burrows are easily spotted because of mounds of excavated soil (Petter, 1961). In Aghanistan, the vegetation in the vicinity of burrows is frequently characterised by high density and low homogeneity (Hassinger, 1973). In observations by Lay (1967) from Iran, "clearly defined, well-used trails spreading from burrow systems suggest that these jirds follow established trails in their movements".

Reproduction. Gestation lasts 22-23 days but is prolonged in lactating females (35-40 days); litter size is $1-9$, mostly $3-7$, and varies between regions (Pavlinov et al., 1990). Young are weaned at 21-30 days and reach sexual maturity at $10-16$ weeks; females may have 3-4 litters annually (Nowak, 1999). Peak breeding season in Rajahstan, India, is from July to August (Roberts, 1997). In Iraq, pregnant females were trapped during all months, including the winter period. Pregnancy rate between November and February varied from 42.9 \% to 66.7 \% (51.6 \% on average; $\mathrm{N}=61$ ) and mean number of embryos per female was 7.2-8.0 (average for 61 females = 7.7; Kadhim, 1998). Sex ratio is balanced and T. indica lived seven years in captivity (Roberts, 1997).

Two juveniles (body mass of 51 and 54 g , respectively) reported by Lehmann (1969) were collected near Ceylanpınar in mid-May (ZFMK).

Food. Water dependant, the gerbil requires green vegetation throughout the year (Misonne, 1975) and cannot survive on the same dry diet as Meriones libycus and M. crassus (Petter, 1961). Diet consists of roots, seeds and bulbs in addition to green plant matter; insects, cutworms and caterpillars are consumed as well. They also eat eggs and young birds and are cannibalistic (Nowak, 1999). Diet depends on the
season, with seeds being most important during winter and rhizomes during the hot period (Harrison \& Bates, 1991). In Rajasthan, India, insects are an important component of their diet after the monsoon in September and October (Roberts, 1997). The Indian gerbil also stores small quantities of food in underground burrows (Pavlinov et al., 1990).

Predation. Found in owl pellets in Syria (Shehab et al., 2004) and Iraq (Nadachowski et al., 1990); some Syrian records relate to a barn owl Tyto alba (Kock, 1998). In Pakistan, they are preyed upon by the barn owl (Mushtaq-ul-Hassan et al., 2004), and in India by the Indian grey mongoose (Herpestes edwardsi), the jungle cat (Felis chaus; Roberts, 1999), the Indian eagle owl (Bubo bengalensis; Ramanujam, 2006) and spotted little owl (Athene brama; Ali Shah \& Azhar Beg, 2001).

## Genus: Meriones Illiger, 1811

Medium-sized ratlike gerbils with tail of about the same length as head and body. Pelage is soft or even silky in some specimens, tail is with a dark crest on its tip and there are frequently light areas about the face. Hind feet are only slightly lengthened for leaping. Skull shape is typical of gerbils, with long and narrow rostrum and an expanded brain-case. Bullae vary in size, from small to very swollen. Alveolar process is well developed on the outer wall of mandibular rhamus. Upper incisors have a longitudinal groove. Molars are hypsodont with prismatic enamel pattern and no traces of cusps. Proximal baculum is simple and its expanded basal portion varies between species (Fig. 165).

Jirds inhabit clay and sandy deserts in northern Africa and southwestern and central Asia. Seventeen species are currently recognised (Musser \& Carleton, 2005) and six of them were also reported from Turkey. Turkish jirds are in two distinct subgenera (out of four recognised by Pavlinov et al., 1990): Parameriones Heptner, 1937, includes M. persicus while the remaining Turkish jirds classify into Pallasiomys Heptner, 1933.

Meriones tristrami has already been reported for Turkey by Danford \& Alston (1880)"from the stony hill-sides at Kaisariyeh" (= Kayseri) as "Gerbillus erythrurus, Gray". Although G. erythrourus of


Figure 164. Jird Meriones. Drawing: J. Hošek.

Grey is a junior synonym of $M$. libycus (Musser \& Carleton, 2005), it is beyond doubt that the animals reported by Danford \& Alston actually belong to $M$. tristrami, the only jird occurring in Central Anatolia (Kumerloeve, 1975). Heptner (1934) provided the first evidence of $M$. persicus (as $M$. rossicus) and $M$. vinogradovi in Turkey. The remaining species, which are all of very marginal occurrence in the country, were subsequently added by Misonne (1957; Meriones libycus and M. sacramenti [= M. crassus]) and Kurtonur et al. (1996; Meriones meridianus [= M. dahli]). Number of species reported for Turkey differs among authorities: three in Doğramacı (1989a; M. persicus, M. tristrami, M. vinogradovi), four in Kumerloeve (1975; M. tristrami, M. vinogradovi, M. persicus, M. libycus) and in Kurtonur et al. (1996; M. tristrami, M. vinogradovi, M. meridianus, M. crassus), and six in Demirsoy (1996) and Yiğit et al. (2006c; same species as in Kurtonur et al., 1996, plus M. persicus and M. libycus).


Figure 165. Baculum of jirds occurring in Turkey:
a - Meriones vinogradovi, b, c - M. libycus, d - M. crassus, $\mathbf{e}-$ M. dahli, f - M. persicus. For M. tristrami see Fig. 171. Redrawn from: a, d, e - Yiğit et al. (1997c); b - Harrison \& Bates (1991); c - Mamkhair et al. (2007); f - Yiğit \& Çolak (1999). Not to scale.


Figure 166. Sole of jirds: a - Meriones tristrami ( 25 km south of Gaziantep, Turkey); b - M. vinogradovi (Tell Abiad, Syria; IRSNB); c - M. crassus (modified from Osborn \& Helmy, 1980); d - M. libycus (Chah-e-Dad Khoda, province Kerman, Iran); e - M. dahli (Bolšoj Araks River valley, Armenia; ZMMU); f-M. persicus (Pir Sohrab, Baluchestan, Iran). Not to scale.

## Key to species

1 Soles bare (Fig. 166f)

## M. persicus

1* Soles at least partly hairy (Fig. 166a-e)

2 Bullae not much expanded, bony auditory meatus does not reach squamosal root of zygoma (Fig. 167a)

2* Bullae greatly expanded, bony auditory meatus in close apposition to the posterior root of zygoma (Fig. 167b,c)

3 Buff streak on throat and chest; black brush on tail's tip extensive (Fig. 168e,f); sole pigmented (Fig. 166b)
M. vinogradovi

3* Throat and chest plain white; black brush on tail's tip normally less extensive, with white hairs in some populations (Fig. 168a-d); sole not pigmented (Fig. 166a)
M. tristrami

4 Back grey
M. dahli

4* Back buff

5 Claws pale; mastoid portion expanded behind occipitals in dorsal view (Fig. 189); supramental triangle nearly as high as long, open posteriorly (Fig. 167b); $1^{\text {st }}$ upper molar 3-rooted (Fig. 191)

## M. crassus

5* Claws dark; mastoid portion does not expand much behind occipitals (Fig. 195); supramental triangle smaller, normally closed posteriorly by a dorsally expanded hamular process (Fig. 167c); $1^{\text {st }}$ upper molar 4-rooted (Fig. 197)
M. libycus


Figure 167. Occipital region of jirds. a - Meriones tristrami (Ceylanpınar, Turkey); b - M. crassus (Tell Bderi, Syria); c - M. libycus (Gonbadli, Khorassan, Iran). hp - hamular process; prz - posterior root of zygoma; st - supramental triangle; $\mathbf{t b}$ - tympanic bulla. Posterior rim of bony auditory meatus is shown by an arrow. Sources of material: ZFMK (a), SMF (b, c). Scale bar = 5 mm .

## Tristram’s jird - Meriones tristrami

Meriones tristrami Thomas, 1892. Type loc.: Dead Sea Region, Israel.
Meriones blackleri Thomas, 1903. Type loc.: İzmir, Turkey.
Meriones blackleri lycaon Thomas, 1919. Type loc.: Karadağ, about 80 km southeast of Konya, Turkey.
Meriones blackleri intraponticus Neuhäuser, 1936. Type loc.: Tosya, Kastamonu, Turkey.
Meriones tristrami kilisensis Yiğit \& Çolak, 1998. Type loc.: 15 km northeast of Kilis, Gaziantep.


Figure 168. Inter- and intraspecific variation in a black terminal tail tuft of jirds. a-Meriones tristrami from Haruniye, district Adana; b-M. tristrami from Bedirge; c - M. tristrami from Belen; d - M. tristrami from Pozantı; $\mathbf{e}-$ M. vinogradovi from Armenia; $\mathbf{f}-$ M. vinogradovi from Tell Abiad, Syria; g, h - M. crassus from Cairo, Egypt; i - M. libycus from Kabul, Afghanistan; j - M. dahli from the Araks River valley, Armenia; $\mathbf{k}-$ M. persicus from Azerbaijan. Sources of material: a-d, g-i - ZFMK; e, j, kZMMU; f - IRSNB. Not to scale.

## Taxonomy

Although already reported under its current name by Ellerman (1941), M. tristrami was nearly uniformly referred to as M. blackleri until the middle of the $20^{\text {th }}$ century (e.g. Neuhäuser, 1936; Ellerman, 1948; Ellerman \& Morrison-Scott, 1951).

## Description

External characters. Large jird with the tail of variable length, either shorter or longer than head and body (77.4-125.4 \% of head and body length; mean $=103.5 \%)$, depending on population. The ovate ears are fairly large; anterior margin is with a raw of silky
hairs. Eyes are large; the diameter is about 8 mm . Fore feet are evidently shorter than the hind ones; palms are bare, with five pads (three on bases of digits). The hind sole is hairy except for its distal portion including heel (Fig. 166a); pads are small and indistinct. Front claws are up to $3.4-3.8 \mathrm{~mm}$ long, hind ones $2.4-3.8 \mathrm{~mm}$. Pelage is dense, long (9-15 mm ) and fine. A narrow mid-ventral gland is longer in males than in females. Tail is wide at base, than gradually tapering towards a tip. It is densely covered by short hairs which entirely conceal underlying annulations; terminal brush is poorly developed (hairs up to $13-15 \mathrm{~mm}$ long). Mystacial vibrissae are long (up to 55 mm ).

Colour. Dorsal side is finely speckled pale greyish fawn to dull red brown, darker on forehead, along the spine and on rump. Even within the same population grey shades dominate in some specimens, buff shades in others. Slate grey band extends from hair bases over half of their length. Belly is plain white; hairs all white or rarely with a short grey basal band. Sides and cheeks are lighter than back; demarcation line is sharp. Immature individuals are greyer than


Figure 169. Tristram’s jird Meriones tristrami from Jordan. Photo: J. Vogeltanz.
adults. Eyes are encircled with grey-buff hair. White postauricular tuft is clearly visible but there is no distinct white postorbital spot. Ears are grey and buff; feet white dorsally with grey-brown palms and soles. Claws are pale, amber white. Tail is bicoloured, frequently with a distinct demarcation along sides; dorsal side mingled by short buff and blackish hairs; ventral side mainly buff. Black or black-and-white terminal brush restricted to a dorsal side of a terminal one-quarter of the tail; white hairs restricted to a


Figure 170. Skin of Meriones tristrami in dorsal and ventral view. Based on a male from Cihanbeyli near Tuz Gölü, Turkey. Photo: C. Mlinar.

a

b


C

d

e

f

g

Figure 171. Variation in shape of proximal baculum in Meriones tristrami from Turkey. a - Kilis (Yiğit \& Çolak, 1998), b, c - Karadağ Mts., Karaman (Yiğit et al., 1998c), d, e - İğdır, Aralık (Kefelioğlu, 1997); f, g - Diyarbakır (Coşkun, 1999a). Not to scale.
terminal tip in a bicoloured brush and present also on its ventral side.

Nipples. Four pairs of nipples, two pairs of pectoral and two pairs of inguinal, respectively (Harrison, 1972; Coşkun, 1999a).

Penis. Glans is covered with spikes throughout its dorsal surface and on a ventral side at a proximal base (Pavlinov et al., 1990). Proximal baculum consists of an expanded spade-like basal portion and elongated distal stalk. Basal spade is variable in shape and apex of the stalk is expanded in some specimens (Fig. 171). In a sample from Ceylanpnar, the proximal baculum was 3.44 mm long (range $=3.06-$ 4.06 mm ) and 1.52 mm wide (range $=1.00-2.34 \mathrm{~mm}$; Coşkun, 1999a). The shaft is without terminal ossicles (Harrison \& Bates, 1991).

Skull is rather delicately built for its size. It is moderately deep (braincase height across bullae equals to $41.2 \%$ of condylobasal length; range $=$ 38.6-45.6 \%). The dorsal profile of the skull is uniformly convex with slight depression at the frontoparietal suture. The tips of the nasals project in front of the incisors. Skull wider across zygomatic arches (55.3-62.5 \% of condylobasal length; mean $=59.2$ \%) than across braincase (breadth across bullae on


Figure 172. Skull and mandible of Meriones tristrami, based on an adult male from Ceylanpınar (ZFMK). Scale bar = 5 mm .
average 56.0\% of condylobasal length; range = 50.260.6\%). The zygomatic arches are slender, with a tendency in older animals to dorso-ventral flattening; anterior root of zygoma expanded in lateral view. Rostrum is long and narrow. Nasals, with a rounded apex, expand backwards to orbital level. Anterior margin of masseteric plate rounded or straight; masseteric knob well developed; lacrimal bones are large. Diastema long; incisive foramens relatively short, hardly reaching level of molars. Posterior palatal foramens are of modest size. Pterygoids short, slightly divergent backwards; interpterygoid fossa short, relatively wide and trapezoid. Frontals not expanded and parietals of normal size. Fronto-parietal suture wedged. Interparietal is of modest size and usually of ovate shape. Supraorbital ridges not greatly expanded, just reaching parietals posteriorly; brain-case rounded and weakly ridged. Bullae not much inflated; bullar length relative to condylobasal length is on average 33.1 \% (range = 29.5-37.2 \%). Not much of mastoid portion is seen in dorsal view and the rim of bony auditory meatus does not reach squamosal root of zygoma. Supramental triangle ovate and of modest size. The mandible is slender; angular and articular
processes are large and subequal; coronoid process is rudimentary. The alveolar process on the outer wall of mandibular rhamus is well pronounced.

Teeth. Upper incisors are opistodont, with longitudal groove which is shifted slightly laterally. The enamel is yellow to orange on upper incisors and of lighter tints on the lower ones. Molar row is shorter than diastema and the two rows are widely apart. Molars are hypsodont, with no traces of cuspidation and with more or less prismatic enamel pattern. Molars decrease in size and complexity in anterior-toposterior direction. Two lingual and two labial re-entrant angles cut $1^{\text {st }}$ molars into three transverse plates. There is one fold on each side on $2^{\text {nd }}$ molars resulting in two transverse plates while $3^{\text {rd }}$ molars are simple and rounded. Angles nearly meet in the middle in young individuals but are increasingly shallow with age until finally lost in very old animals. Enamel pattern and molar size is hence much affected by abrasion (Fig. 174). First molars have three roots, $2^{\text {nd }}$ molar two roots (rarely an additional accessory root) and the last molar is single rooted (Coşkun, 1999a).

Dimensions are given in Table 36. Males are significantly larger than females (Ejgelis, 1980; Table 35).


Figure 173. Skull and mandible of Meriones tristrami, based on an adult female from Harruniye (ZFMK). Scale bar = 5 mm .


Figure 174. Upper (upper row) and lower molars (lower row) in Meriones tristrami. Age-dependent molar abrasion is in increase from left (the youngest) to right (the oldest). Lingual side is to the left, anterior is at the top. Based on specimens from (a, d) Birecik, Gaziantep; (b) Ceylanpınar; (c) Alişam, Elaziğ; (e) Ar Raqqa, Syria; (f) Kayseri. Sources of material: $\mathbf{a}-\mathbf{e}-$ SMF; $\mathbf{f}-$ BMNH. Scale bar $=1 \mathrm{~mm}$.

|  | males |  | females |  |
| :--- | :---: | :---: | :---: | :---: |
|  | N | mean | N | mean |
| Head and body | 23 | 155.7 | 27 | 139.4 |
| Tail | 22 | 137.4 | 27 | 131.2 |
| Hind foot | 23 | 31.8 | 26 | 31.3 |
| Ear | 23 | 20.0 | 26 | 22.3 |
| Weight | 23 | 108.9 | 26 | 83.2 |
| Condylobasal length | 18 | 40.3 | 18 | 36.3 |
| Zygomatic breadth | 19 | 21.0 | 21 | 20.2 |
| Maxillary tooth-row | 22 | 5.5 | 25 | 5.2 |
| Bulla length | 20 | 13.2 | 25 | 13.1 |

Table 35. Means for external and cranial dimensions of Meriones tristrami from Transcaucasia separately for sexes. Based on Ejgelis (1980).

Chromosomes. Diploid number of chromosomes is stable $(2 N=72)$ but fundamental number of autosomal arms varies between 76 and 86 (Qumsiyeh et al., 1986; Qumsiyeh, 1996; Zima \& Král, 1984). Five chromosomal forms have been reported so far from Turkey, with $\mathrm{NF}_{\mathrm{a}}=72-82$ (Table 37). Both heterochromosomes are biarmed in the majority of Turkish populations studied so far; the X chromosome is invariably large while the Y chromosome varies from medium to large size. In animals from Doğubayazıt both heterosomes are reportedly acrocentric (Yiğit et al., 2006a).

Animals from the Aegean coast have the lowest number of autosomal arms $\left(\mathrm{NF}_{\mathrm{a}}=72\right.$; one bi-
armed pair and 34 acrocentric pairs), while the highest number of metacentrics is characteristic of the Doğubayazıt population from the eastern edge of Anatolia $\left(\mathrm{NF}_{\mathrm{a}}=82\right.$; six biarmed pairs and 29 pairs of acrocentrics). The most widespread chromosomal form is seemingly the one with 78 autosomal arms (4
pairs of metacentrics and 31 pairs of acrocentrics).

## Variation

Traditional subspecific taxonomy relied on colouration of back and tail brush, size and body proportions; the subspecies characters are not definitive how-

|  | M. t. blackleri |  |  | Megean coast. lycaon <br>  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | Central Anatolia |  |
| Head and body | 18 | 133.5 | $120-151$ | 53 | 138.7 | $117-170$ |
| Tail | 18 | 143.4 | $128-151$ | 52 | 139.2 | $115-162$ |
| Hind foot | 20 | 33.8 | $29.0-37.0$ | 53 | 35.3 | $31.0-40.0$ |
| Ear | 18 | 20.8 | $19.0-21.0$ | 53 | 20.6 | $17.5-24.0$ |
| Weight | 14 | 71.1 | $51-110$ | 29 | 92.9 | $61-130$ |
| Condylobasal length | 17 | 34.4 | $31.5-36.1$ | 43 | 35.4 | $31.6-39.3$ |
| Zygomatic breadth | 17 | 20.0 | $18.7-22.1$ | 43 | 21.6 | $18.9-23.3$ |
| Maxillary tooth-row | 17 | 5.9 | $5.5-6.4$ | 44 | 5.9 | $5.4-6.5$ |
| Bulla length | 16 | 11.2 | $10.5-12.0$ | 44 | 11.8 | $10.7-13.0$ |


|  | M. t. intraponticus Black Sea coast |  |  | Adana region |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | min - max | N | mean | min - max |
| Head and body | 22 | 142.1 | 126-171 | 6 | 132.2 | 119-144 |
| Tail | 21 | 150.4 | 142-164 | 6 | 135.2 | $127-145$ |
| Hind foot | 22 | 37.3 | 34.0-40.0 | 5 | 32.4 | $31.0-34.0$ |
| Ear | 22 | 21.3 | 19.0-23.0 | 5 | 20.0 | 19.0-21.0 |
| Weight | 20 | 85.9 | 60-120 | 7 | 81.3 | 58-100 |
| Condylobasal length | 22 | 35.9 | 33.3-39.0 | 16 | 34.4 | 32.0-37.5 |
| Zygomatic breadth | 22 | 21.4 | 19.6-26.6 | 13 | 20.2 | 19.1-22.1 |
| Maxillary tooth-row | 22 | 6.0 | $5.6-6.6$ | 15 | 5.9 | $5.5-6.3$ |
| Bulla length | 20 | 11.9 | 10.9-13.0 | 15 | 11.1 | 10.2-12.4 |


|  | M. t. kilisensis |  |  |  | M. t. bogdanovi <br> South-East Anatolia |  |  | East Anatolia, Iran <br>  |  | N | mean | $\min -\max$ | N | mean | $\min -\mathrm{max}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Head and body | 78 | 133.6 | $106-155$ | 11 | 137.5 | $125-147$ |  |  |  |  |  |  |  |  |  |
| Tail | 78 | 134.9 | $103-167$ | 9 | 136.1 | $131-150$ |  |  |  |  |  |  |  |  |  |
| Hind foot | 78 | 32.1 | $30.0-37.0$ | 11 | 33.0 | $31.0-35.0$ |  |  |  |  |  |  |  |  |  |
| Ear | 78 | 19.2 | $17.0-22.0$ | 11 | 20.5 | $19.0-22.0$ |  |  |  |  |  |  |  |  |  |
| Weight | 76 | 73.8 | $42-130$ | 6 | 85.5 | $80-93$ |  |  |  |  |  |  |  |  |  |
| Condylobasal length | 77 | 33.9 | $29.5-39.0$ | 13 | 35.7 | $34.4-37.2$ |  |  |  |  |  |  |  |  |  |
| Zygomatic breadth | 78 | 20.3 | $17.5-23.1$ | 13 | 21.6 | $20.5-22.6$ |  |  |  |  |  |  |  |  |  |
| Maxillary tooth-row | 83 | 5.7 | $5.1-6.4$ | 13 | 5.6 | $5.3-6.2$ |  |  |  |  |  |  |  |  |  |
| Bulla length | 58 | 11.7 | $10.9-13.3$ | 11 | 11.8 | $10.9-12.9$ |  |  |  |  |  |  |  |  |  |

Table 36. External and cranial dimensions of Meriones tristrami from Turkey and adjacent regions. Subspecific names follow Yiğit et al. (1998c). Based on Neuhäuser (1936), Yiğit et al. (1997c, 1998c), Yiğit \& Çolak (1998), Coşkun (1999a), specimens in BMNH, FMNH, NMNH, SMF and ZFMK, and our own material.

Table 36. (continues from previous page)

|  | Syria |  |  |  | Island of Kos |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |  |
| Head and body | 3 | 136.7 | $135-140$ | 1 | 146 |  |  |
| Tail | 1 | 140 |  | 1 | 150 |  |  |
| Hind foot | 3 | 31.6 | $31.3-32.0$ | 1 | 35.0 |  |  |
| Ear | 2 |  | $18.5 / 19.2$ | 1 | 21.0 |  |  |
| Weight | 3 | 83.3 | $80.5-86$ | 1 | 110 |  |  |
| Condylobasal length | 31 | 35.4 | $32.0-39.5$ | 7 | 36.0 | $34.9-37.5$ |  |
| Zygomatic breadth | 22 | 20.9 | $19.4-22.7$ | 6 | 21.2 | $20.3-22.4$ |  |
| Maxillary tooth-row | 34 | 6.1 | $5.1-6.9$ | 8 | 5.8 | $5.2-6.4$ |  |
| Bulla length | 32 | 12.2 | $11.2-13.3$ | 7 | 11.0 | $10.4-11.9$ |  |


| Region | Locality | $\mathrm{NF}_{\mathrm{a}}$ | NF | M | A | X | Y |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| West | İzmir | 72 | 76 | 2 | 68 | lM | mM |
| South-east | Kilis | 74 | 78 | 4 | 66 | lM | lM |
| South-east | Ceylanpınar | 78 | 82 | 8 | 62 | lM | mM |
| Central | Karadağ | 78 | 82 | 8 | 62 | lM | mM |
| North | Tosya | 78 | 82 | 8 | 62 | lM | mM |
| North | Tosya | 80 | 84 | 10 | 60 | lM | lM |
| East | Doğubayazıt 84 | 86 | 12 | 58 | lA | sA |  |

Table 37. Variation in the karyotype of Meriones tristrami from Anatolia. Diploid number is constant $2 \mathrm{~N}=72 . \mathrm{NF}_{\mathrm{a}}-$ fundamental number of autosomal arms; NF - fundamental number of chromosomal arms; M - number of biarmed autosomes; A - number of acrocentric autosomes; X and Y - heterochromosomes ( l large, m - medium, s - small, M - biarmed, A - acrocentric). Karyotypes are arranged according to increasing $\mathrm{NF}_{\mathrm{a}}$ number. Sources: Kefelioğlu (1997), Yiğit \& Çolak (1998) and Yiğit et al. (1998c, 2006a).
ever (Kock et al., 1972; Kock \& Nader, 1983). Yiğit et al. (1998c) revised variation in morphological traits, combined it with chromosomal polymorphism and recognised five subspecies: M. t. blackleri (Aegean coast), M. t. lycaon (Central Anatolia and Hatay), M. t. intraponticus (Kastamonu Province), M. t. bogdanovi Heptner, 1931 (Type loc.: Pirchantapa, Schirimkum [= Milskaja] Steppe, Saljany district, Eastern Transcaucasia; eastern Anatolia in Turkey), and M. t. bodenheimeri Aharoni, 1932 (Type loc.: Kafrun, Syria; range in Turkey: southeastern Anatolia). In the same year when this revision was published, Yiğit \& Çolak (1998a) described another subspecies from southeastern Anatolia (M. t. kilisensis) but did not delimit its range against ssp. bod-
enheimeri. White brush tip is typical of ssp. blackleri and prevails also in intraponticus; in the remaining populations the brush is reported to be mainly black throughout. We saw specimens with white brush tip also in material from southeastern Anatolia, where plain dark colour is otherwise the norm. The only skin we examined from the Aegean Island of Kos had a white tail tip; not surprisingly considering that most likely source of the Kos population is the Aegean coast of Anatolia.

Yiğit et al. (1998c) reported populations from Central Anatolia, and particularly so from eastern Anatolia, to be relatively short-tailed; these differences are not evident from data presented in Table 36. Although back colour varies, Neuhäuser (1936) was unable to correlate colour variation with ecological factors in Turkish material and Osborn (1965) suggested colour types to be segregated within populations. Considerable variation in shade of colour exists in Israel and colouration often resembles shade of the soil in which animals live (Zahavi \& Wahrman, 1957). Mendelssohn \& Yom-Tov (1999) claimed that dark colour develops under a humid environment and is reversible.

Relative length of bullae is fairly stable across Anatolia. In the material we saw, Syrian jirds had, relatively speaking, the longest bullae (34.3 \% of condylobasal length on average; range = 32.5-37.2 $\%$; $\mathrm{N}=29$ ) and those from the Island of Kos had the shortest bullae (mean = 30.6 \%; range $=29.5-32.1$ \%; $\mathrm{N}=7$ ). Ranges however largely overlap in Anatolia and the means for four populations ranged between 32.2 \% and 33.5 \%.

In transect from Israel to Sinai, size associates
positively with mean minimum January temperature, therefore in agreement with Bergmann's rule (YomTov \& Geffen, 2006). Ejgelis (1980) reported on significant size differences between populations in Transcaucasia. Besides, there is a shift in body size in Tristram's jird wherever the species is sympatric with one of its congeners in Israel (Mendelssohn \& Yom-Tov, 1999).

For chromosomal polymorphism see account on the karyotype.

## Distribution

Anatolia, Transcaucasia (Armenia and Azerbaijan), northwestern Iran, northern Iraq, Syria and eastern Mediterranean coast (Lebanon, Israel) as far south as Sinai and southern Jordan. Dot maps were provided by Kock et al. (1972) and Kock \& Nader (1983).

In Asia Minor, Tristram's jird is continuously widespread from the Aegean coast (around İzmir) across Central Anatolia as far east as Kulp on the eastern side of the River Tigris (Fig. 175). The animal is largely absent from the Taurus Mts., from the southern coast except for the vicinity of Adana and Hatay, and from the area around Lake Van. It has so far not been recorded from Hakkari although there
are localities in Iran to the west of Urminian Lake and close to the Turkish border. Eastern localities at Iğdır and Ağrı provinces are more probably connected with the main range in Anatolia via Iran and Iraq, then along the upper flow of the River Murat. Records along the middle flow of the Kızılırmak River are evidently isolates. Tristram’s jird also occupies the Greek Island of Kos off the Aegean coast.

Palaeontology. Meriones is thought to have evolved from the extinct Pseudomeriones Schaub, 1934 (Musser \& Carleton, 2005) which was present in Anatolia since the Miocene (Sümengen et al., 1990). During the Pliocene, Pseudomeriones was abundant in Anatolia (Çalta), while it was rare in the contemporary faunal assemblage from Maritsa (Island of Rhodes) and entirely absent from the Balkans (Tourkobounia-1; Şen \& Bruijn, 1977).

Meriones obeidiensis Haas, 1966, from the Middle Pleistocene of Israel, which was much larger than the recent $M$. tristrami, was suggested to be a common ancestor to two recent jirds of the Near and Middle East, M. persicus and M. tristrami (Tchernov, 1968). The fossil species is documented for a temporal span of 500,000-250,000 years BP while M. tristrami is reported from the Upper Pleistocene


Figure 175. Distribution of Meriones tristrami in Turkey and adjacent regions. For further details on records see Appendix 7.
(about 160,000-120,000 years BP) and is continuously present in Israel afterwards (Tchernov, 1975, 1992). The fossil M. tristrami qatafensis from the Aucheulian of Israel was still much larger than the recent animal and also resembled M. persicus (Tchernov, 1968). Note, however, that Kuss \& Storch (1978) ascribed jirds from the Early Pleistocene of Kalymnos (Dodekanes islands of southeastern Aegean) to M. tristrami. Zahavi \& Wahrman (1957) suggested that Tristram's jird colonised Israel from the north but fossil evidence is more in favour of just the opposite range expansion.

Noteworthy, Meriones is absent from the Middle Pleistocene strata from the Island of Chios (Storch, 1975) and Emirkaya in Central Anatolia (Montuire et al., 1994), as well as from the Upper Pleistocene site at Karayin near Antalya (Storch, 1988). Records of $M$. tristrami from the Upper Pleistocene were reported further south to Turkey, from Israel (Tchernov, 1975, 1988) and Jordan (19,400 years ago; Belmaker et al., 2001). Material identified to a generic level which is $11,500-8,600$ years old is also known from northern Iran (Turnbull, 1975). Tristram's jird emerged in Antalya only during the Holocene (upper Chalcolithic; Storch, 1988), but is now absent from this region. Further two Holocene samples from the Taurus Mts., Bolkar Dağ (undated; Hír, 1991) and Finike (presumably $<7,000$ years BP; Corbet \& Morris, 1967) lack any evidence regarding jirds. Tristram's jird was also not recorded in the Pleistocene layers in Transcaucasia (Vereščagin, 1959).

Molars of recent Meriones do not contain much of phyletic and taxonomic information and are subject to age variation. Wide range of variability as observed in fossil material resulted in taxonomic names which were given to some extreme individuals within the range of variation for recent Tristram's jird (Tchernov, 1968). Fossil evidence is hence unavoidably associated with uncertainties which pose limitations in interpreting fossils. In the opinion by Tchernov (1968), all jirds living in Israel, with the exception of M. tristrami (i.e. M. sacramenti and M. crassus) invaded Levant in post Würm times.

## Habitat

Tristram's jird is one of the most common and widespread jirds in the Near East and has a wide habitat tolerance (Harrison \& Bates, 1991). It is limited to
areas receiving more than 100 mm of rainfall annually (Qumsiyeh, 1996) and needs well drained soil (alluvial deposits, loess, clay soils) although it avoids rocky situations (Pavlinov et al., 1990). The species was reported to be a petrophile in Jordan (Scott \& Dunstone, 2000). Xeric steppes are the main habitat in Iran and in Transcaucasia (Lay, 1967; Ejgelis, 1980) while it is widespread in semi-deserts and Mediterranean habitats in Israel (Zahavi \& Wahrman, 1957). Although Tristram's jird frequently utilizes shrub cover, it is not affected by its removal and does not avoid open sandy areas in coastal dunes in Israel (Kutiel et al., 2000).

Habitats in Turkey are in accordance to the situation elsewhere. Specimens were trapped in dry steppe of short or tall grass, open hillside, among rocky outcrops in desolate steppe, along stone walls, vineyards, orchards, and under bushes. Fields of grain and other crops (watermelon, cotton etc.) are inhabited temporarily but Tristram's jird is permanently present at their margins. Near Kirikhan a specimen


Figure 176. Habitat of Meriones tristrami in Central
Anatolia. a - shores of Lake Burdur (Photo: B. Kryštufek); b - Cihanbeyli, district Konya (A. Kryštufek).
was obtained in pine forest with underlying brushwood (ZFMK). Forests, however, are not inhabited (Lewis et al., 1967). Typical vegetation of open habitats consist of Astragalus sp., Medicago radiata, Euphorbia sp., Festuca sp., Cynodon sp., Thymus spyleus, Ziziphora capitata, Teucrium polium, Polyogonum sp., Salvia cryptantha, Cyperus longus, Carex otrubae, Bolbochoenus maritimus, Scilla biflora, Hordeum sp., Eryngium campestre, Equisetum ramosimum, Atrophaxis billardieri, Crepis sp., Securigera sp., Peganum sp., Agropyron sp., Centranthus longiflorus, Parietaria judaica, Torilis leptophyla (Yiğit et al., 2003).

Altitude. Primarily an inhabitant of lowland steppe habitats. Elevational range in Transcaucasia is from sea level to $2,000 \mathrm{~m}$ a.s.l., but mainly at $100-$ 600 m (Ejgelis, 1980). Tristram's jird goes up to $1,550 \mathrm{~m}$ high in Lebanon (Lewis et al., 1967) and up to $1,600 \mathrm{~m}$ in Israel (Mendelssohn \& YomTov, 1999). Turkish records are from elevations of 100 m (İzmir) up to $1,200 \mathrm{~m}$ (Yiğit et al., 1995) and $1,350 \mathrm{~m}$ (Yiğit et al., 2003). Type series of M. t. lycaon was captured at $1,450 \mathrm{~m}$ a.s.l. ( $4,800 \mathrm{ft}$; information on BMNH specimen tags).

Associates. Throughout its range in Turkey, the Tristram's jird co-occurs with a number of rodent species: Dryomys nitedula, Cricetulus migratorius, Mesocricetus brandti, M. auratus, Microtus levis, M. guentheri, M. hartingi, M. socialis, M. anatolicus, Dipodillus dasyurus, Apodemus witherbyi, A.


Figure 177. Variation in density (number of individuals per hectare) of Meriones tristrami between 1955 and 1970 in two regions in eastern Transcaucasia. Modified from Ejgelis (1980).
mystacinus, Mus macedonicus, M. domesticus and all three Allactaga species. Yiğit et al., (2003) reported its sympatry with Meriones vinogradovi and M. dahli in eastern Anatolia.

Density. Densities in Transcaucasia are 1.5-2.0 individuals per ha and increase to approximately 11 per ha in autumn (rarely up to 45 per ha; Ejgelis, 1980). From 10 to 40 individuals per ha were reported from Israel (Mendelssohn \& Yom-Tov, 1999). Populations fluctuate, both in Transcaucasia (Ejgelis, 1980) and in Israel where Tristram's jird is a pest to agriculture in some years (Zahavi \& Wahrman, 1957).

## Biology

Activity is predominantly nocturnal, but also crepuscular during some times of the year (Lewis et al., 1967). Yiğit et al. (1995) reported the animal to also be diurnal and our observations concur with this. There is a tendency towards nocturnal activity during summer and diurnal acivity in winter (Pavlinov et al., 1990). During winter, animals can stay for days or even weeks in burrows without leaving them (Ejgelis, 1980). Tristram's jird is a solitary species (Mendelssohn \& Yom-Tov, 1999).

Burrows are simple shelters, each with 1-3 entrances and 1.5-2.5 m of tunnels which descend up to 40 cm below surface. Each burrow has up to three storage chambers (cf. also account on food). Breeding burrows are more complex, with 2-5 entrances and a nest (20-30 cm deep); there are also blind alleys and occasionally a storage chamber; the overall length of tunnels is $7-10 \mathrm{~m}$. The winter burrows descend deeper (50-120 cm) and contain several nests and a storage chamber (Pavlinov et al., 1990). Each animal has several burrows in an area of $50 \mathrm{~m}^{2}$ (Petter, 1961). Burrows are usually constructed in the sides of hills and in mounds of earth (Harrison \& Bates, 1991).

Yiğit et al. (1995) distinguished two types of burrows in Turkey: summer and winter ones. The latter were shallow tunnels with 1-2 entrances and an expanded nest chamber (30-40 cm deep and 20 cm in diameter) at the end of a $40-50 \mathrm{~cm}$ long tunnel. Blind alleys (10-20 cm long) were interpreted as being latrines. Summer tunnels had 4-5 entrances and descended 70 cm below surface. Tunnel diameter is about 7 cm .


Figure 178. Entrance to a burrow of Tristram's jird about 25 km south of Gaziantep. Photo: A. Kryštufek.

Reproduction. Reports on gestation period differ: 21-22 days (Mendelssohn \& Yom-Tom, 1999) and 25-29 days (Harrison \& Bates, 1991). Observations on Turkish specimens suggest a gestation of 24-27 days (Yiğit et al., 1995). Breeding season is all year round in Israel (peak from April to September; Harrison \& Bates, 1991) and in Transcaucasia (peak in May; Ejgelis, 1980). Yiğit et al. (1995) reported reproductive activity in Turkey between March and late September and recorded pregnant females from May to September. In museum material of Tristram's jird from Turkey, the juveniles were captured between March and October. Youngsters captured in mid-March near Antakya (ZFMK), with a body mass of 54-62 g, were estimated to be at
least two months old (for increase in body mass during postnatal development cf. Table 2 in Yiğit et al., 1995). Reproductive activity varies among regions of Turkey and strarts earlier in southeastern Anatolia.

Number of embryos is $1-11$ and litter size is $2-8$ (mainly 4-5; Pavlinov et al., 1990) but this varies geographically with smaller litters in the south. Embryo count in Turkey is $3-10$ (mean $=6.3$; Yiğit et al., 1995) and in Transcaucasia the average ranges from 5.2 to 6.4 (Ejgelis, 1980). Litter size in Israel is 1-7 (mean = 3.6; Mendelssohn \& Yom-Tov, 1999). Cubs are weaned at three weeks old. Maximum life expectancy in nature is up to 2.5 years; five years in captivity (Mendelssohn \& Yom-Tov, 1999). Sex ratio is balanced (Ejgelis, 1980).

Food consists of grain and leaves (Mendelssohn \& Yom-Tov, 1999). Opinions on food storages in burrows differ. Mendelssohn \& Yom-Tov (1999) state that large quantities of grain are hoarded in burrows during peak years in Israel; Papanjan (1977) reports caches of 200-700 g in Armenia; winter storage contains up to 5 kg of seeds (Pavlinov et al., 1990). On the other hand, no evidence of storage was found in Lebanon (Lewis et al., 1967) and Turkey (Yiğit et al., 1995).

Predation. Obuch (1994) found M. tristrami in pellets of the eagle owl (Bubo bubo) and tawny owl (Strix aluco) but at low percentages ( $0.7 \%$ and 0.6 \% of small mammals, respectively). A similarly low percentage ( $0.3 \%$ ) was reported from barn owl (Tyto alba) prey in the Menderes Delta (Brinkmann et al., 1990) and from pellets of the long-eared owl (Asio otus) in Diyarbakır Province (1.6 \% Seçkin \& Coşkun, 2006). Tristram’s jird becomes an important part of the owl's diet further south of Turkey with the following figures: $0.5 \%$ of small mammals (barn owl, northern Syria; Shehab \& Al Charabi, 2006), 6.2 \% (barn owl in southern Syria; Shehab, 2005), 29.2 \% (eagle owl in Syria; Shehab, 2004) and 61.0 \% (barn owl in Jordan; Rifai et al., 1998). This jird is also one of main prey items of the barn owl in Israel (Tores et al., 2006). Kasparek (1985) reports from Turkey also predation by Athene noctua. Tristram's jird was found in barn owl pellets on the Aegean island of Kos (Niethammer, 1989).

## Vinogradov's jird - Meriones vinogradovi

Meriones vinogradovi Heptner, 1931. Type loc.: Tabriz, Azerbaijan, Iran.

## Description

External characters. Large and robust jird with tail shorter than head and body (76.0-102.0 \% of head and body length; mean $=89.9 \%$ ). The ovate ears are of moderate size; anterior margin bears a raw of long ( 5 mm ) stiff hairs that cover auditory passage. Fore feet are evidently shorter than the hind ones. The hind soles are hairy except for heel (Fig. 166b); palms are bare. Front claws are up to $3.2-3.8 \mathrm{~mm}$ long, hind ones up to $4.4-4.7 \mathrm{~mm}$. Pelage is dense, long (10 mm on shoulders, 15 mm on hind back) and fine, but less silky than in M. crassus or M. libycus; ventral hairs are shorter ( 8 mm ). Males have a dark narrow mid-ventral gland ( $2-3.5 \times 16-17 \mathrm{~mm}$ ). Tail is wide at base, than gradually tapers towards the tip. It is densely covered by short hairs which entirely conceal underlying annulations; hairs of terminal brush are up to 20 mm long. Mystacial vibrissae are long (up to 50 mm ).


Figure 179. Meriones vingradovi in a characteristic upright position. Redrawn from Petter (1955).

Colour. Dorsal side is finely speckled dull greyish buff, darker on forehead, along the spine and on the rump; hair are plumbeous at bases up to half their length. Belly is white, with greyish or buff shades; hair bases are grey but dark band is less extensive than in dorsal hair. A characteristic buff streak is present on throat and chest; its shape and size vary individually. The streak is $17-60 \mathrm{~mm}$ long and $2-3$ mm wide; in some specimens the strike is expanding either towards the throat or the abdomen. The flanks and cheeks are less grey and lighter; demarcation line is either well defined or obscured. White postauricular tuft is clearly visible. Ears are grey with buff margin. Fore feet are whitish cream; hind feet are dirt whitish above with a light buff lateral streak; soles are buff, their margins are grey. Claws are pale, amber white on front feet, dark amber on hind feet. Tail


Figure 180. Skin of Meriones vinogradovi in dorsal and ventral view. Based on a specimen from Tell Abiad, Syria (IRSNB). Photo: C. Mlinar.


Figure 181. Skull and mandible of Meriones vinogradovi from Ghivragh, Nakhitchevan, Transcaucasia (SMF). Scale bar = 5 mm .
is buff, with orange or grey tints on its proximal part, black dorsally over its terminal one-half; on ventral side the black crest remains restricted to a terminal one-fifth to one-third (Fig. 168e,f).

Nipples. Four pairs of nipples, two pairs of pectoral and two pairs of inguinal (Yiğit et al., 1997c).

Penis. Proximal baculum of a specimen from Turkey is figured by Yiğit et al. (1997c). The expanded base is lanceolate (Fig. 165a).

Skull is similar to M. tristrami but is more robust. It is moderately deep (braincase height across bullae equals on average to $39.6 \%$ of condylobasal length (range = 38.6-41.1 \%). Zygomatic arches are wider (56.5-62.4 \% of condylobasal length; mean $=60.0 \%$ ) than braincase (breadth across bullae on average 53.3 \%; range = 51.2-55.3 \%). Rostrum is long and expanded proximaly, nasals hardly reach the orbital level. Anterior margin of masseteric plate straight vertical or slightly perpendicular; masseteric knob well developed. Anterior root of zygoma not largely expanded in lateral profile. Frontals are expanded, parietals are shifted posteriorly. Fron-to-parietal suture is frequently a straight line. Interparietal is of modest size. Supraorbital ridges not much expand, hardly reaching parietals. Zygomatic arches
slightly concave in medial part, diverge backwards. Diastema is long; incisive foramens wide but relatively short, not reaching level of molars. Posterior palatal foramens are rudimentary. Pterygoids diverge only slightly; interpterygoid fossa mainly narrow and long. Bullae not much inflated; bullar length relative to condylobasal length is on average $31.4 \%$ (range = 27.7-33.3 \%). Not much of mastoid portion is seen in dorsal view and the rim of bony auditory meatus does not reach the squamosal root of zygoma. Supramental triangle is ovate, of comparable size to $M$. tristrami.

Mandible is essentially as in M. tristrami.
Теетн. Upper incisors opistodont, grooved; enamel yellow. Molar pattern as in M. tristrami (Fig. 183). First upper molar with four roots, $2^{\text {nd }}$ molar with two roots; last molar single rooted (Fig. 184).

Dimensions. Males are significantly larger in Transcaucasia (ZMMU material): head and body length (mm): 148-178 in males (mean = 160.7; $\mathrm{N}=15$ ), 140-169 in females (mean = 153.6; $\mathrm{N}=22$ ); body mass (grams): 107-159 in males (mean = 131.5; N $=14$ ), 101-147 in females (mean = 122.3; $\mathrm{N}=22$ ).

Chromosomes. Diploid number of chromosomes is $2 \mathrm{~N}=44$ and fundamental number of autosomal


Figure 182. Skull and mandible of Meriones vinogradovi from Tell Abiad, Syria (IRSNB). Scale bar $=5 \mathrm{~mm}$.


Figure 183. Upper (a) and lower molars (b) of Meriones vinogradovi from Vedi, Araratski range, Armenia (ZMMU). Lingual side is to the left, anterior is at the top. Scale bar $=2 \mathrm{~mm}$.


Figure 184. Alveolar pattern of maxillary molars in Meriones vinogradovi. Based on a specimen from Armenia (ZMMU). Lingual side is to the left, anterior is at the top.
Scale bar $=2 \mathrm{~mm}$.

|  | Transcaucasia |  |  |  | Turkey |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | $\operatorname{mean}$ | $\min -\max$ |  |  |
| Head and body | 46 | 157.7 | $140-180$ | 5 | 158.0 | $137-165$ |  |  |
| Tail | 44 | 141.4 | $127-160$ | 5 | 144.8 | $133-156$ |  |  |
| Hind foot | 46 | 34.3 | $30.0-38.0$ | 5 | 38.4 | $37.0-40.0$ |  |  |
| Ear | 46 | 20.3 | $18.0-23.0$ | 5 | 22.8 | $21.0-25.0$ |  |  |
| Weight | 36 | 125.9 | $101-159$ | 5 | 117.8 | $82-135$ |  |  |
| Condylobasal length | 42 | 37.7 | $35.3-40.6$ | 5 | 36.8 | $34.6-37.9$ | 37.1 | 38.7 |
| Zygomatic breadth | 46 | 22.6 | $20.9-24.4$ | 5 | 23.2 | $21.3-24.2$ | 22.5 |  |
| Maxillary tooth-row | 42 | 6.6 | $6.2-7.0$ | 5 | 6.7 | $6.5-7.1$ | 6.7 | 6.4 |
| Bulla length | 43 | 11.8 | $10.9-12.7$ | 5 | 13.3 | $12.9-13.6$ | 11.5 | 12.1 |

Table 38. External and cranial dimensions of Meriones vinogradovi from Transcaucasia (ZMMU, SMF), Turkey (Yiğit et al., 1997c), and Tell Abiad, Syria (IRSNB).
arms is $\mathrm{NF}_{\mathrm{a}}=74$. There are 9 pairs of metacentric, 7 pairs of submetacentric and 5 pairs of acrocentric autosomes. The X chromosome is the largest metacentric and the Y chromosome is a small metacentric (Zima \& Král, 1984). Same chromosomal set is reported from Turkey, except that the Y chromosome is a small acrocentric (Yiğit et al., 2006a).

## Variation

A monotypic species.

## Distribution

Small range species largely restricted to Transcaucasia and northern Iran but was also reported for Syria and adjacent Turkey; range is mapped in Harrison \& Bates (1991). Range in Transcaucasia is small and limited to the middle course of the River Arkas along the border with Turkey (Šidlovskij, 1976). Lay (1967) reported Vinogradov’s jird from Iran for the provinces of Azerbaijan, Kurdistan, Zanjan, Qazvin and Tehran. Pavlinov et al. (1990) cite also northern Iraq but Vinogradov’s jird is not listed for this country (Hatt, 1959; Mahdi \& Georg, 1969; Kadhim et al., 1977; Harrison \& Bates, 1991).

Heptner (1931) was the first to include $M$. vinogradovi to the list of Turkish rodents, however, he did not provide exact locality ("südlichen Teil des Karstgebietes"). In his subsequent paper (Heptner, 1934) the locality is given as Sardanes (ca 12 km south-east of Oltu, Kars). Misonne (1957) reported M. vinogradovi for southeasternTurkey (locality not specified) which was accepted with no hesitation by Osborn (1965), Kumerloeve, (1975), Atallah (1978), Harrison \& Bates (1991), Demirsoy,
(1996) and Kurtonur et al. (1996); Doğramacı (1989) however ignored it and reported Vinogradov's jird only for eastern Anatolia.

Misonne's (1957) report for Mesopotamia is supported by voucher specimens and we had an opportunity to examine four animals from Tell Abiad, Ar Raqqah, Syria (IRSNB; cf. Figs. 180, 182). Although this material belongs to $M$. vinogradovi, we still see several problems with the presence of the species in Mesopotamia. These concerns are:

1. Misonne (1957) remains the only author who has reported $M$. vinogradovi for Mesopotamia. Jirds of Syria were reviewed recently by Kock (1998) and those of Turkey by Yiğit et al. (1997c, 2006c). All these attempts failed to recognise a single Vinogradov's jird in extensive samples resulting from field surveys which provided rich, new material.
2. Misonne (1957) reported M. vinogradovi to be the most abundant rodent during his visit to the region ( $54.4 \%$ of all rodents trapped in Syria and 62.1 \% in Turkey). Comparative figures for M. tristrami, which all recent surveys found to be the most abundant jird in the area, are 30.5 \% and 21.1 \%, respectively (Misonne, 1957). Such high abundance was never reported for Vinogradov's jird (cf. Ejgelis, 1980). E.g. the Street 1962-1963 expedition to Iran collected 35 specimens of M. tristrami but not a single M. vinogradovi (Lay, 1967).
3. Typical habitats of Vinogradov's jird in Transcaucasia are cool semideserts and high elevation steppe mainly $>700 \mathrm{~m}$ of elevation (see account on habitat). Deep soil is essential for burrowing
and the species does not occur on sands and on a substrate of rocky debris. On the other hand, Vinogradov's jird avoids the hot lowlands which are typical habitat of M. libycus, and does not enter cultivated land (Ejgelis, 1980; Pavlinov et al., 1990). Habitat selection and burrowing activity as reported for M. vinogradovi in Mesopotamia differ fundamentally from the rest of the range: burrowing in moist banks, occurrence in rocky deserts, on sandy substrate and in cultivated fields (Misonne, 1957; Harrison \& Bates, 1991).

In conclusion, records of Vinogadov's jird in Mesopotamia are about 500 km to the west of the established range in Iran. Also, the habitat in Mesopotamia is atypical for what is known about the biology of species in the Iranian plateau (Golvan \& Rioux, 1961). The presence of this species in Mesopotamia therefore requires further verification.

Turkish authors reported two localities in eastern Anatolia with no further details: Aralık and Doğubayazıt (Yiğit et al., 1997c, 2006a,c). Obuch (1994) identified Vinogradov’s jird from the owl pel-
let material collected at Sarikamiş. This record seems reliable since it is within the known range, however no $M$. tristrami were identified in the same sample.

Palaeontology. Fossil history of Vinogradov's jird is not known (Vereščagin, 1959).

## Habitat

Typical habitats in Transcaucasia are cool semideserts and high elevation steppe. Vinogradov's jird requires deep soil for burrowing but does not occur on sands and on a substrate of rocky debris. In mountains, the species is frequently found close to cereal fields. Local populations are isolated to some degree (Ejgelis, 1980; Pavlinov et al., 1990). Habitats around Aralık are predominantly steppic, cool and dry (198 mm of precipitation annually). Dominant plants on dry soils are Equisetum raminosum, Atraphaxis billardieri, Brassicaceae spp., Crepis sp., Medicago sp. and Euphorbia sp. (Yiğ it et al., 2003). Vinogradov's jird avoids hot lowlands and so consequently, reports for Mesopotamia are abnormal also from this point.

Altitude. In Transcaucasia from the valley of the Araks River ( 700 m ) up to $1,500-1,800 \mathrm{~m}$ a.s.l., rare-


Figure 185. Distribution of Meriones vinogradovi in Turkey and adjacent regions. An uncertain record is shown as a diamond. Records: 1 - Sardanes (ca 12 km south-east of Oltu), Kars; 2 - Sarıkamış, Kars; 3 - Doğubayazıt, Ağrı; 4 - Aralık, Ĭğdır. Corresponding referrences: Heptner (1934): 1. Obuch (1994): 2. Yiğit et al. (1997c): 4. Yiğit et al. (2006c): 3.
ly higher (2,000 m; Ejgelis, 1980) but exceptionally up to 2,600 m (Pavlinov et al., 1990).

Associates in Transcaucasia are Meriones libycus, M. tristrami, Microtus arvalis/levis, Allactaga elater and $A$. williamsi. Vinogradov’s jird is the rarest jird and its relative abundance in eastern Transcaucasia is 1 M . vinogradovi : 7 M . tristrami : 17.5 M. libycus (Ejgelis, 1980). Other rodents occurring in the area of Aralık, Turkey, include Spermophilus xanthoprymnus, Mesocricetus brandti, Meriones tristrami, M. dahli, Microtus arvalis, Ellobius lutescens, Apodemus cf. witherbyi and Allactaga elater (Yiğit et al., 2003).

Density is on average 8.7 individuals per ha in Transcaucasia and varies from 7.1 per ha in summer to 9.4 per ha in autumn. Mean densities in peak years are 37 per ha and at population bottoms 5-10 per ha. The summer aggregations on good feeding grounds can have even higher temporary densities, e.g. up to $40-50$ per ha ( $60-80$ per ha in peak years) on scattered patches of halophytic vegetation, but long-term average is much lower (12-14 per ha) (Ejgelis, 1980). Densities varied seasonally within the same population in Armenia from 4.5 per ha to 19.5 per ha. Over the years, numbers varied between 4.0 and 28.6 per ha in one population and 4.0-15.1 per ha in another (Ejgelis, 1980; Fig. 183). In a study from Azerbaijan, the amplitude of population oscillations was 24 -fold during the 18 -year period (Pavlinov et al., 1990).

## Biology

Activity is predominantly diurnal from autumn to spring and peaks at midday. The animals are mainly nocturnal in summer when daily activity is restricted to morning and afternoon hours (Petter, 1961; Pavlinov et al., 1990). A male establishes a long-term association with one or two females which share a common territory and nurse litters together (Pavlinov et al., 1990). Vinogradov’s jirds live in small colonies of 4-5 animals (Petter, 1961).

Burrows were studied in detail by Ejgelis (1980) in Transcaucasia. He found tunnels of a family group to spread over $0.1-0.3$ ha, rarely over $0.5-0.8$ ha. The burrow system has numerous entrances and the total length of galleries exceeds 19 m . There are four or more storage chambers arranged along three metres of a tunnel which is about 30-50 cm below the


Figure 186. Variation in density (number of individuals per hectare) of Meriones vinogradovi between 1955 and 1970 in two regions of eastern Transcaucasia. Modified from Ejgelis (1980).
surface. On the other extreme of complexity are simple temporary burrows with no chambers, with 1-3 entrances and with 60-182 cm of tunnels which descend $25-47 \mathrm{~cm}$ deep. Solitary feeding burrows are longer (580-780 cm of tunnels), 18-31 cm deep, with 5-9 entrances and one or two storage chambers. Winter burrows (4-7 entrances) contain 1-3 nest chambers and a cache; they cover a surface area of 11-16 $\mathrm{m}^{2}$ and have 5.7-10 m of tunnels. Reproductive burrows have up to 14 entrances, tunnel length of 0.8 13.5 m and contain a nest which is $20-48 \mathrm{~cm}$ deep (Ejgelis, 1980). Animals frequently move from one


Figure 187. Burrow systems of Meriones vinogradovi in Transcaucasia. Entrances are shown by circles; C - cache; N - reproductive nest. Modified from Ejgelis (1980).
burrow to another (Pavlinov et al., 1990). Burrows in Iran were described by Petter (1961).

Because post-juvenile dispersal is frequently postponed, young animals normally over-winter with their parents. Therefore a family burrow can contain up to 5-6 adult jirds (Pavlinov et al., 1990).

Reproduction was studied in Transcaucasia by Ejgelis (1980) on a sample of 40,600 Vinogradov’s jirds. Breeding season starts in March (rarely in February) and peaks from March to April-June when up to 25 \% (exceptionally 45 \%) of females are visibly pregnant. Pregnant females can be found at any time of the year but at very low proportion (0.5-1.2 \%) between November and March. The breeding season therefore normally lasts six months. Hence the breeding season is longer in Vinogradov's jird than in other sympatric Meriones species ( $M$. libycus, M. tristrami, M. dahli). Number of embryos is $1-12$ (5.26.2 on average) and litter size is up to $6-8$. Females normally have 2-3 litters annually, occasionally four (Ejgelis, 1980). Gestation lasts 21.5-23 days (Petter, 1955).

Sex ratio is male biased in spring, female biased in summer. Sexual maturity is reached at age of three months but juveniles normally start to reproduce only the following year (Ejgelis, 1980).

Food. Diet is omnivorous and mainly consists of plant material, particularly of seeds. Green plants are an important source of water (Pavlinov et al., 1990). Food is stored for winter and caches contain up to 3.5 kg (Harrison \& Bates, 1991) or up to 40 litres of grain (Petter, 1961).

Predation. Near Sarıkamış, Kars, Obuch (1994) found $M$. vinogradovi in pellets of the eagle owl (Bubo bubo) at a relative abundance of $5.4 \%$ of all rodents ( $\mathrm{N}=1,180$ ); cf. also account on distribution.

Conservation. Vinogradov's jird shows all three aspects of rarity as defined by Rabinowitz (1981): small range, habitat specificity and fairly low population densities. Besides, populations are frequently isolated in a patchy environment. According to Meriones standards, this jird seems to be shifted towards K-strategy in the r-K continuum. Its rarity is further evidenced from the fact that 1962-1963 Street expedition to Iran failed to collect a single specimen (Lay, 1967). In the IUCN Red Data Book Vinogradov’s jird is currently listed as a "Lower Risk (lc)" species (IUCN, 2008). In Turkey Yiğit et al. (2006c)
classified Vinogardov’s jird as an endangered species (EN). Aspects of biology have so far been studied mostly from the epidemiological point of view (Golvan \& Rioux, 1961; Ejgelis, 1980).

## Sundevall's Jird - Meriones crassus

Meriones crassus Sundevall, 1842. Type loc.: Fons Moses (Ain Musa), Sinai, Egypt.

## Description

External characters. Small jird, only slightly larger than M. dahli, with a tail shorter than head and body (78.5-99.3 \% of head and body length; mean $=90.9$ \%). Ears are relatively small, with a crest of stiff hairs along its front margin. Fore feet are evidently shorter than the hind ones. Palms with five distinct pads are margined with a crest of short stiff hairs. The hind soles are hairy (Fig. 166d), palms are nude. There are only two pads on hind foot, a lobed postdigital pad and a single hallucal pad (Osborn \& Helmy, 1980). Pelage is long (up to 14 mm on mid-back) and silky. Tail is densely haired throughout and terminates in a brush (hairs about 15 mm long). Mystacial vibrissae are long (up to 40 mm ).

Colour is subject to much individual variation. Dorsal side is finely speckled sandy buff, darker along the spine; flanks are more greyish-yellow. Ventral side is pure white and the lateral line of demarcation is not sharply defined. Base of dorsal hairs are slate grey; ventral pelage is white to bases. Forehead is of same colouration as mid-back, cheeks are greyish, postorbital and postauricular whitish spots are scarcely marked and not present in all specimens. Ears are buff; hands and feet white to pinkish. Tail dull buff, not more ochraceous than the body, greyish in some specimens; ventral side is paler, occasionally cream or grey washed. Short black hairs are sprayed all over the tail; terminal black brush is present on the distal one-third to one-fifth of the tail's dorsal side. Claws are usually pale.

Nipples. Four pairs, two pectoral and two inguinal, respectively (Kock, 1998).

Penis is covered by minute spines in pentagonal sockets. Distal baculum consists of three cartilaginous processes which are not separated, but joined together at their base and attached to the proximal


Figure 188. Sundevall's jird Meriones crassus from Egypt. Photo: J. Vogeltanz.
baculum by connective tissue (Osborn \& Helmy, 1980). Proximal baculum is $2.3-2.9 \mathrm{~mm}$ long in Turkish material (mean $=2.6 \mathrm{~mm}$; Yiğit et al., 1998b). Expanded basal shaft is short and triangular (Yiğit et al., 1996). Note that measurements reported by Yiğit et al. (1998b) do not match the scale to drawings of bacula provided by Yiğit et al. (1996). The basal expansion is oval-shaped in a specimen from Saudi Arabia figured by Harrison \& Bates (1991).

Skull is deep and wide, broader across the tympanic bullae (braincase breadth across bullae averages 62.9 \% of condylobasal length; range $=59.8-$ 70.3 \%) than at the most expanded point of zygoma (zygomatic breadth averages 58.3 \% of condylobasal length; range $=55.8-60.3 \%$ ). Rostrum is relatively short but slender and nasals are strongly projected forwards. Masseteric plate curved round in front; anterior root of zygoma less expanded than in other jirds. The nasals are narrow in dorsal view, pointed at the tip and expanding posteriorly to a level of enlarged lacrimals. Interorbital constriction only slight-
ly broader than the rostrum; supraorbital ridges expand from lacrimals to parietals. Zygomatic arches diverge backwards. Parietals are expanded while inteparietal bone is relatively small. Diastema is long; incisive foramens long and narrow, nearly reaching level of molars. Posterior palatal foramens long and narrow, shifted towards the posterior part of $1^{\text {st }}$ upper molar. Posterior margin of hard palate behind $3^{\text {rd }}$ molars but not shifted as backwards as in M. tristrami. Pterygoids diverge posteriorly, the interpterygoid fossa is triangular. Bullae more inflated than in any other jird in Turkish fauna; bullar length relative to condylobasal length is on average 41.3 \% (range = 39.0-44.9 \%). Enlarged mastoid portion is clearly seen in dorsal view and expands behind the occipitals. The rim of bony auditory meatus is grossly swollen anteriorly and in close apposition to the posterior root of zygoma. Supramental triangle nearly as high as long, open posteriorly. Mandibular body deep, coronoid process leaned against articular process. Alveolar process well pronounced.

Tеетн. Upper incisors opistodont, grooved. Enam-


Figure 189. Skull and mandible of Meriones crassus, based on an adult female from Tell Bderi in Syria (SMF).
Scale bar $=5 \mathrm{~mm}$.
el on upper incisors light yellow to yellow, pale orange on lower ones. Molar pattern shows no peculiarities in comparison with other jirds (Fig. 190). Number of alveoli in Syrian material is as follows (anterior to posterior): 3, 2, 1 in the maxillary row, and 4, 2, 1 in the mandibular row (Fig. 191). In Turkish specimens Yiğit et al. (1998b) scored three alveoli for $1^{\text {st }}$ lower molar.

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 30 | 128.5 | $118-139$ |
| Tail | 29 | 116.6 | $105-130$ |
| Hind foot | 31 | 30.2 | $27.0-34.0$ |
| Ear | 31 | 15.9 | $13.0-17.5$ |
| Weight | 24 | 65.1 | $42-94$ |
| Condylobasal length | 32 | 32.8 | $30.5-34.6$ |
| Zygomatic breadth | 29 | 19.3 | $18.0-20.5$ |
| Maxillary tooth-row | 34 | 5.6 | $5.0-6.0$ |
| Bulla length | 34 | 14.0 | $13.2-14.8$ |

Table 39. External and cranial dimensions of Meriones crassus charon from Turkey and adjacent regions. Based on Yiğit et al. $(1996,1997 \mathrm{c})$, and specimens in BMNH and SMF.

Dimensions are given in Table 39. Petter (1961) reported 150 g as maximum body mass. Males are significantly larger than females in Egypt (Osborn \& Helmy, 1980) and Israel (Krasnov et al. 1996). Mendelssohn \& Yom-Tov (1999) provided the following data for body mass: $86 \pm 13 \mathrm{~g}$ in males, 72 $\pm 19 \mathrm{~g}$ in females. Body mass changes among years and animals lose weight during dry winters (Krasnov et al. 1996).

Chromosomes. In Turkish Sundevall's jirds, the diploid number of chromosomes is $2 \mathrm{~N}=60$ and fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=72$. Seven autosomal pairs are bi-armed of decreasing size and the remaining (22 pairs) are acrocentric. Both heterosomes are biarmed, the X chromosome is one of the largest chromosomes and the Y chromosome is approximately three-quarters of its size (Yiğit et al., 1998b). Fundamental number of autosomal arms varies, being $\mathrm{NF}_{\mathrm{a}}=68$ in Egypt and Iran (Nadler \& Lay, 1968), and $\mathrm{NF}_{\mathrm{a}}=70$ in Jordan (Qumsiyeh et al., 1986).


Figure 190. Upper (a) and lower molars (b) of Meriones crassus (same specimen as in Fig. 189). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

## Variation

Sundervall's jirds from Iran, Iraq and Syria belong to subspecies M. c. charon Thomas, 1919 (Type loc.: Ahvaz, Kuzistan, Iran), which was originally described as a separate species (Thomas, 1919). Yiğit et al. (1998b) ascribed Turkish material to this race, similarly as did Kock (1998) with Syrian animals. In comparison to the nominate race and to $M$. c. swinhoei (Scully, 1881; Type loc.: Gatai, Afghanistan), M. c. charon shows less expanded bullae. Bullae are about $38 \%$ of the occipitonasal length in $M$. c. crassus and M. c. swinhoei, as opposed to 35-36 \% in M. c. charon (Ellerman, 1948); for comparison between the nominate race and charon see Fig. 90 in Petter (1961; p. 198). Note, however, that subspecies are not sharply delimited (Harrison \& Bates, 1991).

Diploid number is stable across the range, fundamental number varies however (Pavlinov et al., 1990); e.g. Benda \& Sádlová (1999) reported 12 biarmed chromosomes from Jordan (eight in Turkey; cf. above).


Figure 191. Alveolar pattern of maxillary (a) and mandibular (b) molars in Meriones crassus. Based on two different individuals from Syria (SMF). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

## Distribution

Sundervall's jird has a wide range in the so-called Saharo-Sindian desert belt (Atallah, 1978; Qumsiyeh, 1996) and occupies Palaearctic northern Africa (from Morocco to Egypt, Sudan and Niger), Sinai, the Near East (Israel, Jordan, Syria, Iraq), Arabia, Iran, Turkmenistan, Afghanistan, and Pakistan. Its northern range in Africa largely coincides with the extent of the Sahara (Petter, 1961). Southeastern Turkey is on the very northern border of this range. In Turkey, Sundevall's jird is restricted to the vicinity of Şanlı Urfa along the border with Syria (Fig. 192). Yiğit et al. (1996) suggested that the range might extend a further ca 150 km north where mountains shape the eastern and western borders of its Turkish range.

We assume that a report of M. sacramenti for Tel Fidan Davud near Şanlı Urfa by Misonne (1957) might be the earliest evidence of the occurrence of Sundevall's jird in Turkey. Within its present taxonomic scope, M. sacramenti is restricted to a small area in Israel and Sinai (Musser \& Carleton, 2005)


Figure 192. Records of Meriones crassus in Turkey: 1 - "Şanlıurfa civarındaki" (= neigbourhood of Şanlı Urfa); 2 - "Şanlı Urfa province near to border to Syria". Corresponding referrences: Yiğit et al. (1997c): 1. Yiğit et al. (1998b): 2. Diamond indicates an unspecified record.
but was listed in the synonymy of $M$. libycus (Aharoni, 1932) or of M. crassus (Ellerman, 1941; Ellerman \& Morrison-Scott, 1951) in Misonne's time. At that period libycus, crassus and sacramenti were still poorly defined and Ellerman (1941) even synonymised crassus with libycus. A report of $M$. sacramenti for Mesopotamia was accepted with no subsequent comments by Osborn (1965), ignored by Doğramacı (1989a), and linked to M. libycus by Zahavi \& Wahrman (1957) and Baltazard \& Seydian (1960); the last view was subsequently adopted by Kumerloeve (1975) and Kock (1998). Zahavi \& Wahrman (1957) relied on a personal communication by Petter and Misonne which gives certain credit to their interpretation, however does not explain the reason why Misonne (1957) also recognised in his material M. libycus, in addition to M. sacramenti. We suggest that two specimens identified by Misonne (1957) as M. sacramenti were possibly M. crassus. Namely, Misonne (1957), who was familiar with the latter species, was in this case, evidently confused by the relatively small size of bullae in his Mesopotamian material (34 and $35 \%$ of
occipitonasal length, respectively). These values are, however, within the range for Meriones crassus charon (Ellerman, 1948) which occurs in Syria and Turkey (Kock, 1998; Yiğit et al., 1998b). Consequently, the report of M. sacramenti for Tel Fidan Davud near Şanlı Urfa by Misonne (1957) is likely the earliest evidence regarding the occurrence of M. crassus in Turkey and was confirmed recently by Yiğit et al. (1998b).

Palaeontology. Presumably invaded Israel from Africa in post-Würmian times (Tchernov, 1968). Remnants from the Deh Luran sequence in northern Iran are of the Holocene age ( $8,000-3,460$ years BP; Turnbull, 1975).

## Наbitat

Sundervall's jird is the most arid-adapted among Meriones species (Pavlinov et al., 1990) and frequently occurs in desolate areas that are virtually devoid of vegetation. Largely psammophilic in Africa and in the western Near East (sand dunes, dry river beds [wadis], and gravel plains), the species inhabits also steppes further east (Petter, 1961). In Pakistan
M. crassus favours the most barren stony or sandyclay plains with the lowest amount of shrub or herb cover (Roberts, 1997). Broad selection of habitats occupied by the species is likely a consequence of pronounced seasonality (Krasnov et al., 1996). Soil conditions affect the species distribution both directly (burrowing conditions) and indirectly (availability of green vegetation during breeding season; Krasnov et al., 1996).

In Turkey, Sundevall's jird inhabits pastures and steppic habitats (Yiğit et al., 1998b) with vegetation of Hordeum sp., Eryngium sp., Securigera sp., Peganum sp. and Agrophiron sp. (Yiğit et al., 1996).

Altitude. Habitats of Sundevall's jird in Turkey are at an altitude of 500 m (Yiğit et al., 1996). The species is "common below 1,500 m" in Afghanistan (Hassinger, 1973) and was collected close to the sea level in Egypt and Sinai (Osborn \& Helmy, 1980).

Associates. Yiğit et al. (1996) reported Meriones tristrami and Allactaga euphratica to co-occur with M. crassus in Turkey. Sundevall's jird is sympatric with M. tristrami in loess-sand areas in Israel (Mendelssohn \& Yom-Tov, 1999). It co-occurs in Egypt with Jaculus jaculus, Gerbillus gerbillus, G. perpallidus, and occasionally with Meriones shawi and M. libycus (Osborn \& Helmy, 1980). In Baluchistan, Pakistan, M. crassus occupies the same biotope as Gerbillus cheesmani, Jaculus blanfordi, Allactaga ellater and to a lesser extent Meriones libycus (Roberts, 1997). Relations between M. crassus and M. libycus are antagonistic (Petter, 1961).

Density. Common species with low habitat-specificity under desert conditions in Israel (Krasnov et al., 1996). Amr (2000) reports the Saundevall's jird to be one of the most common jirds inhabiting the dry and arid habitats of Jordan. Highest densities in Israel are from sand dunes (1.2-4.0 individuals per hectare) but are lower than 1 per hectare in the majority of other habitat types (Krasnov et al., 1996).

## Biology

Activity. Sundewall's jird is mainly believed to be strictly nocturnal (Petter, 1961) but Amr (2000) states that it comes out for feeding during daytime as well. Harrison \& Bates (1991) similarly reported an observation during daytime and Osborn \& Helmy (1980) trapped one specimen around midday. The highest period of activity appears to be dur-
ing the first hour after twilight (Qumsiyeh, 1996). Hassinger (1973) captured over $75 \%$ of his specimens in Afghanistan between dusk and 10 p.m. Periods of above-ground activity are as short as $5-10$ \% of the dark period of the night in Israel (Krasnov et al., 1996).

Sundewall's jirds remain in close vicinity to their burrows for relatively long periods and then move to another burrow where they stay for another 3-7 nights (Krasnov et al., 1996). Homing abilities are highly developed and specimens are known to return to the burrow from a distance of up to 10 km (Petter, 1968). Sundewall's jirds are gregarious but not highly colonial animals (Qumsiyeh, 1996). Krasnov et al. (1996) found no evidence of coloniality in Israel where individuals were rather solitary, each maintaining a small home range.

Burrows. In a habitat mosaic, the burrows are more frequent in sandy substrate than in rocky peneplain. Lay (1967) reported from Iran fairly simple burrows with 3-4 openings leading to a nest chamber which was up to 2 m deep. All eleven burrows excavated in Turkey had a single entrance of oval shape (greatest diameter 7 cm ) with a passage descending gently up to $30-40 \mathrm{~cm}$ below the surface. The nest chamber ( $25 \times 12 \mathrm{~cm}$ ) was actually the expanded main passage, about $80-90 \mathrm{~cm}$ from the entrance and 20-30 cm deep; it was lined with dried vegetation and sheep wool. All burrows contained a food-storage chamber ( $15-20 \mathrm{~cm}$ in diameter) and had blind-end tunnels; one of them was used as a latrine. Entrances were plugged with dry grass (Yiğit et al., 1996). Petter (1961) reported burrows of various size and complexity, from a simple single-entrance tunnels $<1 \mathrm{~m}$ in length, to a dense network of passages with numerous entrances and spreading over an area up to 6 m in diameter ( $20-30 \mathrm{~m}^{2}$ ). Burrows were mainly shallow and rarely deeper than 50 cm . Complex burrow systems are probably used for several generations. Total length of tunnels per burrow is up to $30-40 \mathrm{~m}$ (Pavlinov et al., 1990).

Hassinger (1973) reported entrances at densities of 100 along 100 m of roadside gulley in one place in Afghanistan and about 1 entrance per $15 \mathrm{~m}^{2}$ on another. Burrows clustered together in Turkey, and were $15-20 \mathrm{~m}$ apart; each was occupied by a single animal (Yiğit et al., 1996).

At the ambient temperature of $26-39^{\circ} \mathrm{C}$ and a rel-
ative humidity of 21.5-77 \% the temperature within the burrow is $25-36^{\circ} \mathrm{C}$ and the relative humidity is 24-78 \% (data from Egypt; Osborn \& Helmy, 1980).

Reproduction. Although captive animals long survive on a diet of dry seeds without access to water, they breed only if green, succulent food is available (Krasnov et al., 1996; Mendelssohn \& YomTov, 1999). Reproduction period is long in Israel, from the end of January till the end of September. All males are scrotal from February and May and proportion of breeding females exceeds 50 \% starting from March. Only the first part of breeding period is successful, while the pups from the late summer and early autumn litters generally do not survive (Krasnov et al., 1996). In Egypt, reproduction lasts from November to June (Osborn \& Helmy, 1980). Reproductive animals were found in Turkey in May and September (Yiğit et al., 1996). Pregnancy lasts 1822 days and females deliver 3-7 cubs (mean $=4.9$; Krasnov et al., 1996). Average litter size is estimated at 3.3 in Egypt (range $=1-5$; Osborn \& Helmy, 1980). Yiğit et al. (1996) reported litters from Turkey with $4,4,5$, and 7 pups, respectively. Two pregnant females from Syria had 3 and 5 embryos, respectively (Kock, 1998).

Food. Feeds on seeds, leaves and insects (Mendelssohn \& Yom-Tov, 1999). Food is cached; Petter (1961) reported caches of up to 250 g of grain and 100 g of other edible items. List of food items was provided by Qumsiyeh (1996): Acacia sp., Cassia acutifolia, Citrullus colocynthis, Peganum hormala, Medicago sp., Zilla spinosa, Anabasis articulate, Mesombryanthemum forskalii, Zygophyllum simplex, Plantago cylindrica and Neurada probumbens among plants; also locusts (Schistocera sp.) and crickets (Orthacantharis sp.). Camel and donkey dung is also consumed. In Israel animals move between patches of vegetation, e.g. in late summer from wadis to plains where Hammada salicornia, a necessary part of $M$. cassus diet, is flowering (Krasnov et al., 1996).

Predation. Preyed upon by the barn owl Tyto alba in Syria (Kock, 1998) and Israel (Rekasi \& Hovel, 1997), and the eagle owl Bubo bubo in Jordan (Amr et al., 1997). Found also in owl pellets in Iraq (Nadachowski et al., 1990).

## Libyan jird - Meriones libycus

Meriones libycus Lichtenstein, 1823. Type loc.: Libyan Desert (frequently reported as "near Alexandria, Egypt"; see Musser \& Carleton, 2005, for comments).

## Description

External characters. Large and robust jird with tail of approximately same length as head and body (85.5-119.0 \% of head and body length; mean = 101.0 \%). The ears are rounded and relatively small. Their anterior edge is with a brush of short hairs and the auditory passage is covered by long hairs. The eyes are conspicious. Fore feet are evidently shorter than the hind ones. The hind soles are partly naked proximally; a naked stripe extends from the heel along the medial side of the foot to slightly beyond the tarsometatarsal joint. Palms are bare; front claws are up to 3.5 mm long, hind ones up to 4.7 mm . Pelage is long ( $8-14 \mathrm{~mm}$ on mid-back) and soft. Dense short hair covers annulation throughout the tail; hairs of terminal brush are up to 25-30 mm long. Mystacial vibrissae are long (up to 55 mm ).

Colour. Back side is pale, slightly grizzled sandy buff or pinkish buff, only slightly darker medially; hair bases are plumbeous; black tips give speckled appearance. Belly is pure white; hairs are white throughout, except on the chin and throat where they are white to the roots. Flanks light buff, demarcation line sharp. Postauricular spot and patch at the ear base are pale and not strongly marked. There is also a white spot on the upper side of eyes. Ears are


Figure 193. Libyan jird Meriones libycus from Syria.
Photo: A. Shehab.
pale grey, feet are white to yellowish; claws are darkly pigmented. Tail ochraceous all around, not much paler below; dorsally black over one third to one-fifth of its terminal length. Brush is black, with few white hairs in some animals. Ventral side of the tail is ochraceous from base to tip. Colour varies throughout the range and some populations are as grey as M. dahli (Pavlinov et al., 1990). Hassinger (1973) recorded moulting specimens from July to November.

Nipples. Females have eight nipples (two pairs of each, pectoral and inguinal; Mamkhair et al., 2007).

Penis. The phalus is cylindrical, 25-30 mm long, and the glans terminates in a small papilla. The bac-


Figure 194. Skin of Meriones libycus in dorsal and ventral view. Based on a specimen from Chah-e-Dad Khoda, province Kerman, Iran. Photo: C. Mlinar.
ulum is $3.5-4.0 \mathrm{~mm}$ long in animals from Damascus, Syria (Mamkhair et al., 2007). Expanded basal shaft of proximal baculum is rectangular (Pavlinov et al., 1990) to oval (Mamkhair et al., 2007).

Skull is similar to M. crassus. It is deep and wide, slightly broader across tympanic bullae (braincase breadth across bullae averages 60.2 \% of condylobasal length; range $=59.2-61.5 \%$ ) than at most expanded point of zygoma (zygomatic breadth averages 59.2 \% of condylobasal length; range = 58.1-58.7 \%). Rostrum as in M. crassus, but braincase relatively smaller. Masseteric plate curved round in front; masseteric knob large. Anterior root of zygoma expanded. In the dorsal view the nasals are narrow; lacrimals are large. Interorbital constriction comparatively broader than in M. crassus; supraorbital ridges expand from lacrimals to parietals. Zygomatic arches diverge backwards. Parietals are expanded and fron-to-parietal suture is straight; parietal is oval. Diastema is long; incisive foramens are shorter and narrower than in M. crassus, not reaching level of molars. Posterior palatal foramens are long and narrow. Pterygoids slightly diverge posteriorly. Bullae are inflated, similarly as in M. crassus albeit to a lesser degree; bullar length relative to condylobasal length is on average 39.3 \% (range = 38.3-40.3 \%). Enlarged mastoid portion is clearly seen in dorsal view but does not expand much behind the occipitals. The rim of bony auditory meatus is grossly swollen anteriorly and in close apposition to the posterior root of zygoma. Supramental triangle is smaller than in $M$. crassus and normally closed posteriorly by a dorsally expanded hamular process.

Mandible is deep, coronoid process is free; alveolar process is well pronounced.

Teeth. Upper incisors opistodont, grooved. Enamel on upper incisors light orange, more yellow on lower ones. Molar pattern as in M. crassus (Fig. 196). First upper molar has four roots, both $2^{\text {nd }}$ molars and the $1^{\text {st }}$ lower molar are with two roots, and both $3^{\text {rd }}$ molars are single-rooted (Fig. 197; Mamkhair et al., 2007).

Dimensions of specimens from Iran and Afghanistan (ssp. erythrourus; cf. below) are given in Table 40. Sexes are of subequal size (Table 41); in a sample from Egypt, mean occipitonasal length of adult males was $38.8 \mathrm{~mm}(\mathrm{~N}=25)$ and of adult females was 38.3 mm ( $\mathrm{N}=28$; Osborn \& Helmy, 1980). Hassing-


Figure 195. Skull and mandible of Meriones libycus from Gonbadli, Khorassan, Iran (SMF). Scale bar $=5 \mathrm{~mm}$.
er (1973) provided dimensions of a large sample from Afghanistan ( $\mathrm{N}=132$ ): head and body 110-162 (mean $=135$ ), tail 111-158 (130), hind foot 31-39 (33), ear 13-21 (17). Body mass in a sample from Egypt was 65-120 g ( $\mathrm{N}=43$; Osborn \& Helmy, 1980); maximal body mass reported was 140 g (Petter, 1961) and 180 g (Mamkhair et al., 2007).

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 7 | 137.4 | $121-165$ |
| Tail | 7 | 138.8 | $124-144$ |
| Hind foot | 7 | 31.1 | $28.0-32.0$ |
| Ear | 7 | 16.7 | $16.0-18.0$ |
| Weight | 3 | 102.0 | $94-115$ |
| Condylobasal length | 6 | 35.2 | $32.9-36.8$ |
| Zygomatic breadth | 4 | 20.6 | $19.6-21.8$ |
| Maxillary tooth-row | 7 | 5.5 | $5.2-5.9$ |
| Bulla length | 7 | 13.7 | $13.1-14.4$ |

Table 40. External and cranial dimensions of Meriones libycus from Iran and Afghanistan. Based on specimens in SMF and ZFMK.

Chromosomes. The diploid number of chromosomes is $2 \mathrm{~N}=44$ and fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=72$. Ten pairs are metacentric, 5
pairs are submetacentric or subtelocentric and 6 pairs are acrocentric. The X chromosome is a large metacentric, the Y chromosome is somewhat smaller submetacentric. Karyotype is stable throughout the range in Asia and Africa (Zima \& Král, 1984). The Libyan jird differs from $M$. vinogradovi in having one autosomal pair biarmed instead of acrocentric.

## Variation

Considerable individual and geographical variation was reported in this species. The Euphrates River separates two subspecies, M. l. erythrourus Gray, 1842 (Type loc.: Sahlabad, Afghanistan) to the east, and M. l. syrius Thomas, 1919 (Type loc.: Karyatein, Syria) to the west (Harrison \& Bates, 1991). These two were the only valid subspecies recognized by Ellerman (1948) in southwestern Asia; list of subspecies expanded shortly afterwards and Ellerman \& Morrison-Scott (1951) listed eight races. Noteworthy, even erythrourus and syrius are closely related (Thomas, 1919) and Ellerman (1948) separated them by the relative size of bullae: bulla longer than 35 \% of occipitonasal length in M. l. erythrourus and shorter than 33 \% in M. l. syrius. In accordance with Thomas (1919), M. l. syrius is also larg-

a

b

Figure 196. Upper (a) and lower molars (b) of Meriones libycus (same specimen as in Fig. 195). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
er on average; mean condylobasal length $=37.4 \mathrm{~mm}$ (range $=33.8-41.0 \mathrm{~mm}$; Mamkhair et al., 2007). Under the presumption that the River Euphrates effectively separates the two races, material from Turkey and adjacent Syria belongs to M. l. erythrourus.


Figure 197. Alveolar pattern of upper (a) and lower (b) molars in Meriones libycus from Syria. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$. Redrawn from Mamkhair et al. (2007).

## Distribution

Widely distributed jird, ranging from North Africa (Rio de Oro to Egypt) through Sinai, Arabia (where absent from southern and western parts of the peninsula), Jordan, Iraq, Syria, Transcaucasia, Iran, Turkmenistan and Afghanistan to Pakistan, Kazakhstan, and Xinjiang in western China (Pavlinov et al., 1990; Musser \& Carleton, 2005).

|  | Transcaucasia |  |  |  | Syria |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | males |  | females |  | males |  | females |  |
|  | N | mean | N | mean | N | mean | N | mean |
| Head and body | 67 | 137.9 | 82 | 134.1 | 15 | 151.7 | 14 | 152.7 |
| Tail | 64 | 124.4 | 77 | 125.1 | 10 | 164.4 | 7 | 166.7 |
| Hind foot | 67 | 31.3 | 83 | 31.1 | 15 | 36.7 | 14 | 36.3 |
| Ear | 67 | 18.1 | 83 | 18.0 | 15 | 18.7 | 14 | 18.6 |
| Weight | 67 | 81.8 | 83 | 78.7 | 14 | 115.9 | 13 | 120.1 |
| Condylobasal length | 42 | 36.2 | 66 | 35.8 | 15 | 37.1 | 14 | 37.8 |
| Zygomatic breadth | 45 | 20.2 | 67 | 20.0 | 13 | 22.6 | 10 | 22.7 |
| Maxillary tooth-row | 61 | 5.1 | 78 | 5.2 | 15 | 6.0 | 14 | 6.3 |
| Bulla length | 43 | 12.6 | 70 | 12.7 | 15 | 16.0 | 14 | 16.1 |

Table 41. Means for external and cranial dimensions of Meriones libycus from Transcaucasia (Ejgelis, 1980) and from Damascus, Syria (Mamkhair et al., 2007) separately for sexes.

The first report for Turkey is from Harran (Misonne, 1957) and has not been confirmed in recent surveys by Yiğit et al. (1997c, 2003, 2006c). In any case, the nearest certain records of M. libycus southward of Harran are not very far from the TurkishSyrian border (Harrison \& Bates, 1991). Next report for Turkey is from near Belen in Hatay, from where Obuch (1994) identified four specimens of $M$. libycus from Strix aluco pellets. This record is less reliable than the one by Misonne (1957) for two reasons. First, M. libycus is absent from the coastal belt of the eastern Mediterranean and is missing also in Israel (Mendelssohn \& Yom-Tov, 1999) and Lebanon (Lewis et al., 1967; Musser \& Carleton, 2005). Second, Obuch (1994) did not recognize in the Belen sample a single $M$. tristrami, which does, however, occur in the region. In any case, the presence of $M$. libycus in Turkey needs further attention and indisputable evidence of confirmation

Although Libyan jird occupies eastern Transcaucasia, it cannot be expected in eastern Anatolia. The Transcaucasian range is nearly entirely along the River Kura (Šidlovskij, 1976) and all the records in

Georgia are on its eastern bank and further eastward (Bukhnikashvili, 2004).

Palaeontology. Reported from the Middle Pleistocene on the Apšeron Peninsula in eastern Azerbaijan (Vereščagin, 1959).

## Наbitat

The Libyan jird is well adapted to an arid environment. It survived in captivity for one month at a constantly high ambient temperature of $32^{\circ} \mathrm{C}$ and low relative humidity ( $50 \%$ ), and tolerated body mass loss of up to 10 \% due to desiccation (Petter, 1961).

Preferred habitats are low-lying areas while steep mountain slopes and rocky regions are avoided. The Libyan jird inhabits vegetated arid landscape (steppes, semi-deserts and deserts) on clay, loess, gravel or sandy substrate; hard soil is the most suitable. Preferred are dry, exposed places, although mesic spots are inhabited in deserts (Osborn \& Helmy, 1980; Pavlinov et al., 1990). In Syria, semi-arid places covered with dense vegetation (especially glassworth Anabasis syriaca) are preferred (Mamkhair et al., 2007). It is a psammophile in Jordan (Scott \&


Figure 198. Distribution of Meriones libycus in Turkey and adjacent regions. Dubious report is shown by a diamond.
Records: 1 - Topboğazı Geçidi, Belen, Hatay; 2 - Harran, Şanlı Urfa. Corresponding references: Obuch (1994):

1. Misonne (1957): 2.

Dunstone, 2000). Slopes provide suitable habitats because water runoff allows a greater amount of vegetation than the surrounding land (Atallah, 1978). Characteristic vegetation is of medium-to-high density, of low shade, in one or two strata, clumped in distribution and of low to high homogeneity (Hassinger, 1973). Barren ground is rarely utilized but Libyan jirds do not avoid salty sand (Osborn \& Helmy, 1980). This jird has successfully adapted to cultivated landscape (fields and gardens). Misonne (1957) captured specimens in fields around Harran. Mamkhair et al. (2007) found the Libyan jird to be quite common along the highways where large quantities of water accumulate after the rainfall which stimulates fresh vegetation.

Altitude. From the Mediterranean coast in Egypt (Osborn \& Helmy, 1980) up to $2,300 \mathrm{~m}$ a.s.l. in the Tjan Shan Mts. (Pavlinov et al., 1990). Elevation of the record near Belen is $1,000 \mathrm{~m}$ a.s.l. (Obuch, 1994).

Associates in Transcaucasia are Meriones vinogradovi, M. tristrami, Microtus arvalis/levis, Allactaga elater and A. williamsi. The Libyan jird was the most abundant Meriones species in eastern Transcaucasia; the ratio is approximately 17 M . libycus : 7 M. tristrami : 1 M. vinogradovi (Ejgelis, 1980).

In the Eastern Mediterranean region, the Libyan jird shares its habitat with at least two of the following gerbils: Meriones crassus, Dipodillus dasyurus, Gerbillus henleyi, G. nanus and Psammomys obesus (Atallah, 1978; Amr et al., 2004). In Pakistan, the Libyan jird was collected along with Cricetulus migratorius, Rhombomys opimus and Gerbillus cheesmani (Roberts, 1997). In colonies of the great gerbil (Rhombomys opimus) and inhabited also by the Libyan jird, the ratio is 1 M . libycus to 3 . opimus (Lay, 1967). In the southeastern corner of the Mediterranean realm, the Libyan jird rarely co-occurs with Shaw’s jird (M. shawi); M. shawi occurs near the sea while M. libycus is found more inland (Osborn \& Helmy, 1980; Qumsiyeh, 1996).

Density. Common species throughout its wide range. In the steppes and semi-deserts of Afghanistan, Hassinger (1973) captured Libyan jirds in every locality sampled below $2,000 \mathrm{~m}$ a.s.l. and Amr (2000) reported it to be common all over the Syrian Desert. Densities vary from low ( $1-10$ per ha) to high (12-52 per ha) and can reach even higher values in


Figure 199. Variation in population density (number of individuals per ha) of Meriones libycus between 1954 and 1970 in two regions of eastern Transcaucasia. Modified from Ejgelis (1980).
years of pronounced population peaks (e.g. 319 per ha in Transcaucasia; Pavlinov et al., 1990). The amplitude of population oscillations is about 100-fold in eastern Transcaucasia, from 0.2 per ha to 27 per ha (Ejgelis, 1980). Between 1956 and 1970, one clear peak occurred in Transcaucasia (in 1964) but not all regions showed the outbreak (Fig. 199).

## Biology

Ejgelis (1980) examined various aspects of biology in eastern Transcaucasia on an incredible sample of 300,000 specimens.

Activity. Active at every hour during day or night (Harrison, 1956a; Hassinger 1973; Atallah, 1978; Mamkhair et al., 2007). In Algeria, activity is mainly nocturnal in summer, both diurnal and nocturnal in colder periods, and strictly diurnal in winter when the animals were seen in the morning and in late afternoon, but not around midday (Pavlinov et al., 1990). During the coldest parts of the winter, Libyan jirds very seldom emerge above ground, relying on caches instead (Roberts, 1997).

When disturbed, jirds utter a warning note resembling a ticking sound (Harrison \& Bates, 1991), simultaneously hitting the ground with hind feet (Mamkhair et al., 2007). Animals can be frequently observed standing on hind feet in front of a burrow (Mamkhair et al., 2007; Fig. 201). When running fast, the reddish tail is held erect at an angle of ninety degrees to the body (Harrison, 1956a).

Diameter of activity ( $100-240 \mathrm{~m}$ ) is density de-


Figure 200. Burrow system of Meriones libycus in
Transcaucasia. Entrances are shown by circles; C - cache; $\mathbf{N}$ - reproductive nest. Modified from Ejgelis (1980).
pendent and is larger at low densities (Pavlinov et al., 1990). Roberts (1997) reported from Pakistan average home range diameters of 44.9 m in males and 39.9 m in females. In autumn, jirds move up to 100-150 m from their burrows (Gromov \& Erbajeva, 1995). The Libyan jird is social (Mamkhair et al., 2007) and several adults of both sexes can share the burrow system (Pavlinov et al., 1990); Roberts (1997) described it as a gregarious animal.

Burrows vary in complexity from simple shelters to an extensive system of tunnels. Shelter tunnels have 1-6 entrances, are up to $1-2 \mathrm{~m}$ long, $20-$ 60 cm deep and do not expand into chambers. Winter dens are particularly elaborate, with several tens of entrances, extensive passages ( $>20 \mathrm{~m}$ ) and have up to 8 caches about 35-40 cm deep. Nest chambers are deeper than caches (85-150 cm; Pavlinov et al., 1990) and bedded with finely shredded vegetable fibres (Harrison \& Bates, 1991). Different types of burrows are normally located close to one another and shelter as many as several tens of family group members. Central burrow system is frequently in a hummock, up to 3 m in diameter, surrounded by storage departments and summer nests which are 10-15 m away from the main winter nest (Pavlinov et al., 1990). Burrows are mainly beneath clumps of perennial bushes or under the cover of coarse grasses and annual herbs (Harrison \& Bates, 1991; Mamkhair et al., 2007). The entrances are marked on the outside by a pile of excavated soil and dry plants (Atallah, 1978), or are occasionally hidden under piles of dried date palm fronds or olive branches (Osborn \&

Helmy, 1980). Entrances to burrows are not sealed (Roberts, 1997).

The Libyan jird utilizes also burrows of the great gerbil (Rhombomys opimus), sand rats (Psammomys sp.) and ground squirrels. In Turkmenistan, at high population densities of the Libyan jird, up to 80-90 \% of the yellow ground squirrel (Spermophilus fulvus) burrows are occupied by jirds but only after ground squirrels enter hibernation (Pavlinov et al., 1990). In the Eastern Mediterranean region, small gerbils (Gerbillus spp.) often construct their burrow as an offshoot from the burrows of Libyan jirds, both utilizing the same entrances (Atallah, 1978). In Pakistan, the marbled polecat (Vormela peregusna) is often found living inside burrows constructed by $M$. libycus (Roberts, 1997).

Reproduction goes all year-round in the south, but is absent during the winter further north (reproducing period from February-March to November). Breeding season lasts 8-12 months in Transcaucasia, from January-March to October-December, depending on the year (Ejgelis, 1980). Nearly all adult females are pregnant (87-99 \%) at the beginning of the breeding season; the proportion drops afterwards to 0-76 \% (Pavlinov et al., 1990). Similarly, the mean litter size declines from the beginning of the breeding season in early spring (mean litter $=6.0-8.3$ ) towards the summer and autumn (mean litter $=3.3-5.5$; Pavlinov et al., 1990). Number of embryos per female is between 2 and 13; mean is higher in the north (56) than in the south (3-4; Pavlinov et al., 1990). In Transcaucasia, the average number of embryos varies between 5.6 and 5.8 among regions and from 3.7 to 6.6 between months (Ejgelis, 1980).

Females normally deliver a single litter in their first year of life and three litters during the following years (Pavlinov et al., 1990). Sexual maturity is reached at three months (Šidlovskij, 1976); males are sexually adult when they reach a body mass of 80 g (Roberts, 1997). Sex ratio fluctuates in Transcaucasia: proportion of males is 38.9-63.5 \% and of females 36.5-60.1 \% (Ejgelis, 1980). In some regions of Transcaucasia, the sex ratio was constantly male biased (56.5-58.7 \%), while in others females dominated over males at all times (53.8-56.0\%; Ejgelis, 1980).

The Libyan jird can survive in nature over four winters (Klevezal \& Povališina, 1970).


Figure 201. Libyan jirds Meriones libycus at entrances to their burrows in Syria. Photo: A. Shehab.

Food eaten by the Libyan jird includes seeds, green plant matter and insects (beetles and orthopterans). Up to 41-44 \% of a diet in Turkmenistan consists of seeds and as many as one hundred plant species are consumed (Pavlinov et al., 1990). Hallophytes are consumed because of their high water content (Pavlinov et al., 1990). Anabasis syriaca is the main food in Syria (Mamkhair et al., 2007). Citrullus colocynthis, a common desert annual plant, is preferred in northern Saudi Arabia, but almost every species of desert shrub within the reach of the Libyan jird is consumed (Atallah, 1978). In the Near East, food varies seasonally. Green matter, rhizomes and bulbs predominate in spring and early summer while seeds are the main diet afterwards, particularly in autumn. Roberts (1997) recorded the following plants consumed in Pakistan: seeds of Chrysopogon spp., young shoots of Bromus spp., leaves of Sephora mol-
lis and Lycium barbarum, and bulbs of Allium, Scilla, and Tulipa species. Food is stored in extensive underground caches (up to $150 \times 80 \times 30 \mathrm{~cm}$ ) which contain $12-15 \mathrm{~kg}$; grain constitutes a major part of stored food. In cereal fields, up to 30 kg of grain can be stored in a single cache (Pavlinov et al., 1990). In Central Asia, the Libyan jird is able to destroy crops down to the level of 4-17 kg of grain per ha left for harvest and is hence a pest to agriculture. Up to 20 \% of vegetation is occasionally removed in pastures (Gromov \& Erbajeva, 1995).

Predation. Recorded in owl pellets in Iraq (Nadachowski et al., 1990). The Libyian jird is the principal prey of the marbled polecat (Vormela pregusna) and is possibly also preyed upon by the booted eagle (Hieraaetus pennatus) and the long-legged buzzard (Buteo rufinus; Roberts, 1997). In Syria, it was identified in barn owl (Tyto alba) pellets, but not in the
diet of other owls. The diaurnal activity of the Libyan jird presumably reduces the opportunity for this species to be preyed upon by nocturnal owls (Mamkhair et al., 2007).

## Dahl's jird - Meriones dahli

Meriones meridianus dahli Shidlovsky, 1962. Type loc.: foothills of Vardanis (Saraibulak) Ridge, Sadarak steppe, Armenia.

## Taxonomy

Originally described as a subspecies of M. meridianus (Pallas, 1773) and nearly uniformly reported as such until very recently. Dahl's jird is geographically isolated from the range of M. meridianus (Corbet, 1978). As shown by Dyatlov \& Avanyan (1987) these two jirds do not hybridise in captivity and thus behave as distinct biological species. Pavlinov et al. (1990) therefore separated M. dahli from the scope of M. meridianus, a step followed also by Musser \& Carleton (2005). Dahl’s jird differs from $M$. meridianus in dark grey dorsal colour (sandy brown with yellowish or rusty shades in M. meridianus); the latter also tends towards a more expanded posterior portion of mastoids and a larger posterior palatal foramen.

The Turkish population of $M$. dahli was mainly reported as M. meridianus (Demirsoy, 1996; Yiğit et al., 1997c, 1998b; Özkurt et al., 2001; Kryštufek \& Vohralík, 2001). Kurtonur et al. (1996) probably first identified Turkish material as a subspecies dahli, while Yiğit et al. (2006c) applied dahli as a species name.

## Description

External characters. The smallest jird in Turkey. Tail massive, on average as long as head and body (84.8-118.7 \%; mean = 100.2 \%), densely haired throughout, with a terminal pencil of hairs up to 20 mm long. Ears moderately long, whiskers long (up to 55 mm ). Fore feet small, palms naked, with four fingers; claws are 3.3-3.5 mm long. Hind feet are much longer, with densely haired soles; five toes bear amber claws (length 3.1-4.2 mm). Pelage is dense and silky, $9-10 \mathrm{~mm}$ long on shoulders, 14 mm on back, shorter ( 8 mm ) on belly. Mature males have a mid-
ventral gland, about 18 mm long and 2.5 mm wide.
Colour. Dorsal side grey with sandy shades, flanks sandy grey, belly pure white. Demarcation line is distinct. Some specimens show narrow buff stripe along flanks. Dorsal hairs grey and ventral hairs white to bases. Head dark grey, eyes encircled by indistinct whitish ring. Lips are whitish, cheeks grey, and shoulders of same colour as flanks. Ears are pale buff grey, with no contrasting post-auricular tuft. Tail


Figure 202. Skin of Meriones dahli in dorsal and ventral view. Based on a female from the Araks River valley, Armenia (ZMMU). Photo: C. Mlinar.


Figure 203. Skull and mandible of Meriones dahli. Based on an adult female from the Arkas River valley, Armenia (ZMMU). Scale bar $=5 \mathrm{~mm}$.
is rusty, darker above than below although not distinctly bi-coloured. It is interspersed by black hairs which are absent on the ventral side. Black terminal brush was present in all Armenian specimens we examined; Yiğit et al. (1998b) reported a specimen from Turkey with a white tail tip.

Nipples. Females have eight nipples.
Penis. Baculum, as figured by Yiğit et al. (1997c), is characterised by extensively expanded, pentagonal basal shaft (Fig. 165e). Proximal baculum is 3.9-4.1 mm long (Yiğit et al., 1998b). Note that measurements reported by Yiğit et al. (1998b) do not match scale to drawings of bacula in Yiğit et al. (1997c).

Skull deeper than in M. crassus, its height across bullae slightly less than one-half of condylobasal length (42.9-47.0 \%; mean $=44.6$ \%). Rostrum is relatively short while the brain-case is expanded. Nasals strongly project forwards, but hardly reach orbital level posteriorly. Masseteric plate curved round in front; anterior root of zygoma heavy. Lacrimals are comparably small. Interorbital region broad, not much constricted; supraorbital ridges well developed, expanding backwards towards the occipital region. Zygomatic arches diverge backwards. Frontoparietal suture is nearly straight transversely; inter-
parietal is of modest size. Diastema is long; incisive foramens relatively wide, reaching level of molars. Posterior palatal foramens short but wide, placed at the contact of $1^{\text {st }}$ and $2^{\text {nd }}$ molars. Posterior margin of hard palate behind $3^{\text {rd }}$ molar but not shifted as backwards as in M. tristrami. Pterygoids are nearly parallel. Bullae much inflated, but less so than in M. crassus. Enlarged mastoid portion clearly seen in dorsal view, but does not expand posteriorly to occipitals. The rim of bony auditory meatus is grossly swollen anteriorly and in close apposition to the posterior root of zygoma. Supramental triangle is closed posteriorly. Skull is slightly broader across bullae (59.4-61.9 \% of condylobasal length; mean $=60.6$ \%) than across zygomatic arches (57.3-61.6 \%; mean = 59.0 \%).

Mandibular body deep, coronoid process leaned against articular process. Alveolar process of modest size.

Teeth. Upper incisors opistodont, grooved. Enamel is dark orange, rarely yellow orange on upper incisors, paler on lower ones. Molar pattern shows no peculiarities in comparison with other jirds (Fig. 204). Number of roots is 3, 2, 1 in maxilla, 2, 2, 1 in the mandible (Yiğit et al., 1998b).


Figure 204. Upper (a) and lower molars (b) of Meriones dahli (same specimen as in Fig. 203). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.

Dimensions are given in Table 42. In a sample from Armenia, males are significantly larger than females (Table 43).

Chromosomes. Diploid number in Turkish population is $2 \mathrm{~N}=50$ and fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=74$. The karyotype consists of 28 bi-armed and 22 acrocentric elements. Both heterosomes are submetacentric; the X chromosome is larger but difference in size is not excessive (Yiğit et al., 1998b).

## Variation

Dahl's jird is considered to be a monotypic species. Turkish animals are on average bigger and range is shifted towards higher values (Table 42). E.g., a body mass over 60 g is rare in the Armenian population (five animals of 51 examined; ZMMU collection).

## Distribution

Dahl's jird populates a small range in Armenia and adjacent Turkey, and also possibly occurs in Iran. In Armenia, it is confined to sandy lowlands along the Araks River to the south of Erevan (Pavlinov et al., 1990) and in Turkey to a sandy belt that extends to the north of Mt. Ararat. It is known in Turkey only from Aralık, İğdır (Özkurt et al., 2001).

Palaeontology. Fossil history is not known (Vereščagin, 1959).

## Habitat

Dahl's jird depends entirely on a sandy substrate throughout its range; it is frequently found in isolated patches of light sands with intrusion of small stones (Pavlinov et al., 1990). The only habitat populated in Turkey is a dense thickset of Equisetum ramossisimum and Atrophaxis billarddieri on a sandy substrate (Yiğit et al., 1998b, 2006c; Özkurt et al. 2001). Ejgelis (1980) reported bushy vegetation of tamarisk and other shrubs to be scarce in Dahl's jird habitat in Transcaucasia.

Altitude. Largely restricted to the lowlands along the Araks River. Turkish populations live at about 900 m a.s.l. (Özkurt et al. 2001).

Associates. The only rodents found in Turkey syntopically with M. dahli are Allactaga williamsi

|  | Turkey |  |  |  |  | Armenia |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\mathrm{max}$ |
| Head and body | 18 | 123.0 | $110-135$ | 51 | 117.4 | $102-132$ |
| Tail | 18 | 123.5 | $116-130$ | 50 | 117.2 | $107-134$ |
| Hind foot | 18 | 33.4 | $31.0-36.0$ | 51 | 28.3 | $25.0-30.0$ |
| Ear | 18 | 15.1 | $14.0-16.0$ | 51 | 14.0 | $13.0-16.0$ |
| Weight | 18 | 63.5 | $54-80$ | 51 | 49.9 | $37-70$ |
| Condylobasal length | 17 | 31.3 | $30.4-32.7$ | 42 | 29.9 | $28.3-31.3$ |
| Zygomatic breadth | 18 | 18.7 | $18.2-19.4$ | 33 | 17.6 | $16.5-18.7$ |
| Maxillary tooth-row | 18 | 5.3 | $4.8-5.6$ | 40 | 5.0 | $4.7-5.5$ |
| Bulla length | 18 | 13.1 | $11.9-13.9$ | 42 | 11.3 | $10.4-12.5$ |

Table 42. External and cranial dimensions of Meriones dahli from Turkey (Yiğit et al., 1997c) and Armenia (ZMMU), respectively.

|  | males |  |  |  | females |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |  |
| Head and body | 26 | 121.8 | $112-132$ | 25 | 112.7 | $102-126$ |  |
| Tail | 25 | 117.1 | $107-134$ | 25 | 117.4 | $109-127$ |  |
| Hind foot | 26 | 28.8 | $25.0-30.0$ | 25 | 27.8 | $26.0-29.5$ |  |
| Ear | 26 | 14.2 | $13.0-16.0$ | 25 | 13.7 | $13.0-15.0$ |  |
| Weight | 26 | 54.8 | $44-64$ | 25 | 44.7 | $37-70$ |  |

Table 43. External dimensions of Meriones dahli from Armenia according to sex. Specimens in ZMMU.
and Cricetulus migratorius (Özkurt et al., 2001). In a habitat mosaic M. dahli is restricted to a sandy substrate while a further two jirds ( $M$. vinogradovi and M. tristrami) occupy patches of soil (Pavlinov et al., 1990; Özkurt et al., 2001).

Density. Locally common. Trapping success varies between 14-24 individuals per 100 trap nights in autumn to 23-31 per 100 trap nights in spring (Ejgelis, 1980). Densities of 20-90 per ha during 19581969 declined to $2-5$ per ha in 1980s due to habitat degradation (Anonymus, 1987).

## Biology

Activity. Özkurt et al. (2001) invariably trapped Dahl's jirds during the night; captive specimens were most active at dusk and late in the evening, never
during daytime. Contrary to this, Pavlinov et al. (1990) reported nocturnal activity in spring and summer, while the animals are active all day long in autumn. Although Dahl's jirds possess individual burrows, animals use tunnels of their neighbours as well. Therefore home ranges overlap widely (Pavlinov et al., 1990), and the animals live in colonies in Turkey (Özkurt et al., 2001). Diameter of activity during three nights was up to 110 m , but mainly $50-80 \mathrm{~m}$ (Pavlinov et al., 1990).

Burrows are mainly simple, with 1-3 entrances; overall length of tunnels is $3-4 \mathrm{~m}$. Nest chamber is up to 50 cm below surface in a simple burrow, up to 200 cm in a more complex winter burrow (Ejgelis, 1980; Pavlinov et al., 1990). Neighbouring burrows are 15-20 m apart in Turkey (Özkurt et al., 2001).


Figure 205. Distribution of Meriones dahli. Record: 1. - Aralık, Ĭğdır, ca 900 m a.s.l. (Özkurt et. al., 2001).

Reproduction. Reproductive period lasts from April to August, rarely into September (Ejgelis, 1980) or from March to November (Pavlinov et al., 1990); in Turkey Özkurt et al. (2001) collected reproductive animals from late June to late October. Proportion of pregnant females varies between 10 \% (September) and 80 \% (July; Ejgelis, 1980). Gestation period is 24-27 days (Özkurt et al., 2001) and females have up to 2-3 litters annually. Captive females were pregnant when three months old and 21.5 g heavy (Ö zkurt et al., 2001). Litter size is $2-7$ (mean $=5.1$; Ejgelis, 1980). Six females collected in Turkey had 6 or 7 embryos (mean $=6.5$ ) and two captive females gave birth to five cubs each (Özkurt et al., 2001). Newborns weigh 2.45 g and are weaned at one month old and weigh on average 12.7 g (Özkurt et al., 2001). Breeds well in captivity (Anonymus, 1987).

FOod contains green vegetable matter and seeds; seeds are also occasionally found in underground storage (Pavlinov et al., 1990).

Predation. Preyed upon by various snakes, diurnal raptors and owls (particularly the eagle owl Bubo bubo), and carnivores (fox Vulpes vulpes and stone marten Martes foina; Anonymus, 1987).

Conservation. Habitats in Armenia are under the process of degradation through overgrazing and cutting bushes for firewood. A considerable decline in population densities was thus recorded and species is included into the Red Data Book of Armenia (Anonymus, 1987). Because of its small range, high habitat specificity and declining populations, Dahl's jird is also considered to be globally threatened and classified as "Endangered" (IUCN, 2008).

## Persian jird - Meriones persicus

Gerbillus persicus Blanford, 1875. Type loc.: Kohrud (= Quohrud), 72 miles north of Isfahan, Iran (Lay, 1967).

## Description

External characters. Large jird with tail generally longer than head and body. In a sample from Armenia, tail is on average 102.7 \% of head and body length (range $=80.0-128.0 \%$ ), and $62 \%$ of specimens had the ratio $>100 \%$. In three specimens from

Turkey tail length relative to head and body was 100.6, 103.3 and 115.8 \% (Yiğit \& Çolak, 1999). Ears are relatively large, margined with stiff hairs. Fore feet are evidently shorter than hind ones; soles and palms are bare (Fig. 166f). There are four subdigital pads on soles, followed by small posterior tu-


Figure 206. Skin of Meriones persicus in dorsal and ventral view. Based on a specimen from Pir Sohrab, province Baluchestan, Iran. Photo: C. Mlinar.


Figure 207. Persian jird Meriones persicus. Photo: J. Vogeltanz.
bercles. Front claws are long ( $3.5-3.9 \mathrm{~mm}$ ), those on hind toes measure $3.6-4.5 \mathrm{~mm}$. Pelage is dense and long ( 13 mm on shoulders, 17 mm on rump); belly hairs are shorter ( 10 mm ). Hairs are silky soft. Mystacial vibrissae are long ( $53-60 \mathrm{~mm}$ ). Tail is densely haired throughout with a terminal brush (up to 25-27 mm long).

Colour. Back side is buff to rusty, slightly grizzled and darker medially; hair bases are plumbeous; black tips give speckled appearance; hairs are grey at their base. Flanks are pale buff or rusty buff in darker specimens. Belly is pure white with hairs white throughout. Demarcation line is sharp, particularly so in darker animals. Cheek are pale buff, lips white; forehead of same colouration as back but duller. Clear white spot on the upper or postero-dorsal eye margin. Ears buff grey, stiff hairs on their margin white. Fore feet white, hind feet white dorsally; palm is dark brown pigmented; claws are amber white. Tail is distinctly bicoloured, dorsally of same colour as back and usually with black stripe; ventral side is greyish white to rusty. Blackish grey terminal tuft spreads well over the terminal one-third of the tail; brush less
extended on ventral side. Colour varies and specimens from arid regions tend to be darker.

NippLes. There are eight nipples (Harrison, 1972).
Penis. Glans penis is cylindrical. Baculum consists of proximal shaft and three cartilaginous processes. Dimensions for proximal baculum (length $\times$ width, mm ) in two specimens from Turkey were: 4.4 $\times 2.1$ and $4.4 \times 2.6$ (Yiğit \& Çolak, 1999). Proximal margin of basal expansion is rounded (Fig. 165f).

Skull is similar to that of M. tristrami but relatively narrower across zygomatic arches; zygomatic breadth relative to condylobasal length averages 56.6 \% (range = 51.7-60.1 \%). Zygomatic arches less expanded posteriorly, nearly parallel in some animals; posterior zygomatic root shifted more backward; braincase relatively shorter and rostrum proportionally longer. Nasals blunt at apex; posteriorly not reaching level of lacrimals. Braincase narrower than zygomatic arches, making up on average 55.2\% of condylobasal length (range $=52.6-57.8 \%$ ). Skull not very deep; height of braincase across bullae relative to condylobasal length on average $40.5 \%$ (range $=38.0-45.3 \%$ ). Anterior margin of masseteric plate


Figure 208. Skull and mandible of Meriones persicus from Tehran, Iran (ZFMK). Scale bar $=5 \mathrm{~mm}$.
straight and perpendicular; masseteric knob well developed. Anterior root of zygoma expanded in lateral view. In dorsal view the frontals expanded and parietals shifted posteriorly. Fronto-parietal suture forms a straight line. Interparietal is of modest size, ovate or nearly so. Supraorbital ridges do not expand much, hardly reaching parietals. Diastema is long; incisive foramens are ovate, not reaching level of molars. Posterior palatal foramens narrow. Pterygoids long, diverge posteriorly; interpterygoid fossa triangular. Bullae not greatly inflated; length of bullae on
average less than one-third of condylobasal length (30.6\%). Not much of mastoid portion seen in dorsal view and the rim of bony auditory meatus does not reach squamosal root of zygoma. Supramental triangle ovate or compressed anteriorly, comparatively smaller than in M. tristrami. Mandible shows no peculiarities in comparison to M. tristrami. Coronoid process is relatively heavy, angular process slender and alveolar process fairly small.

Teeth show no peculiarities in comparison to $M$. tristrami (Fig. 209). Incisors slightly more robust,

|  | Turkey |  |  | Armenia, Iran |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | $\operatorname{mean}$ | $\min -\max$ |
| Head and body | 3 | 159.0 | $149-164$ | 51 | 162.8 | $132-185$ |
| Tail | 3 | 170.0 | $154-190$ | 50 | 167.0 | $136-186$ |
| Hind foot | 3 | 43.3 | $41.0-45.0$ | 51 | 38.3 | $30.0-42.0$ |
| Ear | 3 | 25.6 | $25.0-27.0$ | 51 | 23.2 | $19.4-26.0$ |
| Weight | 3 | 107.7 | $90-122$ | 34 | 120.5 | $75-172$ |
| Condylobasal length | 4 | 39.5 | $37.4-40.8$ | 50 | 37.6 | $34.4-41.4$ |
| Zygomatic breadth | 4 | 22.5 | $21.7-23.0$ | 39 | 21.2 | $19.3-23.5$ |
| Maxillary tooth-row | 4 | 6.5 | $6.1-6.8$ | 49 | 6.3 | $5.9-6.9$ |
| Bulla length | 3 | 12.7 | $11.8-13.6$ | 46 | 11.5 | $10.0-14.4$ |

Table 44. External and cranial dimensions of Meriones persicus from Turkey (Neuhäuser, 1936; Yiğit \& Çolak, 1999), Armenia and north Iran (ZMMU, BMNH, ZFMK).


Figure 209. Upper (upper row) and lower molars (lower row) of Meriones persicus from Armenia (ZMMU). Agedependent molar abrasion is in increase from left (a - the youngest) to right (c - the oldest). Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
with yellow or orange enamel on front surface. First upper molar with three roots; $2^{\text {nd }}$ molar with two roots and $3^{\text {rd }}$ molar single rooted.

Dimensions are given in Table 44. Ejgelis (1980) found no secondary sexual dimorphism in cranial dimensions, however, males were bigger in external dimensions and body mass. Animals over 150 g are rare in a sample from Armenia (17.6\%).

Chromosomes. Diploid number in a population from Turkey is $2 \mathrm{~N}=42$ and the fundamental number
of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=74$. Autosomal set consists of 17 bi-armed pairs; the remaining three pairs are acrocentric. Both heterosomes are medium sized and bi-armed; the Y chromosome is not much smaller than the X chromosome (Yiğit \& Çolak, 1999).

## Variation

Geographic variation is not heavily pronounced and authors disagree on the number of geographic races; Pavlinov et al. (1990) recognized three subspecies while Gromov \& Erbajeva (1995) accepted five subspecies as being valid. Animals from Turkmenistan are pale and with long auditory bullae, those from Afghanistan are dark, and the tail is less hairy in material from Transcaucasia (Pavlinov et al. (1990). Ellerman (1948) ascribed material from southwestern Asia to the nominate race, while Neuhäuser (1936) applied subspecific name rossicus for a specimen from Oltu. Meriones rossicus Heptner, 1931, was described as an independent species (Type loc.: Arzni, 20 km north of Erevan, Armenia) but is now regarded as a subspecific name for Transcaucasian populations (Ellerman \& Morrison-Scott, 1951; Šidlovskij, 1976). Ejgelis (1980) found significant differences in size between populations from Transcaucasia.

## Distribution

Southern Transcaucasia, eastern Turkey, northeastern Iraq (Kurdistan; Harrison \& Bates, 1991), Iran, Turkmenistan, Afghanistan and Pakistan west of the River Indus (Musser \& Carleton, 2005). The Persian jird is widespread in Iran (Lay, 1967), Afghanistan (Hassinger, 1973) and in the mountains of Baluchistan in Pakistan (Roberts, 1997). Transcaucasian range is small, restricted to the middle course of the River Araks in southern Azerbaijan, Nakhichevan, and southern Armenia (Šidlovskij, 1976).

Turkey is on the very northwestern margin of the distribution range. Only four localities are known from easternmost Anatolia (Fig. 210). The Persian jird was first recorded for Turkey by Heptner (1934; as $M$. rossicus). One of his three localities (Oltu) was subsequently confirmed by Yiğit \& Çolak (1999). Yiğit et al. (2006c) extended range to Yüksekova, Hakkâri.

Palaeontology. Storch (1980) identified Late Glacial jirds from Atli Tepeh Cave (Gorgan Province,


Figure 210. Distribution of Meriones persicus in Turkey and adjacent regions. Records: 1a - Olty (= Oltu), Kars; $\mathbf{1 b}$ - Sardanes (ca 12 km south-east of Oltu), Kars; $\mathbf{2}$ - Kulpy (= Tuzluca), İğdır; $\mathbf{3}$ - Yüksekova, Hakkâri. Corresponding references: Heptner (1934): 1a, 1b., 2. Yiğit et al. (2006c): 3.
northeastern Iran) as $M$. cf. persicus. $\mathrm{C}^{14}$ dating suggested their age was approximately $11,400-12,400$ years BP. Jirds of the same taxonomic allocation were reported also from $14,400 \pm 760$ years-old material of Palegawra Cave in northeastern Iraq and from the Zarzian and Baradostian layers from Iranian Kurdestan (Turnbull, 1975). See also comments under M. tristrami. Vereščagin (1959) reported a Holocen record (estimated age of 3,000-4,000 years) from approximately 100 km southeast of Erevan (Armenia).

## Habitat

Main habitats are barren rocky hill and mountain sides in the mountainous landscape and on dry foothills. Characteristic vegetation is of low density, low shade, in one stratum, clumped in distribution and of low-to-high homogeneity (Hassinger, 1973). As a rock-dwelling (petrophile) rodent, the Persian jird occupy screes, accumulations of rocky debris and rubble, rocky outcrops, chunks of conglomerate, dry watercourse habitats and stone walls in orchards and vineyards. The animal was reported to utilize caves in Iran (Lay, 1967). The Persian jird does not enter
cultivated areas but aggregates around them on hilly slopes. Lay (1967) reported an extraordinary case from Iran of a colony existing near a true deciduous forest and even ranging into it. In Pakistan, the Persian jird is mainly replaced at low altitudes and in broad valleys by Meriones libycus (Roberts, 1997) although Pavlinov et al. (1990) reported cases of its spreading into plains up to 100 km away from the nearest foothills in southern Turkmenistan. Because of patchy distribution of rocky habitats, populations of the Perisan jird are frequently isolated (Pavlinov et al., 1990).

The Persian jird's habitat around Oltu was described as a mountain steppe. Yiğit \& Çolak (1999) also noted that the animal occured on hill slopes around grain fields but did not establish itself within cultivations.

Altitude ranges from close to the sea coast up to the mountains. Although largely associated with mountainous landscapes, the Persian jird does not go very high into the mountains in Transcaucasia. It was mainly found between 500 and $1,500 \mathrm{~m}$ a.s.l., while records above $1,800-2,000 \mathrm{~m}$ of elevation are


Figure 211. Habitat of Meriones persicus at Pir Sohrab, Baluchestan, Iran. Photo: V. Vohralík.
rare (Ejgelis, 1980). Captures are up to $1,830 \mathrm{~m}$ a.s.l. ( $6,000 \mathrm{ft}$ ) in Kurdistan, Iraq (Harrison, 1956b; Hatt, 1959), 2,130 m (7,000 ft) in Iran (Lay, 1967), $2,500 \mathrm{~m}$ in Afghanistan (Hassinger, 1973) and 3,250 m in Pakistan (Roberts, 1997).

Associates. The Persian jird is sympatric in Transcaucasia with Meriones tristrami, M. dahli and M. vinogradovi (Šidlovskij, 1976); sympatry of these jirds is postulated also for Turkey (Yiğit \& Çolak, 1999). The same habitat is shared by mouse-like hamsters (Calomyscus sp.) in Iran and Afghanistan and by Apodemus sp. in Iran (Niethammer, 1965; Lay, 1967).

Density. Densities in optimal habitats are between 1-6 and 10-15 individuals per ha; around fields there can be up to 15-20 animals per ha, rarely up to 30 per ha (Pavlinov et al., 1990). Density varies in Transcaucasia from 1.0-2.5 per ha to 2.5-6.0 per ha; highest densities recorded are 8.9 and 14 per ha, respectively (Ejgelis, 1980). Densities are lowest in spring ( 1.5 per ha) and highest in late summer-autumn (12.9 per ha) in Pakistan (Roberts, 1997). Population densities fluctuate over years; sharp peaks are typical of relatively high density populations while low density populations remain for several consecutive years at numbers close to zero (Ejgelis, 1980; Fig. 209).

## Biology

Activity. Largely nocturnal but opinions on diurnal activity differ. Pavlinov et al. (1990) reported Persian jirds to be active during the daytime at high population densities. In the opinion of Šidlovskij (1976) circadian activity varies seasonally, being


Figure 212. Variation in population density (number of specimens per ha) of Meriones persicus between 1957 and 1970 in two regions of east Transcaucasia. Modified from Ejgelis (1980).
nocturnal in summer and also diurnal during winter. The Persian jird undergoes short periods of torpidity during winter (Roberts, 1997).

Males mark and defend territories. Females have smaller homes ranges ( $80-600 \mathrm{~m}^{2}$ ) than males (Pavlinov et al., 1990). Mean greatest distance travelled by a single animal in Pakistan was 35.4 m in females and 61.2 m in males (Roberts, 1997).

Burrows. Although Persian jirds frequently shelter among rocks, they will dig their own burrows if substrate permits. Digging into soft soil on slopes is also reported from Turkey (Yiğit \& Çolak, 1999). An animal usually has the main burrow and several shelters dug around the periphery; entrances are $20-50 \mathrm{~m}$ apart. Summer burrows are simple, mainly without a nest. Winter burrows are more complex and elaborate, usually with 2-4 (up to 8-10) entrances, $2-3$ storage chambers ( $20 \times 40 \times 30 \mathrm{~cm}$ ) and a nest chamber (usually lined with soft grasses; Roberts, 1997) which is $30-110 \mathrm{~cm}$ below the surface; total length of tunnels is up to 20 m (Petter, 1961; Pavlinov et al., 1990).

Burrows of Persian jirds are utilized by mouselike hamsters (Calomyscus sp.) in Afghanistan (Niethammer, 1965) and by scorpions, tenebrionid beetles, toads, lizards and snakes in Iran (Lay, 1967).

Reproduction. The Persian jird is mainly a seasonal breeder. Reproduction starts in March in Turkmenistan (Pavlinov et al., 1990) and Roberts (1997) reported the first litters from Pakistan
in April. In Transcaucasia, the peak in reproduction (highest proportion of gravid females) is in March (in warm regions), in March-April (in semideserts) and from May to July (in high elevation steppe; Ejgelis, 1980). Ejgelis (1980) found up to $31 \%$ of females per sample to be pregnant (altogether 21,400 specimens studied). Gestation period is about 28 days (Roberts, 1997). Number of embryos is $2-11$, more in the north (4-11 in Turkmenistan) than in Azerbaijan (2-8); litters mainly contain 4-5 pups (Pavlinov et al., 1990). Mean litter size in Pakistan (based on embryos and placental scars) was 3.5 (Robert, 1997). Juveniles wean at two months old and participate in reproduction only the following season. Females have 1-3 litters annually and population increase from spring to autumn is at most 3.5fold (Pavlinov et al., 1990).

Food. Vegetarian; diet mainly consists of seeds; green plant matter is mainly consumed in spring (Pavlinov et al., 1990). Roberts (1997) claimed that Persian jirds are omnivorous, subsisting on grass roots, stem, seeds, fallen berries and insects. Grains and seeds are cached in underground burrows for winter consumption. Such caches were reported to contain 8 litres of Onobrychis sp. seeds (Petter, 1961), Bromus danthoniae ears (Pavlinov et al., 1990), Bromus sp., Elymus sp., Hordeum sp.,

Festuca sp. and Medicago sp. (Lay, 1967).
Predation. In Pakistan, they are preyed upon by foxes (Vulpes vulpes griffithi), stone martens (Martes foina) and scop owls (Ottus brucei and O. scops; Roberts, 1997). Also found in owl pellets in Afghanistan (Niethammer, 1965).

## Genus: Dipodillus Lataste, 1881

Small to medium-sized gerbils of slender form, with a long tail and lengthened hind feet; plantar surface is hairless. Dipodillus was originally described as subgenus of Gerbillus Desmarest, 1804, and subsequently considered that way (e.g. Ellerman \& Morrison-Scott, 1951; Lay, 1975; Corbet, 1978; Harrison \& Bates 1991; Yiğit et al., 1997b; Mendelssohn \& Yom-Tov, 1999). Pavlinov et al. (1990) elevated Dipodillus to generic rank, a view adopted also by Musser \& Carleton (2005). Thirteen species, which are included into Dipodillus, occur in Africa to the north of Sahel, in Arabia and adjacent southwestern Asia (Pavlinov et al., 1990; Musser \& Carleton, 2005). The single species known from Turkey is of very marginal occurrence in the country and was reported for the first time fairly recently (Yiğit et al., 1997b).


Figure 213. Dipodil Dipodillus. Drawing: J. Hošek.

## Wagner's dipodil - Dipodillus dasyurus

Meriones dasyururs Wagner, 1842. Type loc.: Sinai.

## Taxonomy

Until very recently, Wagner’s dipodil was invariable reported as Gerbillus dasyurus, and was frequently allocated into a subgenus Hendecapleura Lataste, 1894 (e.g. Yiğit et al., 1997b). Musser \& Carleton (2005) synonymysed Hendecapleura with Gerbillus s. str. and allocated D. dasyurus into the subgenus Petteromys Pavlinov, 1982.

## Description

External characters. The smallest gerbil in Turkish fauna. Body form slender and graceful, head relatively large, eyes large, ears moderate. Tail longer than head and body (106.3-154.4 \%; mean $=125.7$ $\% ; 119.8-149.4 \%$; mean $=137.1 \%$ in material from Jordan; Abu Baker \& Amr, 2003a), densely haired throughout its length. Hairs are short at tail base, than getting longer and forming a distinct terminal brush. Front feet evidently shorter than lengthened hind feet. Plantar surface hairless, with five pads (the two proximal pads are the largest); of the six palmar tubercles the proximal two are larger. Number of fingers is four on front foot, five on hind foot; claws are
dark and relatively large. Mystacial vibrissae are long ( 38 mm ) and mainly white. Pelage is dense, silky and long ( 11 mm on mid-back).

Colour varies locally and geographically, therefore we based this account partly on Yiğit et al. (1997b) who described coloration in a sample from Turkey. Dorsal fur is pale yellowish-brown with fine agouti pattern, flanks are bright yellow, belly is white; demarcation along flanks is distinct. Dorsal hairs are slate grey on the proximal two-thirds of length; those on belly are pure white to base. Feet are white. The ear is buff-grey at base, grey towards the tip, and covered with short white hairs. Indistinct facial markings include white supraorbital and postorbital spots. The tail is bicoloured, greyish-brown above, paler below. Its terminal one-quarter is blackish brown on dorsal side, white to grey below.

Nipples. Four pairs of mammae (Amr, 2000).
Penis. The surface of the penis is covered with minute spines in small, circular pockets. The baculum is of long proximal stalk which is expanded basally, and of three separate cartilaginous digitigrate process (Yiğit et al., 1997b). Basal stalk is about 2.2 mm long (estimated from Fig. 3 in Yiğit et al., 1997b). A distal portion is of variable size (cf. Yiğit et al., 1997b, and Abu Baker \& Amr, 2003a).

SkuLL is narrow and moderately deep. Zygomatic


Figure 214. Wagner’s dipodil Dipodillus dasyurus. Photo: J. Vogeltanz.


Figure 215. Skull and mandible of Dipodillus dasyurus. Based on an adult male from As Salihiyah (between Al Mayadin and Abu Kamal), Syria (SMF). Scale bar $=5 \mathrm{~mm}$.
arches only slightly converge anteriorly; width across zygoma relative to condylobasal length is 55.6-60.9 \% (mean $=57.4$ \%). Long, narrow rostrum tapers towards its tip. Nasals are nearly parallel, long and reaching anterior level of orbit. Lacrimals are large and rectangular. Interorbital constriction exceeds width of rostrum; it is flat, margined with weak supratemporal ridges. Braincase is large, covered entirely by parietals and a triangular interparietal. Braincase breadth relative to condylobasal length accounts for slightly less than zygomatic width (50.857.5 \%; mean = 53.4 \%). Diastema is long; incisive foramens are long and narrow (longer than maxillary tooth-row). Second pair of palatal foramens is small, located at the level of $1^{\text {st }}$ molar. Pterygoids converge towards posterior hard palate, interpterygoid space is consequently triangular. Bullae are of moderate size, accounting for 31.0 \% of condylobasal skull length (range = 26.5-35.2 \%). Dorsal profile is slightly convex; occipital region is rounded. Nasals project far in front of incisors. Mandible is low; angular process is more powerful than the articular one; alveolar process is weak.

Teeth. Upper incisors are weak and narrow, opistodont and with a medially shifted longitudinal groove. Enamel is pale orange (upper incisors), yel-low-orange on lower ones. Molars are hypsodont, cuspidate in juveniles; enamel patter is essentially as in other gerbils, i.e. of transverse plates separated by inner and outer re-entrant angles (Fig. 216). Labial loops (salient angles) tend towards smaller size and lingual re-entrant angles are deeper. First upper molars are with three transverse loops, $2^{\text {nd }}$ ones by two loops, while the last molar is much reduced, being of circular shape with traces of bi-laminate pattern in younger animals. As with other gerbils, molar pattern strongly depends on tooth-wear. Number of alveoli: 4, 3, 1 (maxillary row); 2, 2, 1 (mandibular row; Yiğit et al., 1997b).

Dimensions are given in Table 45. Males are significantly smaller in head and body length ( $88.1 \pm 0.75$ mm in males $v .93 .8 \pm 0.65 \mathrm{~mm}$ in females), but are heavier ( $22.2 \pm 0.1 \mathrm{~g}$ in males $v .20 .9 \pm 0.1 \mathrm{~g}$ in females; Shenbrot et al., 1997). Osborn \& Helmy (1980) found sexes to be subequal in Egypt. Wagner's dipodils grow in Israel from summer to win-
ter, but not from winter to summer. Growth is less expressed in dry years; seasonal changes of body mass are also more evident in males than in females (Shenbrot et al., 1997). Body mass varies between years, and is lower in years following high winter precipitation and at high population densities (Shenbrot et al., 1997). On the basis of body mass, Shenbrot et al. (1997) distinguished three age groups: juveniles ( $<15 \mathrm{~g}$ ), subadults ( $16-18 \mathrm{~g}$ ) and adults ( $>21$ g ); animals with body mass $19-21 \mathrm{~g}$ were classified as subadults if they were sexually immature or inactive (Shenbrot et al., 1997).

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 46 | 91.4 | $82-109$ |
| Tail | 46 | 115.9 | $100-126$ |
| Hind foot | 46 | 24.8 | $23.3-27.0$ |
| Ear | 41 | 13.7 | $12.0-15.0$ |
| Weight | 46 | 21.2 | $13-31$ |
| Condylobasal length | 28 | 23.6 | $22.0-25.1$ |
| Zygomatic breadth | 35 | 13.9 | $13.2-14.8$ |
| Maxillary tooth-row | 33 | 4.2 | $3.9-4.5$ |
| Bulla length | 33 | 8.9 | $8.1-9.4$ |

Table 45. External and cranial dimensions of Dipodillus dasyurus from Turkey and Syria. Based on Yiğit et al. (1997b), Çolak et al. (1999) and specimens in SMF.

Chromosomes. Diploid number of chromosome in Turkish Wagner's dipodil is $2 \mathrm{~N}=60$; fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=76$. Four autosomal pairs are bi-armed, the remaining 25 pairs are acrocentric. The X chromosome is the largest metacentric, the Y chromosome is the smallest acrocentric (Yiğit et al., 1997b). Although the diploid number is stable (Pavlinov et al., 1990) fundamental number of chromosomal arms varies in Jordan $\left(\mathrm{NF}_{\mathrm{a}}=66,68\right.$, 70; Qumsiyeh et al., 1986).

## Variation

The colouration is variable and changes over short distance. Light greyish-yellow animals with brown tail tip occupy deserts and dark reddish-brown ones with black tail brush occur elsewhere (Mendelssohn \& Yom-Tov, 1999). The two colour morphs are figured in Ferguson (2002; Plate 47). Dark brown form is more common in the lava desert in Jordan (Abu Baker \& Amr, 2003a). Desert populations also have longer bullae (Mendelssohn \&


Figure 216. Upper (a) and lower molars (b) of Dipodillus dasyurus (same specimen as in Fig. 215). Scale bar $=1 \mathrm{~mm}$.

Yom-Tov, 1999). Turkish animals (condylobasal length: 22.0-25.1 mm; mean $=23.6 \mathrm{~mm} ; \mathrm{N}=33$; Yiğit et al., 1997b) seem to be smaller than their southern counterparts from Jordan (23.0-26.6; mean $=24.7 \mathrm{~mm} ; \mathrm{N}=21$; Abu Baker \& Amr, 2003a, and SMF specimens) and Yemen (25.1-26.6 mm; mean $=25.8 \mathrm{~mm}$; SMF). Note however, that statistics by Yiğit et al. (1997b) also possibly involves immature animals. Size in Wagner's dipodil associates negatively with annual precipitation and mean minimum January temperature in transect from Israel to Sinai (Yom-Tov \& Geffen, 2006).

## Distribution

Range covers Sinai, Arabia, and marginally the Eastern Desert in Egypt. Further north, the species is present in Israel, Lebanon, Jordan, Syria and Iraq. The Euphrates River is only exceptionally transgressed into Mesopotamia. Turkey, where the animal is known from two localities (Fig. 217), is on the northern range margin.

Palaeontology. Fossil Gerbillus (which might also involve Dipodillus) was reported already from


Figure 217. Distribution of Dipodillus dasyurus in Turkey and adjacent regions. Records: $\mathbf{1 - 1 0} \mathrm{km}$ east of Kilis; 2 Ceylanpınar, Şanlı Urfa. Corresponding referrence: Yiğit et al. (2003).
the Upper Pliocene beds on the Apšeron Peninsula in Transcaucasia (Vereščagin, 1959) and afterwards from various Pleistocene sites in Israel, Libya and Algeria (Turnbull, 1975). Wagner's dipodil is known from the Late Auchelian (about 250,000 years ago) of Israel (Tchernov, 1988, 1994).

## Habitat

Throughout its range, Wagner’s dipodil was reported from rocky steppes, salt flats, thickets of low thorny trees on edges of cultivated fields, bushes on the sea shores, moist, densely vegetated patches in arid landscape and limestone cliffs (Shenbrot et al., 1997). In Israel, the animal selects relatively soft soil mixed with stones (Shenbrot et al., 1997) and occupies rocky habitats, including sandstone hills (Zahavi \& Wahrman, 1957). Harrison \& Bates (1991) characterised the species as an inhabitant of rocky steppe desert and many authors (Zahavi \& Wahrman, 1957; Scott \& Dunstone, 2000; Abu Baker \& Amr, 2003b) described it as a petrophile or a rock dweller. In Jordan, rocky areas with low vegetation (Anabasis sp., Artemisia sp., Atriplex sp., Halogeton sp.) are preferred, but sandy soil is avoided
(Hatough-Bouran, 1990; Abu Baker \& Amr, 2003a). Specimens in Turkey were captured "...in rocky hills, with poor soil and vegetation" (Yiğit et al., 1997b). The following plants were reported from Turkish localities: Hordeum sp., Eryngium sp., Securigera sp., Peganum sp., and Agropyron sp. (Yiğit et al., 2003).

Shenbrot et al. (1997) found Wagner’s dipodils at various densities in six different habitat types of the Negev highlands of Israel. Preferred habitat was hilly landscape with deep loess and wide dry river beds (wadis) with vegetation of Anabasis articulate, Atriplex halimus, Artemisia herba-alba, Salsola schweinfurthii and Noaea mucronata. Next in order of preference were wadis with sandy gravel soil (with Retama raetam, Moricandia nitens, Tamarix nilotica and Artemisia monosperma) or with thin loess (with Anabasis articulate, Atriplex halimus and Artemisia herba-alba). Sand dunes were avoided, but specimens were occassionaly trapped there during high population densities in the preferred habitats.

Altitude of records ranges from 400 m below sea level (Dead Sea) up to 2,000 m in the mountains of Sinai (Petter, 1961).

Associates. The following rodents co-occur with Wagner's dipodil in Turkey: Mesocricetus auratus, Cricetulus migratorius, Meriones tristrami, Microtus guentheri, Apodemus mystacinus, and Mus domesticus (Çolak et al., 1999). In the Near East, the dipodil is associated with Acomys russatus in the lava desert (Jordan; Abu Baker \& Amr, 2003a), A. dimidiatus (Israel; Mendelssohn \& Yom-Tov, 1999) and Jaculus jaculus (Jordan, Hatough-Bouran, 1990). Associates in Egypt are Sekeetamy calurus, Dipodillus nanus, Acomys cahirinus, A. russatus and Eliomys melanurus (Osborn \& Helmy, 1980). Gerbillus nanus Blanford, 1875, excluds Wagner’s dipodil from sandy soil (Qumsiyeh, 1996).

Density. Common species. Densities fluctuate strongly between years, possibly in relation to annual level of precipitations (Shenbrot et al., 1997). In the Negev highlands of Israel populations varied over three years between 7.3 and 32.3 per ha in a preferred habitat; they were lower elsewhere (0.2-12.0 per ha; Shenbrot et al., 1997). Mean home range in Israel was 10.7 m and 8.9 m for males and females, respectively (Mendelssohn \& Yom-Tov, 1999).

## Biology

A detailed study was conducted in the Negev highlands in Israel (Shenbrot et al., 1997). Aspects of biology are nearly unknown in Turkey.

Activity is strictly nocturnal. Wagner's dipodil is not gregarious in its activity (Harrison \& Bates, 1991).

Burrows were described from Israel (Shenbrot et al., 1997) and Jordan (Hatough-Bouran, 1990). Wagner’s dipodils dig simple tunnels; complex burrows are rare. Most burrows have 1-3 openings (up to five) with a diameter of $2.5-3.0 \mathrm{~cm}$ (Israel) or 4-8 cm (Jordan). Overall tunnel length is 45-175 cm (nearly 3 m in complex burrows; Shenbrot et al., 1997) and average tunnel volume in Jordan was 0.29-4.2 dm ${ }^{3}$ (Hatough-Bouran, 1990). Burrows contain a single nest, occasionally a storage chamber (two at most), and up to two blind alleys (HatoughBouran, 1990). Nest of dried plant material is typical for complex burrows (Shenbrot et al., 1997). Entrances are plugged with sand during day to re-
tain a favourable microclimate (Osborn \& Helmy, 1980). Wagner's dipodils also frequent burrows of Psammomys obesus and Meriones libycus (Atallah, 1978). In steppes and along cultivated land the burrows are mainly constructed under rocks and behind stone walls (Atallah, 1978).

Reproduction. Wagner's dipodil is an opportunistic breeder and demonstrates a long breeding period. Shenbrot et al. (1997) captured reproductively active males from January to November and females from February to October. Between May and August the proportion of reproductive females exceeded 50 \%. Reproductive activity varies between years, depending on rainfall. Duration of pregnancy was reported as 18-22 days (Shenbrot et al., 1997) or 2426 days (Al-Khalili \& Delany, 1986), and litters contain 3-7 cubs (Shenbrot et al., 1997). The highest proportion of subadults in a population is in August and September. Longevity in the field is up to 2.5 years, more than four years in captivity (Shenbrot et al., 1997).

Reproductively active dipodils were collected in Turkey between mid-April (a lactating female and a scrotal male) and late August (pregnant females and scrotal males). Two females had 3 and 4 embryos, respectively (Çolak et al., 1999). Captive females produced four litters with $3,4,4$, and 7 cubs, respectively. Çolak et al. (1999) estimated litter size for the Turkish population to be 5.7 on average (range $=$ 3-9) which might be an error possibly resulting from inaccurate placental scar counts.

Food mainly consists of seeds and annual herbs (especially Medicago sp.), but also of invertebrates, particularly snails (Harrison \& Bates, 1991; Mendelssohn \& Yom-Tov, 1999). Hatough-Bouran (1990) found in caches Anabasis articulate, Atriplex halimus, Seitlitzia rosmarinus, Halocnemum strobilaceus, Halogeton alopecuroides and Artemisia herba-alba. Shenbrot et al. (1997) maintained captive animals on a diet of millet seeds and leaves of Atriplex halimus.

Predation. Main prey of the barn owl (Tyto alba) in Israel (Rekasi \& Hovel, 1997). Also found in pellets of the little owl (Athene noctua) (5.1 \% of remnants) in Jordan (Amr et al., 2004).

## Family: Spalacidae Gray, 1821

Mole rats are a small group of subterranean rodents occupying the Eastern Mediterranean, Africa, Eastern Europe and various parts of Asia. They are well defined morphologically and relatively reliably traceable in the fossil record. Spalacidae in their current scope includes four subfamilies: Spalacinae Gray, 1821 (with Spalax), the eastern Palaearctic zokors Myospalacinae Lilljeborg, 1866, the African mole rats Tachyorictinae Miller \& Gidley, 1918, and the Oriental bamboo rats Rhyzomyinae Winge, 1887 (Musser \& Carleton, 2005). A similar taxonomy was already advocated by Ognev (1947). In the past, as now mole rats in the genus Spalax, were nearly uniformly recognised as being an independent family Spalacidae (e.g. Miller, 1912; Topachevskii, 1976; Ellerman \& Morrison-Scott, 1951; Corbet, 1978; Savić, 1982a; Harrison \& Bates, 1991; Gromov \& Erbajeva, 1995), or in a subfamily Spalacinae within the family Muridae (Musser \& Carleton, 1993; Kryštufek \& Vohralík, 2001). Changes in the taxonomic ranking did not affect the scope of Spalacinae (cf. Musser \& Carleton, 1993, 2005).

The number of genera within Spalacinae has changed over time. While some authors recognised a single genus (Spalax; e.g. Miller, 1912; Méhely, 1913; Ognev, 1947; Ellerman \& MorrisonScott, 1951; Corbet, 1978; Harrison \& Bates,
1991), others found a two genera solution (Spalax and Microspalax) more appropriate (Topachevskii, 1976; Savić, 1982a). Because Microspalax Nehring, 1898, is preoccupied by Microspalax Megnin \& Trouessart, 1884 (Acari), it was replaced by Nannospalax Palmer, 1903 (Gromov \& Baranova, 1981; Savić \& Nevo, 1990; Nowak, 1999; Musser \& Carleton, 1993; Kryštufek \& Vohralík, 2001). Topachevskii (1976) further divided Nannospalax into two subgenera, Microspalax (with ehrenbergi) and Mesospalax Méhely, 1909 with leucodon and nehringi. Méhely (1913) had already recognised three subgenera within Spalax in much the same manner: Microspalax (the ehrenbergi group), Mesospalax (leucodon and nehringi sensu Musser \& Carleton, 2005), and Macrospalax Méhely, 1909 (giganteus and the microphthalmus group). Note that the taxonomic scope of Macrospalax matches Spalax sensu Topachevskii (1976). Morphological differences between Spalax and Nannospalax are stable enough to be of practical use on fragmentary fossil material as well (Bruijn, 1984). Besides, the two genera show very different cytogenetic properties. Nannospalax is characterised by low diploid numbers (nearly invariably $2 \mathrm{~N}<60$ ) of mainly acrocentric chromosomes ( $\mathrm{NF} \leq 92$ ) and by a proliferating chromosomal speciation. Spalax, on the other hand, has high diploid numbers ( $2 \mathrm{~N}=60$ or 62 ) of biarmed chromosomes ( $\mathrm{NF} \geq 120$; L’apunova et al., 1971) and shows a slow rate of chromosomal speciation.


Figure 218. Mole rat Spalax. Drawing: J. Hošek.

The number of species within Nannospalax has been a long-standing source of disagreements and conflicting views. Taxonomy underwent phases of splitting (e.g. four species and 12 subspecies recognised by Méhely, 1913) and clumping (e.g. Harrison \& Bates, 1991, with S. leucodon as the only species); now the taxonomy is evidently entering a phase of extensive split (see under Spalax).

Spalacinae first appeared in the Lower Miocene in the northeastern corner of the Mediterranean (Balkans and Anatolia; Ünay, 1996). The most diverse early fossils are known from Anatolia (Ünay, 1999). Molecular (Catzeflis et al., 1992) and fossil evidence (Hugueney \& Mein, 1993) produced comparable divergence time estimates for the emergence of mole rats from the murid-cricetid stock (about 19 million years ago). The extinct genus Pliospalax Kormos, 1932 (latest Miocene to Villanyian) is a possible ancestor of the recent Spalax which emerged in the Ruscinian times (Kowalski, 2001). The oldest record of Pliospalax is that of P. marmarensis from the Early Middle Miocene of Pasalar in southwestern Turkey (Ünay, 1996). Mole rats were already an abundant rodent group in Central Anatolia (16.3\% of all rodent specimens found in Çalta) in the Late Pliocene (Şen \& Bruijn, 1977), when the environment was a steppic one (Şen, 1978). Şen (1977) published a photograph of a beautifully preserved skull of Pliospalax macoveii (Simionescu, 1930) from Çalta which already showed all the essential characteristics of recent mole rats. Noteworthy, mole rats remained restricted to their current distributional range throughout their evolutionary history.

Spalacinae are more subterranean than any other muroid group and are also the only eyeless and effectively blind rodents. They are chisel-tooth diggers, thus loosening the soil with lower incisors and using the lower jaw as a shovel. The excavated soil is then pushed behind the body by fore and hind limbs and later transported to the surface using the hind feet. The presence of mole rats is easily detected by large mole hills which are frequently arranged in a line. The diet is herbivorous and consists mainly of bulbs, tubers and roots; reproduction is slow. Musser \& Carleton (2005) recognised 13 species of mole rat, all in the genus Spalax. Dental formula is: $1 / 1,0 / 0$, $0 / 0,3 / 3=16$.

## Genus: Spalax Güldenstaedt, 1770

## Taxonomy

The three species as recognised from Turkey have been at the heart of a taxonomic dispute for decades. The central phenomenon of their evolution is chromosomal speciation on the one hand and convergent morphology on the other. As a consequence, the traditional taxonomy only with difficulty delimited morphologically very similar species (e.g. Ellerman \& Morrison-Scott, 1951). As suggested by chromosomal research, each of the morphological species is most probably a collection of sibling species, which putatively evolved through chromosomal rearrangements. To make the problem even more puzzling taxonomically, cytotypes are largely allopatric or at most parapatric. Hybridization between different cytotypes occurs in parapatric zones. The hybrids are at least partly fertile, although they show a lower level of fitness than parental animals. There is no evidence of gene flow between different cytotypes. Four cytotypes of S. ehrenbergi from Israel developed post-mating chromosomal incompatibilities and pre-mating behavioural mechanisms (Nevo et al., 2001). Some of the cytotypes from Israel are highly divergent with the estimated time of divergence from $0.18-0.75$ to $2.00-2.35$ million years ago (Nevo et al., 2001). It has therefore been argued for long time that splitting produces a more realistic taxonomy in mole rats than clumping (Nevo et al., 1995).

The traditional morphological species is certainly not an adequate approach in the mole rat taxonomy. Another extreme option is in the recognition of each cytotype as a distinct species. Currently, such a solution is frequently advocated by Turkish authors (e.g Coşkun et al., 2006) but has already been applied to S. leucodon in Europe. Savić \& Soldatović (1984) recognised, entirely on chromosomal grounds, 13 species and a further 10 subspecies in southeastern Europe alone. In their practice, taxonomic names were applied to all known cytotypes with no clear criteria for ranking cytotypes as species or subspecies. Unsurprisingly, such taxonomy did not receive support (e.g. Musser \& Carleton, 1993, 2005). Recent formal recognition of the four Israeli S. ehrenbergi cytotypes as distinct species was accompanied by the evidence from various independent data sets (Templeton, 1999; Nevo et al., 2001). The addi-
tion of these four species to the list of World Mammals (Musser \& Carleton, 2005) however, produced an unbalanced taxonomy in the ehrenbergi group, which is further complicated by unresolved nomenclatural questions (see under that species).

Various authors claim that S. leucodon and/or S. ehrenbergi are actually superspecies, i.e. monophyletic assemblages of closely related and morphologically cryptic species. The superspecies, however, is not a taxonomic category. It might be perhaps more appropriate to designate cytotypes as evolutionary significant units (ESU’s; Moritz, 1994) within currently used species names. In any case, we feel that for the time being, a conservative approach is the only sound alternative to avoid excessive cytotypebased splitting which could easily produce an unbalanced taxonomy.

The independent specific position of Spalax ehrenbergi has been recognised even in times of the most conservative mole rat taxonomy (e.g. Ellerman, 1948; Ellerman \& Morrison-Scott, 1951) and is also currently widely accepted (see under that species). In phylogenetic reconstructions by Nevo et al. (1995, 2001), S. ehrenbergi emerged as a monophyletic unit while S. nehringi appeared to be paraphyletic. Divergence time between S. ehrenbergi and S. nehringi (1.4 million years; Nevo et al., 1995) is
possibly an underestimate since it is within the range of divergences between cytotypes of S. ehrenbergi in Israel (0.18-2.35 million years; Nevo et al., 2001).

## Key to species

1. Third upper molar usually with two isolated enamel islands (Fig. 219a-e); parietal width never less than its length, even in full grown specimens (Figs. 244, 248); upper incisors frequently with longitudinal grooves (Fig. 220); upper incisor narrower ( $<2.1 \mathrm{~mm}$ in majority of specimens) ${ }^{1)}$
S. ehrenbergi

1* Third upper molar usually with one isolated enamel island (Fig. 219h-k); parietal width frequently much less than its length in full grown specimens (Figs. 223, 226, 234, 237); upper incisors ungrooved; upper incisor wider ( $>2.1 \mathrm{~mm}$ in majority of specimens) ${ }^{1)}$

2 Nasals with a medial slit-like depression; $1^{\text {st }}$ upper molar with 1 or 2 (rarely 3) roots (Fig. 221b,c)
S. xanthodon


Figure 219. Variability in enamel pattern in $3^{\text {rd }}$ upper molar in Spalax ehrenbergi (upper row) and S. xanthodon (lower row). Spalax ehrenbergi: a - Israel, Mi’ilya; b - Turkey, Antakya; c - Turkey, Elazığ; d, f - Syria, Aleppo; e - Syria, Damascus. Spalax xanthodon (all from Turkey): g - Akşehir; h - Island of Gökçeada; i - Beyşehir; j - Ankara; k - Savaştepe, Balıkesir; $\mathbf{I}$ - Erzurum. Age is in increase from left (the youngest) to right (the oldest). Lingual side is to the left, anterior is at the top. Based on specimens in SMF (a, c, d, l), ZFMK (b, g, i), BMNH (e), NMNH (f), FMNH (j, k), and our own material (h). Not to scale.


Figure 220. Skull of Spalax ehrenbergi in frontal view. Note the enlarged infraorbital foramen (if) and grooved incisors (indicated by an arrow). Based on a specimen from Elazığ, Turkey (SMF). Scale bar $=5 \mathrm{~mm}$.

2* Nasals without a medial slit-like depression; $1^{\text {st }}$ upper molar with 3 or 4 (rarely 2 ) roots (Fig. 221a)
S. leucodon
${ }^{1)}$ Although width of the upper incisor overlaps (range $=1.2-2.6 \mathrm{~mm}$ in S. ehrenbergi, $1.4-3.7 \mathrm{~mm}$ in the remaining two species), only 11 specimens of S. ehrenbergi (= ca $15 \%$ of a total sample) exceeded 2.1 mm versus 13 specimens in $S$. leucodon and $S$. xanthodon ( $=8.7 \%$ ) with the incisor narrower than 2.1 mm .

## Lesser mole rat - Spalax leucodon

Spalax typhlus leucodon Nordmann, 1840. Type loc.: Near Odessa, Ukraine.
Spalax monticola turcicus Méhely, 1909. Type loc.: Makrikeui near Constantinople (Méhely, 1913); given as Makri-Koi, Constantinople, by Ellerman \& Morrison-Scott (1951); defined as Bakırköy, İstanbul, by Kıvanç (1988). Note that Bakırköy is already integrated into the rapidly expanding city of İstanbul, consequently the population in the type locality has possibly been extirpated.

## Taxonomy

For delimitation between S. leucodon and S. xanthodon, see account under the latter. Kıvanç (1988) pooled mole rats form Thrace and Marmara into a subspecies Spalax leucodon turcicus. Chromosomal and allozyme evidence placed specimens from Bolu (identified as turcicus by Kıvanç, 1988) within S. xanthodon (cf. Nevo et al., 1995; Sözen 2004;


Figure 221. Alveolar pattern of $1^{\text {st }}$ upper molar in Spalax leucodon (a) and S. xanthodon (b, c). Based on BMNH specimens from Gelibolu in Turkish Thrace (a), İzmir (b), and Ankara (c). Anterior is at the top, lingual is to the left. Scale bar $=1 \mathrm{~mm}$.

Sözen et al. 2006). Due to the lack of convincing evidence on the occurrence of $S$. leucodon on the Asiatic side of the Marmara and Bosporous straits, we therefore restrict its range to Europe.

Savić \& Soldatović (1984) considered the cytotype from Turkish Thrace with $\mathrm{NF}_{\mathrm{a}}=74$ to be an independent species S. turcicus.

## Description

Since the lesser mole rat most closely resembles $S$. xanthodon, see also under that species. If not otherwise stated, the details provided below relate to material from Turkish Thrace.

External characters. Medium sized mole rat. Nostril pad is wide, 12.5 mm long and 6.5 mm high. Front claws are 5.4 mm long, hind ones are shorter $(4.5-5.2 \mathrm{~mm})$. Hair is dense and soft, up to $10-13$ mm long on mid-back; ventral hairs are shorter (ca 5 mm ).

Colour. The lesser mole rats are mainly grey or buff brown. On average, $S$. leucodon is darker than $S$. xanthodon, and does not attain the pale extremes of the latter. Colour is variable, even in Turkish Thrace. A specimen from Gelibolu is buff-yellow, much lighter than a skin from Edirne which is brownish grey. Belly is slate grey in both animals, but washed with buff shades in the skin from Gelibolu; upper chest and throat are grey. Lateral line is obscured, particularly so in the Gelibolu specimen. Forehead is grey, brush of stiffened hairs is yellowish to buff, paws are whitish (Gelibolu) or greyish (Edirne). White or yellow spots which are typical for some of the Balkan populations of S. leucodon were not seen in Thracian animals.


Figure 222. Skin of Spalax leucodon in dorsal and ventral view. Based on a female from Karaağaç, Edirne, Turkish Thrace. Photo: C. Mlinar.

Nipples. There are six nipples, two inguinal and one pectoral pair, respectively.

Penis and male genitalia were described in detail by Kratochvíl (1964) on the basis of material from eastern Hungary. The club-like glans is simple, lengthened and slightly expanded distally. The opening of urethra is surrounded by two lobes. The baculum is a simple shape, flat, and expanded basally. Basal part is cartilaginous. Length is $6.0-8.6 \mathrm{~mm}$ (Ognev, 1947).

Skull differs from the condition in S. xanthodon mainly in having a massive and broader rostrum; width of rostrum is $30.7-45.5 \%$ of rostrum length (mean $=37.4 \%$; $\mathrm{N}=109$; material from the Balkans and the Carpathian Basin). Nasals also tend to be broader. Zygomatic arches are widely expanded, their width equals $72.5-85.4 \%$ of condyloba-
sal length (mean $=78.0 \%$ ). Braincase is fairly shallow (34.9-47.3\% of condylobasal length; mean = $41.2 \%$ ). Nasals have a blunt tip and converge posteriorly; naso-maxillary suture is either broad or much restricted (about 2 mm wide). Interpterygoid fossa is broad and the posterior hard palate is straight or inconspicuously dentate. Posterior palatal foramina are shifted more backward than in S. xanthodon, and are separated by a high and narrow medial septum. Mandible is heavy with a powerful and laterally expanded alveolar process (Fig. 224).

Teeth are identical to those in S. xanthodon. Enamel is yellow-orange on upper incisors, yellow or cream-white on lower ones. Number of maxillary alveoli in a specimen from Gelibolu is 3 ( $1^{\text {st }}$ and $2^{\text {nd }}$ molar) and 1 ( $3^{\text {rd }}$ molar); the same count we also found in an animal from Thessaloniki, Greece. Topachevskii (1976) provides the following figures for the maxillary molars: $2-4$ roots on $1^{\text {st }}$ molar, 2-4 roots on $2^{\text {nd }}$ molar, and 3 roots on $3^{\text {rd }}$ molar; mandibular row: 1 or 2 roots on $1^{\text {st }}$ molar, 2 roots on $2^{\text {nd }}$ molar, and 2 or 3 roots on $3^{\text {rd }}$ molar.

Dimensions are given in Table 46. Males are larger than females (Savić, 1982b). Maximum body mass in the southern margin of the Carpathian Basin is 365 g in males and 328 g in females (Savić, 1982b).

|  | N | mean | min - max |
| :--- | :---: | :---: | :---: |
| Head and body | 14 | 185.8 | $167-222$ |
| Hind foot | 16 | 23.0 | $18.0-25.2$ |
| Weight | 16 | 198.9 | $162-274$ |
| Condylobasal length | 18 | 43.9 | $39.9-47.1$ |
| Zygomatic breadth | 16 | 35.0 | $32.0-37.2$ |
| Maxillary tooth-row | 18 | 7.6 | $6.9-8.5$ |

Table 46. External and cranial dimensions of Spalax leucodon from Turkish Thrace. Based on Kurtonur (1972), Savić (1982b), specimens in BMNH, and our own material.

Chromosomes. Highly polymorphic species with no less than 29 cytotypes so far reported from Europe. Diploid number varies between $2 \mathrm{~N}=46$ and 2 N $=58$, and fundamental number of chromosomal arms ranges from $\mathrm{NF}_{\mathrm{a}}=72$ and $\mathrm{NF}_{\mathrm{a}}=94$ (Peshev, 1983; Savić \& Soldatović, 1984; Sözen, 2004). Populations from European Turkey have diploid number of chromosomes $2 \mathrm{~N}=56$ but fundamental number of autosomal arms varies, being $\mathrm{NF}_{\mathrm{a}}=72$ in a population from Erceabat in Gelibolu (Sözen, 2004)


Figure 223. Skull and mandible of Spalax leucodon, based on a female from Karaağaç, Edirne, Turkish Thrace.
Scale bar $=5 \mathrm{~mm}$.
and $\mathrm{NF}_{\mathrm{a}}=74$ in the rest of Turkish Thrace (Savić \& Soldatović, 1984; Sözen et al. 2006a). Cytotype $\mathrm{NF}_{\mathrm{a}}=74$ consists of two pairs of medium sized metacentrics, five pairs are submetacentrics (mainly of medium size), three pairs of subacrocentrics and the remaining 17 pairs of acrocentric autosomes; the X chromosome is large and submetacentric, the Y chromosome is considerably smaller and acrocentric (Savić \& Soldatović, 1984). Cytotype $\mathrm{NF}_{\mathrm{a}}=$ 72 has 9 pairs of biarmed and 18 pairs of acrocentric autosomes; the X chromosome is medium sized metacentric and the Y chromosome is small acrocentric (Sözen, 2004). Since Sözen (2004) did not


Figure 224. Caudal view of ramus mandibulae of Spalax leucodon (same specimen as on Fig. 223). al - alveolar process; an - angular process; ar - articular process; $\mathbf{c p}$ - coronoid process; $\mathbf{m 3}-3^{\text {rd }}$ molar. Scale bar $=5 \mathrm{~mm}$.
publish a figure of the Ercebat karyotype, we cannot judge whether differences in fundamental autosomal number might be due to arbitrariness in distinguishing between subacrocentric and acrocentric autosomes. Differences in heterosomes seem to be real,


Figure 225. Upper (a) and lower molars (b) in Spalax leucodon. Based on a specimen from Dobrostan, district Plovdiv, central Bulgaria. Anterior is at the top, lingual is to the left. Scale bar $=2 \mathrm{~mm}$.
however. Either of these two cytotypes is known outside Turkish Thrace (cf. Peshev, 1983).

Cytotype $\mathrm{NF}_{\mathrm{a}}=74$ (form turcicus sensu Savić \& Soldatović, 1984) is surrounded by three cytotypes in Bulgaria: 2N = 52, $\mathrm{NF}_{\mathrm{a}}=74$ (Varna) and two closely related cytotypes with $2 \mathrm{~N}=54$ and $\mathrm{NF}_{\mathrm{a}}$ = 82 (Pazardžik) or 92 (Dobrostan); differences between the sites with $2 \mathrm{~N}=54$ are in different number of biarmed (15 and 18 pairs, respectively) and acrocentirc (11 and 8, respectively) autosomal chromosomes (Peshev, 1983).

There seems to be no clear discontinuity in a conventionally stained karyotype between the European S. leucodon and S. xanthodon of Asia Minor. E.g. a cytotype from the vicinity of Karabük and Kastamonu has $2 \mathrm{~N}=56$ and $\mathrm{NF}_{\mathrm{a}}=70$ and its heterosomes are of same size and shape as in Thracian animals (Sözen, 2004; Sözen et al. 2006).

## Variation

Interpopulational variation is obscured by a pronounced individual variation, as is typical of other species of mole rats as well. The taxonomy of S. leucodon is therefore unstable and the taxon is most probably a collection of several allopatric or parapatric species. At the most simplistic end, Topachevskii
(1976) divided S. leucodon into two subspecies, the nominate one, which is on average smaller, and S. l. monticola Nehring, 1898 (Type loc.: Kupres, Bosnia and Herzegovina). Bolkay (1928) provides details on the topotypical material of monticola. The nominate form is mapped for the Carpathian Basin and across Romania further eastward to Moldova and Ukraine; ssp. monticola is reported for the Balkans, including European Turkey (Topachevskii, 1976). In comparison with other European populations of the lesser mole rat (body mass up to 504 g; Straka, 1965), the animals from Turkish Thrace appear to be of small size (Table 46).

On the basis of karyotypes, Savić \& Soldatović (1984) recognised 14 species in Europe and raised cytotype turcicus to the level of an independent species. The high number of acrocentric chromosomes led them to the conclusion that turcicus is one of the oldest chromosomal races within Nannospal$a x$. Chromosomal variation in Turkish Thrace is described above.

The lesser mole rat might have a very low genetic diversity. Major histocompatibility complexes (MHC) which are compulsory for the recognition of any antigen by the vertebrate immune system, showed low polymorphism for both classes of


Figure 226. Skull in dorsal view in Spalax leucodon to show variation in shape. a - an unsexed adult specimen from Gelibolu, Turkish Thrace; b - an adult male from Mudros, Island of Limnos, Greece (type of insularis). Not to scale. Based on BMNH material.
polypeptids in four cytotypes from former Yugoslavia (Nižetić et al., 1988). This is indicative of a past population bottleneck. Results, however, have to be considered with caution due to small sample sizes.

## Distribution

The lesser mole rat is endemic to Europe, where its range is centred in the Balkans, eastern Carpathian Basin, and the steppes on the right bank of the Prut River. Along the Black Sea coast, the animal nearly reaches Crimea. Spalax leucodon therefore occurs in Bosnia and Herzegovina, Montenegro, Greece, Macedonia, Serbia, Bulgaria, European Turkey, eastern Hungary, Romania, Moldova, southern Ukraine, and probably Albania. Occurrence on the Aegean islands is uncertain (see also under S. xanthodon), but a population from the Limnos Island probably belongs to S. leucodon (cf. Fig. 226).

The range in European Turkey is wide, and mole rats presumably occupy the entire region, except for wooded parts on the Istranca Mts.

Palaeontology. Mole rats were common in the Balkans throughout the entire Pleistocene. Recent species S. leucodon emerged in the Middle Pleistocene and its fossil range exceeded the recent one (Kowalski, 2001). Note, however, that Topachevskii (1976) doubts whether the identification of the fossil material is always correct. Santel \& Koenigswald (1998) ascribed mole rats from the Middle Pleistocene strata of the Yarimburgaz Cave in Turkish Thrace to Spalax cf. leucodon.

## Нabitat

The lesser mole rat is common in the open landscape of the Mediterranean and steppic regions, where it occupies various soils, including sands, loess, loam


Figure 227. Distribution of Spalax leucodon in Turkey and adjacent regions. Records: $\mathbf{1}$ - Karaağaç, Edirne; 2 - 1 km south of Koyunbaba, Kırklareli; 3-1 km south of Sofular, Kırklareli; 4-10 km east of Vize, Kırklareli; 5 - Akalan, İstanbul; 6 - Tayakadın, İstanbul; 7a - near Mahmutbey, İstanbul; 7b - Güneyli köyü, İstanbul; 7c - Bağcılar köyü, İstanbul; 7d - Halkalı, İstanbul; 8 - Makri-Koi (=Bakırköy), İstanbul; 9 - Kumburgaz, İstanbul; 10 - Selimpaşa, Silivrı, İstanbul; 11a - 14 km south-east of Çorlu, Tekirdağ; 11b - Yeniçiftlik, Tekirdağ; 12 - Karaevli (= ca 18 km east of Tekirdağ); 14 - Güvenbayırı, Boyalır, Çanakkale; 15 - Eceabat, Çannakale. Corresponding references: Méhely (1913): 8. Kurtonur (1972): 10. Soldatović \& Savić (1978): 11a, 12. Kivanç (1988): 7a, b, c, 9, 14. Sözen (2004): 15. Sözen et al. (2006a): 2, 3, 4, 5, 6, 7d, 11b, 13. Our own data: 1 .
and rendzina. Deep, loose and well drained soil is preferred; forests are avoided as well as a shallow soil layer on rocky substrate, swamps, marshes and periodically flooded land. The animal enters gardens and is found, at least temporarily, on ploughed areas. In the forest zone, it penetrates into clearings.

In sandy and loess soils of the southern Carpathian Basin, the most common plants in the lesser mole rat habitat are: Eryngium campestre, Cynodon dactylon, Centaurea arenaria, Festuca vaginata, F. vallesiaca, F. sulcata, Potentilla arenaria, Alyssum tortuosum, Koeleria glauca, Poa bulbosa, Thalictrum minus, Rindera umbellate, Carex humilis, Ranunculus bulbosus, Teucrium chamaedrys, Chrysopogon gryllus, Thymus glabrescus, Stipa capillata, Adonis vernalis, Agropyrum glaucum, Chondrylla juncea, Daucus carota, Euphorbia cyparissias, and Echinops banaticus (Savić, 1973; Savić et al., 1986). Spalax leucodon is presumably widespread in all open and lowland habitats of Turkish Thrace.

Altitude. Altitudinal generalist, which ranges from close to sea level up to $2,300 \mathrm{~m}$ in the mountains (Savić, 1967, 1982b). Probably restricted to low elevations in Turkish Thrace, and we never observed its characteristic mounds on the Istranca Mts.

Associates. In Turkish Thrace, mounds of the lesser mole rat occur in habitats occupied by Crocidura suaveloens, C. leucodon, Spermophilus citellus, Myomimus roachi, Cricetulus migratoris, Microtus levis, M. hartingi, Apodemus sylvaticus, A. flavicollis, and Mus macedonicus. Further associates are found northwards: Talpa europaea, Cricetus crice-


Figure 228. Habitat of Spalax leucodon at Arpaç near Hasköy, Edirne. Photo: A. Kryštufek.
tus, Microtus arvalis, Apodemus uralensis, Mus spicilegus and Sicista subtilis.

Density varies from <1 individual per hectare, up to 23 per ha. In the northeastern part of its range, reported densities are $0.1-8$ per ha (Topachevskii, 1967), in Bulgaria 1-4 per ha (Straka, 1964) and in southern Carpathian Basin 13.3 per ha (Mikes et al., 1982). Highest density ( 23 per ha) was reported from Bukovina, Ukraine (Topachevskii, 1967). Ploughing results in a significant decrease in mole rat density (Habijan-Mikes et al., 1986).

## Biology

The biology of the lesser mole rat is not known from Turkey.It wasstudied in Bulgaria (Straka, 1964, 1965) and in southern Carpathian Basin (Savić, 1973, 1975). Watson (1961) reported observations on a captive specimen he trapped in "eastern Thrace".

Activity. The lesser mole rat is a solitary, territorial and aggressive animal. Activity is polyphasic, with the main peak during the day-time (1-2 p.m.) and another one during the night ( $1-2$ a.m.; Savić, 1975). Home ranges measure $144-200 \mathrm{~m}^{2}$ (Savić \& Nevo, 1990).

Their daily energy budget during winter amounts to $0.220 \mathrm{kcal} \mathrm{g}^{-1} \mathrm{day}^{-1}$, and for the rest of the year to $0.170 \mathrm{kcal} \mathrm{g}^{-1}$ day $^{-1}$ (Górecki \& Christov, 1969).

Burrows. Just like other mole rats, S. leucodon is nearly exclusively subterranean. Each individual digs its own tunnel system. The basic pattern of such system consists of a main tunnel with several secondary passages branching off. Tunnels (average diameter $7-8 \mathrm{~cm}$ ) are mainly $20-25 \mathrm{~cm}$ below the surface, but can descend as deep as 410 cm (Savić, 1973). Peripheral feeding passages are shallower (1525 cm ), therefore within reach of roots and bulbs. Each system has a single ovate nesting chamber (28 $\times 18 \times 16 \mathrm{~cm}$ ) which is in its centre, $25-50 \mathrm{~cm}$ below the surface. Nest chamber is lined with grass (in the southern Carpathian Basin with Cynodon dactylon and Festuca vaginata) which is brought from the surface. Next to the nesting chamber are small caches; the main storing chamber is $1-2 \mathrm{~m}$ away. Latrines descend 60-130 cm below the surface. Overall length of passages is $65-195 \mathrm{~m}$ (mean $=132 \mathrm{~m}$ ) and they spread over an area of $194-1,000 \mathrm{~m}^{2}$ (mean $=$ $453 \mathrm{~m}^{2}$ ); radius is $26-64 \mathrm{~m}$ (mean $=49.5 \mathrm{~m}$; Savić, 1973).


Figure 229. Mound of soil excavated by Spalax leucodon on a pasture at Arpaç near Hasköy, Edirne. Photo: A. Kryštufek.

Main digging activity occurs over an area of $10-$ $512 \mathrm{~m}^{2}$ (mean $=144 \mathrm{~m}^{2}$ ); radius is $4.8-48 \mathrm{~m}$ (mean $=24.5 \mathrm{~m}$ ). Each animal digs about 1.7 m of new passages daily which produce about 10 kg of excavated soil. Activity varies over the year and is $67 \%$ higher in April than in July. Daily peaks of digging activity are from 11 a.m. to 1 p.m. (main peak), between 7 a.m. and 9 a.m., and again from 5 p.m. to 7 p.m. Mound systems of individual mole rats are spaced by $21-30 \mathrm{~m}$ on average (Savić et al., 1986).

Reproduction. Gestation period is approximately 30 days. Females start breeding during their second year and during their lifetimes, a majority of them deliver only a single litter; a $2^{\text {nd }}$ litter is very rare ( 0.89 \% of females; Savić, 1973). In Bulgaria, the proportion of pregnant females was highest in March (68.4 \%) and of lactating females in April (50\%; Straka, 1965). In the southern Carpathian Basin, litters were similarly born mainly in March and April (Savić, 1973). The last recorded lactating females were found in June (Bulgaria; Straka, 1965) and rarely as late as September in the southern Carpathian Basin (Savić, 1973). Savić (1973) reports only 27 $\%$ of females to be reproductively active in Deliblatska peščara (southern Carpathian Basin), but Straka (1965) gives this proportion as $63.3 \%$. The number of embryos is $1-6$ and a great majority of females in Bulgaria ( $=91.6 \%$ ) have $2-4$ embryos (mean $=3.2 ; \mathrm{N}$ $=107$; Straka, 1965). Counts from the southern Carpathian Basin are lower: range $1-5$ and mean $=2.4$ ( $\mathrm{N}=69$; Savić, 1982b). A higher estimate for mean number of embryos in Ukraine ( $=4.2$; Savić, 1982b)


Figure 230. Burrow system of an adult male Spalax leucodon in Deliblatska peščara, Serbia. $\mathbf{N}$ - nest. Scale bar $=5 \mathrm{~m}$. Modified from Savić (1973).
is probably an artefact due to small sample size ( N $=6$ ). Prenatal mortality is very low and the proportion of resorbed embryos is 2.15 \% (Straka, 1965). Young (weight at birth =6-6.5 g; Savić, 1975) attain a body mass of 137 g (males) and 121 g (females) by the end of May (Straka, 1965). They are weaned at 2-2.5 months old (Straka, 1965). Maximum age reached in captive animals was 3.5 years for females and 4.5 years for males (Savić, 1975).

Sex ratio in the adult population is female biased in the southern Carpathian Basin (1 male : 1.13 females; $\mathrm{N}=981$; Savić, 1975). A skewed sex ratio is even more evident in young animals during spring (1 male : 1.33 females; $\mathrm{N}=147$; Straka, 1965).

Food. Staple diet includes bulbs, roots and tubers, supplemented with green plant matter. Straka (1965) found bulbs and tubers in $90.5 \%$ of stomach content taken from Bulgaria; in 80.9 \% they occupied over one half of the stomach content. Green matter was found in 36.5 \% of stomachs and dominated in $10.1 \%$ of them; it became important in April and dominated in May and June. The most common dietary item are bulbs, tubers and the roots of Agropyrom repens, Cynodon dactylon, Cichorium intybus, Melilotus officinalis, Lotus corniculatus, Taraxacum officinale, Lathyrus tuberosus, Ornithogalum nanum, O. tenuifolium, Senecio sp. and Trifolium sp. Weaned juveniles depend entirely on a green diet (Straka, 1965). In Romania, Popescu \& Torcea (1968) investigated stomach content and identified 27 species of plants from eight families: Solanaceae (1 species), Asteraceae (5), Liliaceae (2), Poaceae (6), Polygo-
naceae (1), Chenopodiaceae (1), Apiaceae (4), and Fabaceae (7). Most frequently consumed were Cynodon dactylon, Sorghum halepense, Agropyron repens, Lanthyrus tuberosus, Medicago sp., Trifolium sp., and Muscari sp. Agricultural plants are consumed whenever available: potatoes, carrot, garlic, onion, beet, turnip, lucerne and cabbage, as well as tulips, sword lilies etc. (Savić, 1973). Daily consumption equals to approximately 36.5 \% of the body mass of an animal (Straka, 1965; range $=14.2-55.0$ \%; Savić, 1973) which gives a rough estimate of 6065 kg of food eaten annually (Straka, 1965). Taking into consideration densities of 1-4 per ha, this would indicate an annual consumption of 65-250 kg per ha.

Popescu \& Torcea (1968) found insects (Hymenoptera and beetle larvae) in six stomachs out of 59 analysed.

Food is stored and reports on caches differ tremendously among authors: 99-500 g in the southern Carpathian Basin (Savić, 1973), 6-700 g in Dobrogea, Romania (Popescu \& Torcea, 1968), and 1220 kg in Bulgaria (Straka, 1965). Eryngium campestre and Cynodon dactylon are the most abundant in such caches in the southern Carpathian Basin, Ornithogalum umbellatum, Colchicum autumnale, Crocus veluchensis, and Verbascum sp. in the hilly regions of Serbia, and Crocus sp., Primula sp., and Geranium rotundifolium in a high mountain pastures in Macedonia (Savić, 1973). Mole rats store chestnuts, beech mast and oak acorns as well (Savić, 1973).

Watson (1961) fed his captive specimen with potatoes, onion, carrot, beet, and large broad beans; beans were preferred. Savić (1973) kept mole rats on a diet of potato (preferred), carrot, onion and garlic, with an occasional supplement of celery, beetroot, and cabbage. Mortality was high in captive animals with a mean life expectancy of 3.1 months for males and 4.4 months for females.

Predation. Savić (1982b) listed the following predators of the lesser mole rat: Bubo bubo, Asio otus, Circus sp., Aquila heliaca, Falco cherrug, Buteo buteo, Mustela putorius, M. eversmanni, M. nivalis, Vulpes vulpes, and Felis silvestris. The proportion of the lesser mole rat in two Asio otus pellet samples from Romania was 0.04 \% and 0.1 \%, respectively. In a sample from Dobrogea, proportions of mole rats over five years were ( $\mathrm{N}=$ total number of preyed upon specimens) $0.7 \%$ in $1958(\mathrm{~N}=698), 0.1 \%$ in

1959 ( $\mathrm{N}=2,558$ ), 0.2 \% in $1960(\mathrm{~N}=2,402), 0.1$ \% in $1961(\mathrm{~N}=11,370)$, and $0.1 \%$ in $1962(\mathrm{~N}=3,996$; Schnapp, 1968).

Conservation. Populations of the lesser mole rat have declined and the range is shrinking in European Turkey (Yiğit et al., 2006c) and in the Carpathian Basin (Németh et al., 1999).

## Anatolian mole rat - Spalax xanthodon

Spalax typhlus xanthodon Nordmann, 1840. Type loc.: Smyrna (= İzmir), Turkey.
Spalax nehringi Satunin, 1898. Type loc.: Kasikoporan (= Kaskoparan köyü = Göle), Kars, Turkey.
Spalax monticola cilicicus Méhely, 1909. Type loc.: Bulgar-Maden (= Bulgar Madeni $=$ Madenköy), Cilician Taurus, Niğde, Turkey.
Spalax monticola anatolicus Méhely, 1909. Type loc.: Burnabad (= Bornova), near İzmir, Turkey.
Spalax monticola armeniacus Méhely, 1909. Type loc.: near Göl (= Göle), Kars, Turkey.
Spalax labaumei Matschie, 1919. Type loc.: Eshischehir (= Eskișehir), Turkey.
Spalax monticola corybantium Hinton, 1920. Type loc.: Murat Dağı, Uşak, Turkey.
Spalax monticola captorum Hinton, 1920. Type loc.: Kanghri (= Çankiri), Turkey.
Spalax monticola vasvarii Szunyoghy, 1941. Type loc.: Sultansuyu - Hara, Malatya, Turkey.
Spalax nehringi tuncelicus Coşkun, 1996. Type loc.: Gömemiş village, 16 km northeast of Tunceli, Turkey (Coşkun, 1996b).
Nannospalax munzuri Coşkun, 2004. Type loc.: Sarıtosun, 5 km southeast of Ovacık, Tunceli, Turkey

## Taxonomy

Authors who recognised mole rats of Asia Minor and the adjacent Transcaucasia as an independent species invariably reported them under the name nehringi (e.g. Topachevskii, 1976; Musser \& Carelton, 1993, 2005; Gromov \& Erbajeva, 1995; Kryštufek \& Vohralík, 2001; see also quotations in a paragraph below). The name nehringi Satunin, 1898, however is preoccupied by xanthodon Nordmann, 1840 (Corbet, 1978) and consequently, we applied the latter name on the grounds of prior-
ity. Lehmann (1966) was perhaps the first to advocate that xanthodon is the oldest available name for Anatolian mole rats. Lehmann, however, did not use xanthodon as a species name because he left the systematic position of the mole rat material collected during "Kumerloeveschen Orientreisen 1953-1965" open.

Anatolian mole rats were considered to be an independent species $S$. nehringi by some students (Felten et al., 1973; Storch, 1988; Topachevskii, 1976; Coşkun, 1996b, 2003, 2004c; Bukhnikashvili \& Kandaurov, 1998; Sözen et al., 2000a; Bukhnikashvili, 2004) although they were more frequently reported under S. leucodon (Steiner \& Vauk, 1966; Felten et al., 1971a; Kock et al., 1972; Šidlovskij, 1976; Doğramacı, 1989a; Kıvanç, 1988; Gülkaç \& Yüksel, 1989; Yüksel \& Gülkaç, 1990, 2001; Nadachowski et al., 1990; Nevo et al., 1995; Demirsoy, 1996; Kurtonur et al., 1996; Ivanitskaya et al., 1997; Özkan, 1987; Sözen \& Kıvanç, 1998; Sözen et al., 1999, 2000b, 2006, 2006a; Yüksel \& Gülkaç, 2001; Yiğit et
al., 2003, 2006c; Sözen, 2004; Kankılıç et al., 2007a, b). Topachevskii (1976) distinguished between leucodon and nehringi and we follow his taxonomy which is based on a thorough morphological revision.

Some of the above authors, who preferred leucodon over nehringi, claimed that Anatolian mole rats are actually only a cluster of chromosomal species, cytotypes or cryptic species within the S. leucodon 'superspecies'. We believe that at this point of the mole rat taxonomy, the main question is whether there are two phylogenetic lineages with the S. leucodon 'superspecies' which are separated by the straits of Marmara. If so, then xanthodon is worthy of recognition as an independent species, no matter that it is very likely a collection of sibling allopatric species which need further assessment using molecular markers. We found morphological characters proposed by Topachevskii (1976) to distinguish reasonably well between S. leucodon and S. xanthodon, thus providing good grounds for applying a bipartite taxonomy. L'apunova et al. (1974) argued that S.


Figure 231. An adult Anatolian mole rat Spalax xanthodon from Çığılkara, Antalya. Photo: A. Kryštufek.


Figure 232. Head of Spalax xanthodon in frontal (left) and semi-lateral view (right). Same specimen as in Fig. 231. Photo: A. Kryštufek.
xanthodon is chromosomally clearly differentiated from S. leucodon group. Although this conclusion was probably valid in the mid-1970s, subsequent research in Turkey has complicated the matter. We are now aware of an incredible chromosomal diversity which obscures putative karyological differences between mole rat populations in Europe and in Asia.

Kıvanç (1988) is the only author who comprehensively revised mole rats in Turkey. He did not distinguish between leucodon and xanthodon (and even synonymised the latter with anatolicus; cf. below) and clumped mole rats of Thrace and the Marmara region into one and the same subspecies (turcicus). The latter act puzzled us already while compiling the checklist of Turkish mammals (Kryštufek \& Vohralík, 2001). Available chromosomal and allozyme evidence place specimens from Bolu (identified by Kıvanç as turcicus) into S. xanthodon (Nevo et al., 1995; Sözen 2004; Sözen et al., 2006). As shown

| No. of <br> roots | upper <br> row |  |  | $1^{\text {st }}$ | $2^{\text {nd }}$ | $3^{\text {rd }}$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 69.6 | 79.3 | 77.2 | $1^{\text {st }}$ | $2^{\text {nd }}$ | $3^{\text {rd }}$ |
| 1 | 27.2 | 20.7 | 13.0 | 100.0 | 163.7 | 78.3 |
| 2 | 3.2 | 0.0 | 9.8 | 0.0 | 0.0 | 5.4 |

Table 47. Variation in number of molar roots in Spalax xanthodon from the area of Kastamonu (in percentages, sample size $\mathrm{N}=92$ ). From Sözen et al. (2006).
by Sözen et al. (2006), mole rats from northwestern Anatolia normally posses one or two-rooted condition of $1^{\text {st }}$ upper molar (Table 47) which is typical for the Anatolian populations, however Kıvanç (1988) diagnosed his turcicus by a three-rooted $1^{\text {st }}$ molar. Recently Yiğit et al. (2006c) mapped S. leucodon only for European Turkey.

It is beyond doubt that the taxonomy of $S$. xanthodon will change considerably in the future and more species will be recognised in Anatolia and Transcaucasia. We expect that molecular data will provide a vital insight into current species limits and past cladogenetic events in the group.

## Description

External characters. Medium sized to large mole rats. Long, cylindrical body is supported by relatively weak limbs; there is no apparent neck and no visible external tail. Head is broadly rounded when viewed from above, wedge-shaped in profile. Nostril pad is large, of triangular outline, $15.3-18.2 \mathrm{~mm}$ broad and $8.0-9.5 \mathrm{~mm}$ high. It is followed by a bristly stiff keel of facial hairs directed outward and upward and extending about half-way to the ear (length of the keel is up to 28 mm ). Rudimentary eyes are entirely covered by skin with no external opening. An external ear is missing but the small auditory opening is margined by a low ridge. Thumb is reduced in both, fore and hind feet, but still bears a claw. Claws are broad,
$5.0-5.5 \mathrm{~mm}$ long on a fore feet and $5.0-5.8 \mathrm{~mm}$ on hind ones; middle claws are the longest. Palms and soles are bare; there are two large pads on palms and five pads on soles; the three pads at hind toe bases are smaller than the posterior two pads. Stiff keel of short hairs extends on the outer side of forearm behind the wrist. Hind feet are particularly weak and soles are narrower than palms. Pelage is long, soft and nondirectional; mid-dorsal hairs are 9-12.5 mm long. Whiskers are scarce and directed forward.

Colour. Pelage is slate grey throughout the length of the hair, except for a short terminal buff band which is frequently absent on the belly. Back colour varies from light buff grey or yellowish buff, to reddish buff and to dull brown. Belly is slate grey, nearly blackish in one extreme and with whitish or silver shades in another. Flanks are darker than back in some individuals, lighter and more buff in others. Lateral line is rarely distinct but never sharp. Lips and nostril pad
are margined in white in some animals. White spot or streak is seen occasionally on a head. Short hair on muzzle is pure grey rather than slate. Nostril pad is brownish, stiff facial keel is cream to yellowish. Palms and soles are brownish below, grey to slate (rarely whitish) dorsally. Claws are amber white.

Nipples. Six, one pectoral and two inguinal pairs, respectively.

Penis has a simple and elongated glans with a three-lobed apex. The glans is covered throughout with small denticles (figured in Ognev, 1947, and Yiğit et al., 2006c). Baculum is of simple shape, elongated and bent dorsally; base is expanded in some populations. Mean length varies between populations from 4.36 to 7.38 mm (Yiğit et al., 2006c). Differences in baculum are significant among cytotypes (Coşkun, 2004c; Yiğit et al., 2006c).

Skull is heavily-built, pronouncedly ridged in adult animals and with a gradually sloping occipi-


Figure 233. Skins of Spalax xanthodon in dorsal and ventral view. a - a female from the Island of Bozcaada; b - a male from 5 km west of Bağdaşan, district Kars. Photo: C. Mlinar.
tal. Infraorbital foramen is much expanded dorsally. Rostrum is more slender than in S. leucodon; rostral width is $27.0-37.8$ \% of the rostrum length (mean $=34.0 \%$; $\mathrm{N}=43$ ). Nasals are expanded anteriorly; apex is usually pointed; naso-frontal suture is at the level of infraorbital openings. Zygomatic arches are widely expanded (zygomatic width relative to condylobasal length $=77.3$ \%; range $=73.9-80.9 \%$ ); interorbital region is broad and flat in juveniles, constricted and ridged in adults. Brain-case is broadly ovate; interparietals become increasingly constricted with advanced age. Skull is as deep as in S. leucodon; height of braincase averages 42.8 \% of the condylobasal length (range = 39.4-46.4 \%). Diastema is long (more than twice the length of the upper molar row) but incisive foramens are small. Posterior palatal foramina are mainly anterior to $2^{\text {nd }}$ molars and are separated by a high and narrow medial septum. Hard palate terminates slightly behind tooth-row; its posterior margin is straight or dentate, depending on the population. Interpterygoid fossa is wide; bullae are relatively small.

Mandible is heavy with a powerful rhamus. Angular process is relatively small and bent laterally; condylar process is heavy and situated low; coronoid process is sickle-shaped and strong; alveolar process is powerful, laterally oriented and higher than the articular process.

Teeth. Upper incisors are orthodont, short but broad and powerful. Lower incisors are much length-
ened. Enamel on front surface is orange, yellow or white. Sözen et al. (2006) scored colour of incisor enamel as 'white' or 'orange' in a sample $(\mathrm{N}=94)$ from the area of Kastamonu. Orange enamel was more common on upper incisors (85.1 \% of specimens) than on lower ones (33.0 \%).

Molars are high crowned, with short roots. First and $2^{\text {nd }}$ molars are subequal and the $3^{\text {rd }}$ molar is clearly smaller; they are all of circular shape. The enamel pattern of lower molars resembles a mirror-image of the upper row. Occlusal surface becomes worn flat early in life and enamel pattern changes as the molars wear down (Fig. 235). Pattern of enamel folding is at first sigmoid. Lingual enamel folds are curved backward and the labial folds are curved forward. First two molars have two labial and a single lingual fold; $3^{\text {rd }}$ molars have a single re-entrant fold on each side. As the crown wears away, the re-entrant folds tend to become isolated as enamel islands. The single enamel island is clearly seen in the middle worn $3^{\text {rd }}$ upper molar. With advanced wear, this island splits into two islets, and traces of the folds are lost entirely in heavily worn molars.

Number of roots is given in Table 47. Three roots on the $1^{\text {st }}$ upper molar were recorded only in ca. $3 \%$ of specimens (Sözen et al., 2006).

Dimensions are given in Table 48, separately for major regions of Turkey. Males are bigger than females. E.g. maximal body mass in a population from the Island of Gökçeada is 522 g in males and 310


Figure 234. Skull and mandible of Spalax xanthodon, based on a female from Erzurum (SMF). Scale bar $=10 \mathrm{~mm}$.
g in females; comparative figures for the Island of Bozcaada are 348 g and 212 g , respectively (Özkan, 1995). In four cytotypes from northwestern Anatolia, the males are on average heavier by 14-60\% (data from Sözen et al., 2006). Maximum body mass in mole rats from Armenia is 295 g in females and 455 g in males (Harutiunian \& Avetissian, 1983).

Chromosomes. Chromosomal variation is the central phenomenon of the mole rat evolution and Spalax xanthodon is as polymorphic in its karyotype as S. leucodon and S. ehrenbergi. This aspect attracted considerable attention (L’apunova et al., 1974; Savić \& Soldatović, 1979; Giagia et al., 1982; Yüksel, 1984; Gülkaç \& Yüksel, 1989; Yüksel \& Gülkaç, 1990, 1995; Nevo et al., 1995; Ivanitskaya etal., 1997; Sözen \& Kıvanç, 1998; Sözen et al. 1999, 2000a,b, 2006, 2006a; Coşkun, 2003, 2004c; Sözen, 2004; Kankılıç et al., 2007a, b). So
far, 28 different cytotypes were described in S. xanthodon, but two reports throw doubt on their authenticity. Diploid number of chromosomes vary from 36 to 60 (possibly 62) and the number of chromosomal arms ranges between 64 and 84 (Appendix 9). The X chromosome is medium to large, subtelocentric, submetacentric or metacentric. The Y chromosome is a small acrocentric, subtelocentric or submetacentric. All known cytotypes with one exception ( $2 \mathrm{~N}=48$, NF = 64 from Armenia; Fig. 236a) occur in Turkey. Despite such excessive variation, the cytotypes show trends in their geographic distribution; see text below. Note that some cytotypes display further minor variations in centromeric position on various chromosomes (Sözen \& Kıvanç 1998; Sözen, 2004).

Diploid number is stable across the Central Anatolian plateau $(2 \mathrm{~N}=60)$. This extensive area is populated by at least eight distinct cytotypes which dif-


Figure 235. Age-dependent variation in enamel pattern of upper (top) and lower molars (bottom) in Spalax xanthodon from Turkey. Anterior is at the top, lingual is to the left. a - Pazarköy, Isparta; b-5 km west of Bağdaşan, Kars; c - Çığlıkara, Antalya; d, g - Erzurum; e - Savaştepe, Balıkesir; f - Balkusan, Konya. Based on specimens in SMF (a, c, d, g), FMNH (e), and our own material (b, f). Age is in increase from left (the youngest) to right (the oldest). Scale bar $=2 \mathrm{~mm}$.

|  | Aegean Anatolia (İzmir) |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | males |  |  |  |  |  |


|  | Taurus Mts. |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | males |  | females |  |  |  |
|  | N | mean | $\min -\max$ | N | mean | min - max |
| Head and body | 16 | 204.9 | $172-220$ | 26 | 193.0 | $180-228$ |
| Hind foot | 16 | 27.9 | $26.0-30.0$ | 26 | 25.7 | $23.5-30.0$ |
| Weight | 2 |  | $150 / 156$ | 10 | 199.6 | $155-238$ |
| Condylobasal length | 15 | 45.9 | $39.5-49.3$ | 24 | 44.3 | $41.0-47.0$ |
| Zygomatic breadth | 14 | 34.4 | $28.5-38.3$ | 25 | 32.6 | $29.7-35.8$ |
| Maxillary tooth-row | 16 | 7.9 | $7.6-8.4$ | 25 | 7.5 | $6.9-8.5$ |


|  | East Anatolia, eastern Black Sea Mts. |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | males |  | females |  |  |  |  |
|  | N | mean | $\min -\max$ | N | mean | $\min -\mathrm{max}$ |  |
| Head and body | 32 | 205.9 | $172-248$ | 42 | 205.7 | $164-237$ |  |
| Hind foot | 32 | 28.2 | $24.0-31.0$ | 42 | 27.6 | $24.0-30.0$ |  |
| Weight | 9 | 194.0 | $170-281$ | 6 | 224.3 | $185-267$ |  |
| Condylobasal length | 32 | 45.2 | $35.7-53.5$ | 41 | 45.1 | $38.4-53.7$ |  |
| Zygomatic breadth | 32 | 34.6 | $26.3-44.4$ | 40 | 35.4 | $28.3-42.6$ |  |
| Maxillary tooth-row | 32 | 7.7 | $6.2-9.0$ | 41 | 7.9 | $6.8-9.5$ |  |


|  | Island of Gökçeada |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | males |  |  |  |  |  |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |
| Head and body | 14 | 210.7 | $173-241$ | 13 | 200.5 | $155-222$ |
| Hind foot | 14 | 24.7 | $23.0-26.0$ | 13 | 24.0 | $21.0-25.0$ |
| Weight | 14 | 278.2 | $160-522$ | 13 | 238.7 | $130-310$ |
| Condylobasal length | 13 | 43.0 | $36.0-48.5$ | 13 | 41.8 | $38.4-44.0$ |
| Zygomatic breadth | 13 | 36.5 | $30.7-41.6$ | 13 | 35.2 | $29.7-37.5$ |
| Maxillary tooth-row | 14 | 8.2 | $7.6-9.0$ | 13 | 8.0 | $7.6-8.3$ |


|  | Island of Bozcaada |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | males |  |  |  |  |  |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |
| Head and body | 7 | 217.4 | $193-243$ | 3 | 194.0 | $175-205$ |
| Hind foot | 7 | 26.3 | $25.0-27.0$ | 3 | 24.0 | $23.0-25.0$ |
| Weight | 7 | 285.7 | $275-348$ | 3 | 203.0 | $195-212$ |
| Condylobasal length | 7 | 44.6 | $40.7-47.0$ | 3 | 40.5 | $38.0-42.4$ |
| Zygomatic breadth | 7 | 37.2 | $33.3-40.3$ | 3 | 33.2 | $31.0-34.7$ |
| Maxillary tooth-row | 7 | 8.3 | $7.6-8.6$ | 3 | 8.1 | $8.0-8.3$ |


|  | NW Anatolia |  |  |  |
| :--- | :---: | :---: | :---: | :---: |
|  | males |  |  | females |
|  | N | mean | N | mean |
| Head and body | 35 | 223.9 | 46 | 201.9 |
| Hind foot | 37 | 28.3 | 50 | 26.4 |
| Weight | 34 | 284.6 | 44 | 206.0 |
| Condylobasal length | 39 | 49.5 | 53 | 45.5 |
| Zygomatic breadth | 39 | 38.4 | 54 | 33.5 |
| Maxillary tooth-row | 40 | 8.2 | 54 | 8.0 |

Table 48. External and cranial dimensions of Spalax xanthodon from Turkey. Based on Steiner \& Vauk (1966), Kıvanç (1988), Özkan (1995), Coşkun (2004c), Sözen et al. (2006), specimens in BMNH, FMNH, NMNH, SMF and ZFMK, and own material.
fer in the fundamental number of chromosomal arms (NF = 72-84; Fig. 236e). Noteworthy, all these cytotypes most likely lack metacentric and submetacentric autosomes and the only biarmed elements in the autosomal set are subtelocentric. The most widespread cytotype with a contiguous range is with $\mathrm{NF}=$ 80 (nine pairs of subtelocentric and 20 pairs of acrocentric autosomes); the X chromosome is medium to large submetacentric and the Y chromosome is small to medium subtelocentric. This cytotype ranges from north of Lake Akşehir and vicinity of Ankara in the west till the Euphrates River in the east. Populations on the northwestern edge of the range of the $2 \mathrm{~N}=$ 60 cytotype are characterized by $\mathrm{NF}=78$; the same fundamental number was retrieved also to the east of Lake Eğirdir, along the lower flow of the Yeşilırmak River, and on the very southeastern range of the $2 \mathrm{~N}=$ 60 form. A discontinuous occurrence of several cytotypes with different fundamental numbers ( $\mathrm{NF}=74$, 78 , and 82) suggests that they evolved independently. The Havza cytotype ( $\mathrm{NF}=77$ ) on the northern edge of the range contains one heteromorphic autosomal pair.

Mole rats with diploid numbers $2 \mathrm{~N}=56$ and 58 are peripheral to $2 \mathrm{~N}=60$ cytotype (Fig. 236d). The fundamental number of chromosomal arms vary from $\mathrm{NF}=68$ to $\mathrm{NF}=78$ (in $2 \mathrm{~N}=58$ ), and is either $\mathrm{NF}=72$ or $\mathrm{NF}=74$ in the $2 \mathrm{~N}=56$ cytotype. Giv-
en a highly dispersed occurrence of these cytoypes, we again suggest their parallel origin. The $2 \mathrm{~N}=54$ chromosomal form shows three distinct fundamental number counts: $\mathrm{NF}=72,74$, and 75 (the last count results from the presence of one heteromorphic autosomal pair). Again, these cytotypes are peripheral to $2 \mathrm{~N}=60$ animals, but also overlap with them (Fig. 236c). The range of the cytotype NF $=74$ is disconnected; the western segment is restricted to the area between the middle flow of the Kızılırmak and Kamış rivers, and the eastern portion is to the east of the Euphrates. Situation with the cytotypes having $2 \mathrm{~N}=50$ and $2 \mathrm{~N}=52$ (both containing populations with fundamental number either $\mathrm{NF}=70$ or 72 ) is analogous to the situation reported above (Fig. 236b). Particularly noteworthy is the cytotype $2 \mathrm{~N}=50$, NF $=70$, which is broadly sympatric with $2 \mathrm{~N}=50$, NF $=72$ in northeastern Anatolia, but occurs also in the western Black Sea Mts. and possibly in the Aegean Anatolia. A unique mole rat population with $2 \mathrm{~N}=40$ and $\mathrm{NF}=72$ is restricted to a small area to the south of Lake Beyşehir (Fig. 236a). Due to the peripheral position of the majority of cytotypes, their diversity is high in the eastern Taurus Mts. and particularly so in the Black Sea Mts. to the west of the Kızılırmak River. E.g., no less than five different cytotypes ( 2 N = 50-58) occupy a relatively small area in northwestern Anatolia: $2 \mathrm{~N}=50$, NF $=70$ (Kaltepe near Ka-
rabük), $2 \mathrm{~N}=52, \mathrm{NF}=70$ (Marmara and vicinity of Bolu), 2N = 54, NF = 72 (isolates around Eflani, Zonguldak, and Başçiftlik in the eastern Black Sea Mts.), $2 \mathrm{~N}=56, \mathrm{NF}=74$ (vicinity of Kastamonu), and 2N = 58, NF = 78 (known only from Sarıkavak).

Northeastern Anatolia is populated by mole rats having $2 \mathrm{~N}=50$ (see above) and $2 \mathrm{~N}=48$. Three cytotypes of the latter, which are evidently separated by the range of the former (Fig. 236a), are characterized by different fundamental numbers: NF $=64$ (known only from Armenia), NF = 68 (small range
to the north of Van), and NF = 71 (due to one heteromorphic pair of automosomes). The Aegean is occupied by mole rats which have one of the lowest diploid numbers recorded in S. xanthodon: $2 \mathrm{~N}=38$ ( $\mathrm{NF}=74$ ). Autosomal complement consists of six metacentric, eight submetacentric, three subtelocentric and one acrocentric pairs; the X chromosome is mainly a large subacrocentric and the Y chromosome is small acrocentric. The same cytotype also occurs on the Aegean island of Lesbos (Giagia et al., 1982) where it has presumably remained unchanged during


Figure 236. Geographic distribution of chromosomal forms in Spalax xanthodon. Cytotypes are arranged according to ascending diploid numbers (2N). Fundamental numbers of chromosomal arms (NF) are shown by symbols; question marks lack of information on NF. Right bottom insert shows two cytotypes which were reported only once but never confirmed since. For further details see Appendix 9.
the island's isolation from the mainland Anatolia, for about the last 10,000 years. Another cytotype of even lower diploid number ( $2 \mathrm{~N}=36$, NF $=70$ ) was reported from the vicinity of İzmir by Sözen et al. (1999) but never confirmed afterwards.

Nevo et al. (1995) reported $2 \mathrm{~N}=62$ cytotypes from a number of localities stretched across the range of $2 \mathrm{~N}=60$ chromosomal races, but none of their reports have been subsequently confirmed (Fig. 236f).

The prevailing mechanism in chromosomal evolution was presumably an increase in diploid number
via Robertsonian mutations with a subsequent reduction in number of biarmed chromosomes. Diploid number of chromosomes correlates negatively with water availability variables, hence, the more stressful the environment, the higher the chromosomal count (Nevo et al., 1995). This pattern was confirmed by (Sözen et al., 2000b) along the environmental gradient from the Taurus Mts. towards Central Anatolia with a progressive Robertsonian series ( $2 \mathrm{~N}=52$ $\rightarrow 56 \rightarrow 58 \rightarrow 60$ ) from mesic towards arid habitats. The increase in diploid number may have several ef-


Figure 237. Dorsal view of skulls in adult Spalax xanthodon from Turkey to show variation in shape. a - a female from the Island of Bozcaada; $\mathbf{b}$ - a female from İzmir (topotype of xanthodon); $\mathbf{c}$ - a female from Çankiri (type of captorum); $\mathbf{d}$ - an unsexed individual from Murat Dağı, Uşak (type of corybanthium); $\mathbf{e}$ - a female from Ankara; $\mathbf{f}$ - an unsexed individual from Ovacık, Tunceli (topotype of munzuri). Based on specimens in BMNH (b-e) and our own material (a); f - redrawn from (Coşkun, 2004). Not to scale.
fects, singly or in combinations (Nevo et al., 1995, 2001): (1) an increase in the recombination potential; (2) a reduction of aberrational losses due to Spalax genome size (8.4-8.6 pg of DNA); (3) the optimization of genes and gene groups' function; (4) a regulation of chromosome folding and cellular machinery.

So far as is known, all cytotypes of S. xanthodon are allopatric, at least on a small scale, with no evidence of parapatry. This contradicts the situation of S. ehrenbergi in Israel, where parapatric cytotypes hybridise over restricted zones of overlapping ranges (Nevo et al., 2001). Cytotypes of S. leucodon are also predominantly allopatric, however several cases of parapatry have been demonstrated (Savić \& Soldatović, 1984).

## Variation

Kivanç (1988) revised mole rats of Turkey (as Spalax leucodon) using morphological characters. He recognised five subspecies: S. l. nehringi, S. l. armeniacus, S. l. cilicicus (synonyms: corybanthium, captorum), S. l. anatolicus (synonym: xanthodon) and S. l. turcicus. All these races were mapped for Anatolia and ssp. turcicus was also reported for Thrace. As stressed above in the account on taxonomy, mole rats from the Marmara region (denoted as turcicus) are not identical to those from the European side of the Bosporus and Dardanelle straits.

Kivanç (1988) was evidently wrong in some details; e.g. Sözen et al. (2000b) showed that chromosomal data are not strictly concordant with two morphological subspecies (nehringi and armeniacus) in part of their ranges. Despite such minor deviations, morphological subspecies recognized by Kivanç are amazingly concordant with main cytotypes occupying Anatolia. This concurrence is particularly obvious in Central Anatolia, the Aegean region and for populations occurring to the east of the Euphrates River. We therefore assume that Kivanç (1988) in his detailed work might recognise main phylogenetic lineages in Anatolian mole rats which makes his revision a solid starting point to any forthcoming phylogenetic study of S. xanthodon.

The determination key by Kivanç (1988) is given below with some modifications. First of all, note that Kivanç clumped leucodon and xanthodon together. Also note that character states in dichotomy 3 of the subsequent key are not concordant with Fig. 4
in Kivanç (1988: p. 13), evidently the consequence of a typographic error in the quoted paper.

## Key to subspecies (based on Kivanç, 1988)

1 Posterior margin of hard palate with protuberance (Fig. 238b); size large

1* Posterior margin of hard palate straight (no protuberance; Fig. 238a); size smaller

2 Foramens on the posterior naso-premaxillary suture; nasals usually do not reach line of posterior border of the infraorbital slit

## S. l. armeniacus

2* Naso-premaxillary suture with no foramens on its posterior part; nasals usually reach line of posterior border of the infraorbital slit
S. l. nehringi
$31^{\text {st }}$ upper molar single rooted; nasals usually shorter than combined length of frontals and parietals; posterior palatal foramen usually anterior to $2^{\text {nd }}$ molar
S. l. cilicicus

3* $1^{\text {st }}$ upper molar with 2 roots; nasals usually longer than combined length of frontals and parietals; posterior palatal foramen usually anterior to $2^{\text {nd }}$ molar

## S. l. anatolicus

3** $1^{\text {st }}$ upper molar with 3 roots; nasals usually shorter than combined length of frontals and parietals; posterior palatal foramen is usually reaching level of $2^{\text {nd }}$ molar
S. l. turcicus ${ }^{1)}$
${ }^{1)}$ Three-rooted condition in populations from the Marmara region (turcicus sensu Kivanç, 1988) is an exception rather than the prevailing morphotype (see above account on dentition).

There is not much size variation between regions and some of the differences (cf. Table 48) might reflect discrepancies among authors in ageing their material.


Figure 238. Variation in a shape of the posterior margin of the hard palate in Spalax xanthodon from Turkey. Anterior is at the top. a - Bolu; b-Erzurum (SMF specimens). M3 - $3^{\text {rd }}$ upper molar; tb - tympanic bulla. Scale bar $=5 \mathrm{~mm}$.

Chromosomal polymorphism is described above. The phylogenetic analysis based on allozyme diversity at 37 gene loci among 20 S. xanthodon populations suggests a basal position for the marginal populations (Aydın, Bolu, Sarıkamış, Erzurum), while those from the central Anatolian plateau are seemingly of younger origin (Nevo et al., 1995).

Genetic diversity within the Anatolian S. xanthodon is low on average. Partitioning of the 76 alleles into widespread, sporadic and localised showed that 79.5 \% of alleles are not widespread (Nevo et al., 1995). Genetic diversity correlates negatively with water availability variables. This factor, oper-
ating through aridity stress, presumably affected allozyme evolution in Anatolian moles rats in a similar way as their chromosomal differentiation (Nevo et al., 1995).

## Distribution

The Anatolian mole rat is nearly endemic to Turkey. In the northeast, its range extends to Transcaucasia, but occupies only an area of $2,000 \mathrm{~km}^{2}$ in southwestern Georgia (Bukhnikashvili \& Kandaurov, 1998). Range is also very restricted in northwestern Armenia where the animal was found only on the western, northern and northeastern slopes of Mt. Alagez and in the lowlands at its foothills (Šidlovskij, 1976). Savić \& Soldatović (1984) and Bukhnikashvili \& Kandaurov (1998) also reported the Anatolian mole rat for northern Iran. Gromov \& Erbajeva (1995) mention S. xanthodon (as S. nehringi) for northern Iraq; this certainly relates to S. ehrenbergi (see under that species).

Another extralimital occurrence of S. xanthodon is on the Greek Island of Lesbos. This is part of a general pattern seen in the eastern Aegean islands. Namely, numerous islands off the western coast of Turkey, although politically part of Greece, belong biogeo-


Figure 239. Distribution of Spalax xanthodon in Turkey and adjacent regions. For further details on records see Appendix 8.
graphically to Anatolia (Laar \& Daan, 1967). The Anatolian mole rat also occurs on a further two islands offshore of the western Anatolian coast, Bozcaada and Gökçeada. Bozcaada, with its surface area of $36 \mathrm{~km}^{2}$ is possibly the smallest isolate with a permanent mole rat population; Gökçeada ( $285 \mathrm{~km}^{2}$ ) is nearly ten-fold larger. Mole rats are widespread on both of these islands (Özkan, 1995).

Spalax xanthodon is widespread in the Aegean and Central Anatolia. Along the Mediterranean coast, the range tentatively follows the seashore (although the animal does not descend close to sea level) as far east as the vicinity of Adana. At that point the distributional border turns northward and follows the line Ala Dağları - Göksun - Malatya (a report for Karadut is based on owl pellets and requires verification). Further east, the range border follows the western bank of the Euphrates and the northern bank of the Murat River till the vicinity of Muş (the available record is from 20 km west of Muş). In eastern Anatolia, mole rats are present southward of the Murat, around Lake Van and further north till Bağdaşan and Ardahan. The northern border evidently does not follow the Black Sea shoreline and the mole rat is also putatively absent from the northwesternmost Marmara. The Anatolian mole rat is evidently allopatric with respect to S. ehrenbergi.

Palaeontology. Anatolia has been continuously populated by mole rats since the Lower Miocene (Ünay, 1996, 1999) and mole rats from the genus Pliospalax were an abundant rodent group in Central Anatolia already in the Late Pliocene ( 16.3 \% of all rodent specimens found in Çalta; Şen \& Bruijn, 1977) when the environment was a steppic one (Şen, 1978).

The Lower Pleistocene mole rats from the Aegean Island of Kalymnos have already been identified as Spalax cf. nehringi (Kuss \& Storch, 1978), while the material found in the Middle Pleistocene strata on the Island of Chios match perfectly the extant $S$. xanthodon (Storch, 1975). From this site Storch (1975) published a photograph of the well preserved cranium of an immature individual. Molars from Emirkaya-2 (Middle Pleistocene) are reportedly indistinguishable from the extant species, even though they were ascribed to S. cf. leucodon (Montuire et al., 1994) or S. cf. ehrenbergi (Șen et al., 1991). The Anatolian mole rat was also present with some in-
termittency from the Middle Palaeolithic through the Upper Palaeolithic into the Holocene near Antalya (Storch, 1988). Corbet \& Morris (1967) did not detect this animal in the Holocene material (presumably < 7,000 years old) from Finike, Antalya, but Hír (1991) found it to be relatively abundant in an undated sample from Bolkar Dağ, the eastern Taurus Mts. Vereščagin (1959) reported from the Caucasus region only the Pleistocene and Holocene remnants of S. microphtalmus and S. giganteus. Both these species have extant ranges to the north of the Caucasus.

## Нabitat

Habitat selection of S. xanthodon is very similar to the one in S. leucodon, and the only difference is that a considerable part of the former's range is under more xeric conditions. The Anatolian mole rat therefore ranges from the Aegean and partly Mediterranean coasts across steppes and semideserts of Central Anatolia to high elevation pastures $>2,000 \mathrm{~m}$ a.s.l. It avoids forests, rocky substrate, swamps and marshes.

Main habitats in the Aegean Anatolia are pastures and a mosaic of small scale cultivations, orchards, brushes, pastures and olive growths. In the calcareous Taurus Mts. mole rats are restricted to deeper soil, frequently at the bottom of conical depressions (dolines), but are absent from the shallow soil layer on the slopes. Many of the patches that provide mole rats enough soil for their burrowing activities are frequently so small that they hardly support more than a single animal. Central Anatolia is the main homeland of S. xanthodon, where the animal abounds in steppes covered by perennial grasses. Vegetation is largely of Salvia cryptantha, Ziziphora capitata, Teucrium polium, Medicago radiate, Astragalus sp., Festuca sp., Cynodon sp., Thymus sp., and Polyogonum sp. Steppes to the east of the Euphrates River are dominated by Astragalus angustifolius, A. microcephalus, Agropyron repens, Echinops ritrio, Salvia aethiops, Senecio vernalis, Hyoscyamus niger, Centranthus longiflorus, Parietaria judaica, Torilis leptophyla, Eryngium campestre, Festuca valesiaca, Eremopoa songarica, Bromus danthoniae, B. tomentellus, Equisetum ramosimum, Atraphaxis billardieri, Ornithogalum sp., Crepis sp., Medicago sp., and Euphorbia sp. (Yiğit et al., 2003). In the high plateau of Central Anatolia we found S. xanthodon to be abundant even in the driest alkaline soil around Lake Tuz, sparsely
covered with vegetation and receiving $<150 \mathrm{~mm}$ of rainfall annually. In marginal regions, the mole rat generally occurs only sporadically, although reasons for this are not always obvious, e.g. in Mt. Keltepe (ca 150 km north of Ankara) which is a marginal lo-
cality, Sözen (2004) recorded mole rats only on the southern and eastern slopes from 1,300 m to 1,850 m a.s.l. (the peak of the mountain is at $2,000 \mathrm{~m}$ ).

Altitude. Vertical range in Anatolia is from close to sea level (lowest record is at 50 m a.s.l.; Nevo et


Figure 240. Habitat of Spalax xanthodon: a - Central Anatolian steppe around Mt. Ercyes, Kayseri; b - arid steppe in Cihanbeyli, Konya; c - arid steppe around Lake Tuz Gölü; d - karstic valley (dolines) in Çığlıkara, Antalya (note that only the bottom of dolines provides soil deep enough for burrowing); e - a high plateau at Yellibeli Geçidi, eastern Taurus Mts., district Konya; f - a valley of the River Gök Çay near Balkusan, district Konya. Photo: B. Kryštufek (a, e), A. Kryštufek (b-d, f).
al., 1995) to 2,600 m (5 km west of Bağdaşan, Kars); Yiğit et al. (2006c) gave 2,900 m a.s.l. as the highest occurrence. However, the animal is most widespread and abundant between 900 and 1,600 m a.s.l. Altitudinal range in Georgia is $700-2,400 \mathrm{~m}$ a.s.l., but optimal habitats are at 1,200-1,600 m (Bukhnikashvili \& Kandaurov, 1998).

Along the southern Anatolian coast, the Anatolian mole rat is largely absent from lower elevations. Along a transect Antalya - Elmalı - Cığlıkara (sea level - $1,750 \mathrm{~m}$ ) we recorded the first mole rats 20 km east of Korkuteli at 950 m a.s.l. Further east in the Taurus Mts., between Antalya and Isparta, they appeared at $1,050 \mathrm{~m}$ a.s.l.

Mole rats frequently go above $2,000 \mathrm{~m}$ a.s.l., but factors determining their upper altitudinal range are not always evident. In the mountains above Ardahan we observed abundant mole rats' digging activity up to $2,000 \mathrm{~m}$ a.s.l., while the only subterranean rodent we recorded on alpine pastures above this elevation was Prometheomys schaposchnikowi.

The two island populations on Gökçeada and Bozcaada occur at low elevations; the highest altitudes for the islands are 700 m and 191 m , respectively.

Associates. Mounds of the Anatolian mole rat occur in habitats occupied by Spermophilus xanthoprymnus, S. taurensis, Cricetulus migratorius, Mesocricetus brandti, Microtus guentheri, M. hartingi,
M. socialis, M. dogramacii, M. anatolicus, M. levis, M. arvalis, M. daghestanicus, Apodemus witherbyi, Mus macedonicus, Meriones tristrami, M. vinogradovi, M. dahli, Allactaga williamsi, and A. elater. Anatolian mole rat is in no place sympatric with $S$. ehrenbergi.

Information on sympatry with another two burrowing rodents of Anatolia (Ellobius lutescens and Prometheomys schaposchnikowi) is contradictory. We did not find mole rats in sympatry with $P$. schaposchnikowi. Coşkun \& Ulutürk (2003) demonstrated that ranges of mole rats (S. xanthodon) and mole voles (E. lutescens) are mutually exclusive in eastern Turkey with a gap of 5-8 km in between. Contrary to this, Yiğit et al. (2003) reported mole rats to be sympatric with E. lutescens at 10 km south of Van and with P. schaposchnikowi in "Kars and Ardahan". Since Yiğit et al. (2003) did not always clearly define their sampling locations, we conclude that a narrow sympatry between these subterranean rodents is not proven.

Density. Mounds by Anatolian mole rats are occasionally very abundant in Turkey, even in its driest and most desolated regions. Yiğit et al. (2006c) reported densities in Anatolia to be up to 6 animals per 0.1 ha. The highest densities in Transcaucasia (8-9 individual per ha) are on mesic meadows 1,5001,600 m a.s.l. (Gromov \& Erbajeva, 1995).


Figure 241. Mounds of soil excavated by Spalax xanthodon in Çığlıkara, Antalya.
Photo: A. \& B. Kryštufek.

## Biology

Biology of the Anatolian mole rat is little known (Gromov \& Erbajeva, 1995) and was mainly studied in Transcaucasia.

Activity is presumably as in the remaining two mole rats occurring in Turkey.

Burrows. Characteristic mounds of unearthed soil are a characteristic feature of the Anatolian landscape. Burrows are evidently very similar to those constructed by the lesser mole rat and consist of a nest chamber, latrine, caches and feeding galleries (Yiğit et al., 2006c).

Reproduction was studied in Armenia between 1978 and 1982 using a sample of 451 mole rats (Harutiunian \& Avetissian, 1983). Minimum body mass for sexually mature animals was 165 g (females) and 147 g (males). Scrotal males with the ongoing spermatogenesis were found all year round, but their proportion peaked in March and April. Breeding season started in January and the last pregnant females were recorded in May. Females had one litter per year and pregnancy lasted at least 26 days. Litter size was $1-6$ (mean $=2.6$; $\mathrm{N}=83$; Harutiunian \& Avetissian, 1983). Proportion of sexually active females and mean litter size depended on body size. Mean number of embryos was 2.3 in size class $165-179 \mathrm{~g}, 2.5$ in $220-239 \mathrm{~g}$, and 3.0 in $280-299 \mathrm{~g}$. Proportion of reproductively active females varied between size classes: 23.0 \% (165-179 g), 39.5 \% (220-239 g) and $50.0 \%$ (280-299 g). Body mass and reproductive success were highly correlated in both cases. Percentage of females participating in reproduction was on average 74.5 \% but varied between years (51.7-89.8 \%). Sex ratio was biased towards females (1 male : 1.4 females) but this changed between years. From 1978 to 1982, the sex ratio varied between 1 male : 0.8 female, and $1: 2.1$ (Harutiunian \& Avetissian, 1983).

In Turkey, the reproductive period lasts from January to July with a peak in February. Litter size is very similar to that of Armenia: range 1-6 and average of about 3 cubs. Sex ratio is female biased (59.2 \%; Yiğit et al., 2006c).

Newborn cubs are 9.0-9.5 g heavy and 50-60 mm long. When they reach $75-85 \mathrm{~g}$, they start exploring underground galleries but green vegetable food is taken only when their body mass reaches $90-100 \mathrm{~g}$. They are weaned at a body mass of 115 g and the last
cubs were found in the maternal nest in early June (Harutiunian \& Avetissian, 1983).

Food habits are reported for Armenia (Harutunian, 1983). Diet mainly consists of bulbs of monocotyledonous plants, roots and tubers; animals also feed above ground. Harutunian (1983) recorded 58 different species of plants from 22 families in their diet: Asteraceae (11 species), Alliaceae (1), Apiaceae (5), Brassicaceae (6), Caryophyllaceae (2), Chenopodiaceae (2), Convolvulaceae (1), Equisetaceae (1), Euphorbiaceae (1), Fabaceae (6), Geraniaceae (1), Iridaceae (2), Liliaceae (6), Plantaginaceae (1), Poaceae (3), Polygonaceae (2), Ranunculaceae (1), Rosaceae (1), Rubiaceae (1), Salicaceae (1), Scrophulariaceae (1), Solanaceae (1), and Violaceae (1). Geranium tuberosum is the most important dietary item and various weeds are consumed in arable fields. Daily consumption equals to 22.2-59.4 \% of the animal's body mass (Harutunian, 1983).

Food is stored in underground caches. Mean amount of stored food was $741-1,556 \mathrm{~g}$ and varied between seasons: $45-3,902 \mathrm{~g}$ in spring $(\mathrm{N}=8)$, $55-$ 285 g in summer $(\mathrm{N}=3), 42-2,510 \mathrm{~g}$ in autumn ( N $=4)$, and $2,700 \mathrm{~g}$ in winter ( $\mathrm{N}=1$; Harutunian, 1983). Gromov \& Erbajeva, (1995) reported stores of potatoes, sugar beet and carrot to contain up to 10 kg or more of food.

Yiğit et al. (2006c) reported damage especially to potatoes, onion, garlic, carrot, and sugar beet. Yüzbaş \& Benli (1995) on the other hand did not consider mole rats to be a pest to agriculture in Turkey.

Predation. Obuch (1994) found mole rats in the pellets of the tawny owl Strix aluco and of the eagle owl Bubo bubo, but percentages were low (2.4 \% and 0.6 \% of small mammals, respectively). In an undated subfossil sample from Bolkar Dağ which evidently results from owl pellet accumulation, mole rats were more abundant, i.e. 5.6 \% of all rodents ( N = 577; Hír, 1991).

Conservation. In Anatolia, the mole rat is in decline due to intensification and the spread of agriculture, destruction of animals as pests, and also as a result of urbanization. The majority of cytotypes are classified as Vulnerable (Yiğit et al., 2006c). Bukhnikashvili \& Kandaurov (1998) consider the Anatolian mole rat to be a species of conservation concern in Georgia as well. The main threats they
face are habitat degradation by agriculture and overgrazing, destruction of mole rat as a pest to crops, and isolation of populations due to habitat fragmentation. Range supposedly shrunk.

## Palestine mole rat - Spalax ehrenbergi

Spalax ehrenbergi Nehring, 1898. Type loc.: Jaffa, Palestine.
Spalax intermedius Nehring, 1898. Type loc.: Tschengenkoi, einige Stunden landeinwärts Iskenderun, nördlichen Syria (= Çengenköy, Arsuz, İskenderun, Turkey, according to Kıvanç, 1988 and Coşkun et al., 2006).
Spalax ehrenbergi var. ceyhanus Szunyoghy, 1941. Type loc.: Ceyhan (about 50 km east of Adana), Turkey.
Spalax nehringi nevoi Coşkun, 1996. Type loc.: Sargüllük, 6 km west of Gaziantep, Turkey (Coşkun, 1996a).

## Taxonomy

Opinions on the phylogenetic position of the Palestine mole rat are contradictory. Topachevskii (1976) considered it to be a primitive form with a less advanced molar pattern than the Middle Pleistocene Spalax odessanus. On the other hand, Nevo et al. (1995) suggested that S. ehrenbergi is a derivative of the Spalax leucodon-nehringi group and the final step in a continuous penetration of mole rats into a stressful, arid environment. Molecular evidence does not provide conclusive results regarding these relations (Nevo et al., 2001).

Students of Turkish mammals largely considered the Palestine mole rat to be specifically distinct from S. leucodon or S. xanthodon (Ellermann, 1948; Ellerman \& Morrison-Scott, 1951; Misonne, 1957; Lehmann, 1969; Lewis et al., 1967; Atallah, 1978; Osborn \& Helmy, 1980; Coşkun \& Bilgin, 1988; Kıvanç, 1988; Doğramacı, 1989; Nevo et al., 1994, 1995, 2001; Demirsoy, 1996; Kurtonur et al., 1996; Ivanitskaya et al., 1997; Sözen \& Kıvanç, 1998; Coşkun, 1999b, 2004,a,b; Sözen et al., 1999; Yiğit et al., 2003; Shehab et al., 2004; Coşkun et al., 2006, 2009). Some authors reported Palestine mole rats under S. leucodon (Reed, 1958; Steiner \& Vauk, 1966; Harrison,

1972; Kadhim et al., 1977; Corbet, 1978; Nadachowski et al., 1990; Harrison \& Bates, 1991; Qumsiyeh, 1996; Mendelssohn \& Yom-Tov, 1999; Amr, 2000; Amr et al., 2004), S. nehringi (Coşkun, 1996a) or even S. micropthtalmus (Ferguson, 2002).

Palestine mole rats from Israel were a model group in intensive evolutionary research for more than three decades. An enormous body of accumulated information was summarised by Nevo et al. (2001). Four sibling species from Israel were first recognized by karyological evidence, but subsequent studies also uncovered differences in body measurements and colour, ear ossicles, baculum shape and size, dental peculiarities, and in a broad array of physiological and behavioural quantitative traits. Cytotypes do hybridise in nature. While the hybrids are at least partly fertile, their overall fitness is lower than that of their parents (Savić \& Nevo, 1990). Genetic evidence derived from proteins and DNA sequences failed to detect genetic introgression across hybrid zones (Nevo et al., 2001). Therefore, different cytotypes have been formally named as a distinct species.

While proposing new names for four Israeli cytotypes, Nevo et al. (2001) did not strictly follow the rules set by the International Code of Zoological Nomenclature (ICZN, 1999). Because ehrenber$g i$ is based on material from Israel (Jaffa) one of the new names is unavoidably its junior synonym. As the type locality of S. ehrenbergi is from the hybrid zone of two cytotypes and therefore also of the newly proposed names, namely of S. carmeli Nevo, Ivanitskaya, Beiles, $2001(2 \mathrm{~N}=58)$ and S. judaei Nevo, Ivanitskaya, Beiles, 2001 ( $2 \mathrm{~N}=60$ ), its cytogenetic identity is not known. Consequently, Nevo et al. (2001) reserved ehrenbergi to designate the superspecies but recognised no species per se (Musser \& Carleton, 2005). Such a solution is formally inappropriate and the status of the name ehrenbergi is to be formally clarified (Musser \& Carleton, 2005). Musser \& Carleton (2005) accepted the validity of all four species named by Nevo et al. (2001), but curiously applied ehrenbergi for populations occurring outside Israel. If the name ehrenbergi cannot be properly defined and hence applied to one of the newly established species occupying Israel, it would be more appropriate to use for the non-Israeli mole rats from the ehrenbergi complex the oldest name which
is not based on the material from Israel. Two such names are available for mole rats of Turkey and adjacent regions, Spalax intermedius and Spalax kirgisorum.

Spalax kirgisorum Nehring, 1898 was described on the basis of skull and skeleton which Nehring obtained from W. Schlüter. It was claimed that the material originated from Ryn Peski in the steppes of western Kyrgyzia (now western Kazakhstan; Topachevskii, 1976). Nehring's mole rat material was studied subsequently by Méhely (1913) who concluded that S. kirgisorum is actually a member of S. ehrenbergi group. Although Méhely expressed doubts whether the type was correctly labelled, he accepted the assertion by Nehring that such a suspicion is groundless. Méhely (1913), still not entirely convinced, supposed for a short time that small mole rats might range from the Near East to Kyrgyzia. A subsequent examination of Spalax giganteus Nehring, 1898, from western Kazakhstan, convinced Méhely that the two mole rats are very distinct. Although Méhely (1913) recognised S. kirgisorum to be a valid species, he did not speculate on a possible
locality where the type might originate from. Thus, the type locality of kirgisorum remains unknown (Topachevskii, 1976). Ellerman \& MorrisonS cott (1951) stated it to be Syria, but this is under question. Although reasons for such a decision are not given, this opinion was accepted, e.g. by Harrison \& Bates (1991). Kıvanç (1988) in his review of Turkish mole rats still continues to report Kyrgyzia ('Kırgız stepleri') as the type locality.

Description of Spalax intermedius Nehring, 1898, was based on a specimen collected in "... Tschengenkoi, einige Stunden landeinwärts von ... Iskenderun im nördlichen Syria" (Nehring, 1898). Tschengenkoi was said to be a distance of several hours by walk inland from İskenderum, therefore within the political borders of modern Turkey. Kıvanç (1988) identified Tschengenkoi as Çengenköy near Arsuz, Hatay. Méhely (1913) who synonymised intermedius with kirgisorum, on grounds of page priority, did not specify type locality for the former. Ellerman \& Mor-rison-Scott (1951) gave type locality of intermedius as Syria with no additional arguments.

Nevo et al. (1995) and Ivanitskaya et al.


Figure 242. Palestinian mole rat Spalax ehrenbergi from 25 km west of Şanlı Urfa. Photo: A. Kryštufek.
(1997) concluded that several cytotypes from Turkey are genetically isolated and thus act as an independent biological species. This was misunderstood by Coşkun et al. (2006) who concluded that "Nevo et al. (1995) have pointed out that each chromosomal form must be assigned to a separate biological species". Although further studies will most likely demonstrate that many cytotypes are actually an independent species, it is probably not appropriate to claim a specific status for each cytotype. The time of divergence between four 'chromosomal' species occurring in Israel and derived from DNA-DNA hybridization ranges from $2.00-2.35$ to $0.18-0.75$ million years (Nevo et al., 2001). Hence, cytotypes are of very different age in Israel and similar situation can also be expected for Turkey.

## Description

External characters. Small mole rats of the same body proportions as the previous two species. Nostril


Figure 243. Skin of Spalax ehrenbergi in dorsal and ventral view. Based on a female from 25 km west of Şanlı Urfa. Photo: C. Mlinar.
pad is triangular in outline, $10.8-14.4 \mathrm{~mm}$ broad and $8.0-9.4 \mathrm{~mm}$ high; it is followed by a brush of stiffened hairs directed outward and upward and extending about half-way to the ear, just like in the remaining mole rats. Eyes are rudimentary and the Palestine mole rat is effectively blind (Haim et al., 1983). Thumb is reduced in both, fore and hind feet, but still bears a claw. Palms and soles are bare; there are two large pads on palms and five pads on soles; the three anterior pads at toe bases are smaller than the posterior two. Claws are broad, $4.0-4.5 \mathrm{~mm}$ long on forefeet and $4.3-5.0 \mathrm{~mm}$ on hind feet. Pelage is long, soft and nondirectional; mid-dorsal hairs are $7.0-8.5 \mathrm{~mm}$ long, those on the belly measure $6.0-7.0 \mathrm{~mm}$. Whiskers are scarce and directed forward.

Colour. Hairs are slate grey; those on back and flanks have a short terminal band of dull buff or brown colour. Head and ventral side are invariably slate; where buff hair tips are worn out (particularly on the rump) the animal looks predominantly slate grey. There is no clear demarcation along flanks. Yellowish or creamy brush of stiffened hairs contrasts grey background colour of the head. Fore-feet are brown and hind feet are covered by grey hairs on dorsal side. Claws are amber brown. Mole rats living to the south of Turkey are frequently more bright reddish; some populations have a high proportion of animals with irregular white spots on the belly and less frequently also on the back.

Nipples. There are two pairs of inguinal nipples (Amr, 2000).

Penis was studied in four cytotypes from Israel (Simson et al., 1993). The phallus is relatively simple and glans ic covered by microscopic papillae. The opening of urethra is surrounded by $2-3$ lobes, depending on the cytotype. The baculum has the shape of a simple club; it is $5-7.5 \mathrm{~mm}$ long (of which $0.5-$ 1.0 mm belongs to the cartilaginous base) and bent dorsally. The base is $2-5$ times wider than the tip. The baculum is characteristic of four cytotypes from Israel and its size does not depend on overall body size (Simson et al., 1993). Yiğit et al. (2006c) provide details on Turkish populations. The penis is simple, with two or three-lobed apex and glans is covered by spines. Baculum is of simple structure and strongly bent dorsally; it is $4.73-7.59 \mathrm{~mm}$ long.

Skull resembles condition seen in previous two species, but is smaller and less ridged. Two major


Figure 244. Skull and mandible of Spalax ehrenbergi, based on a female from 25 km west of Şanlı Urfa. Scale bar = 5 mm .
crests on the brain-case (the sagittal and the lambdal) develop only with old age, and are never as prominent as in the larger $S$. xanthodon. Interorbital constriction tends to be relatively wider and the entire skull is of paedomorphic appearance. Zygomatic arches are less expanded than in the larger species and zygomatic breadth makes up 68.5-79.9 \% of the condylobasal length (mean $=73.8 \%$ ). In comparison to $S$. leucodon or $S$. xanthodon, the occipital region is less inclined and brain-case is slightly shallower; height of brain-case averages 41.7 \% of condylobasal length (range $=35.0-45.6 \%$ ). Posterior margin of hard palate is broad, smooth or with a medial denticle; interpterygoid fossa is broad. Mandible shows no peculiarities.

Teeth in general, resemble situation found in the remaining two species of mole rats, but there are several differences. Incisors, the upper ones in particular, are with two or three longitudinal grooves (Fig. 220); grooves are shallow and are worn out in some specimens. Enamel is yellow to intense orange on upper incisors and yellowish white or pale yellow on lower ones. Eruption-rate of the incisors is rapid to compensate for their excessive wear by excavation; males use their incisors more than females (Zuri \& Terkel, 2001). Molars are high crowned, with short roots. First and $2^{\text {nd }}$ molars are subequal and $3^{\text {rd }}$ molar is much smaller; they are all of circular shape.


Figure 245. Age-dependent variation in enamel pattern of upper (top) and lower molars (bottom) in Spalax ehrenbergi from Turkey. Anterior is at the top, lingual is to the left. a - a juvenile from Çeylanpınar; b - a subadult from 25 km west of Şanlı Urfa; c - an adult from Adana; d - an old specimen from Tarsus. Based on specimens in ZFMK (a, c), NMNH (d), and our own material (b). Scale bar $=2 \mathrm{~mm}$.


Figure 246. Alveolar pattern in Spalax ehrenbergi from Çeylanpınar. a - upper, $\mathbf{b}$ - lower row. Lingual is to the left and anterior is at the top. Redrawn from Coşkun (1991).

Occlusal surface becomes worn flat early in life and the enamel pattern changes as the molars worn down (Fig. 245). Two islands of enamel are clearly seen in moderately worn $3^{\text {rd }}$ upper molar. With advanced wear, the anterior island splits into two and the molar has up to three enamel islets (Fig. 219f).

Number of roots in the molars is 3 ( $1^{\text {st }}$ and $2^{\text {nd }}$ upper molars), $1-3$ ( $3^{\text {rd }}$ upper molar), 2 ( $1^{\text {st }}$ lower molar) and 2 or 3 ( $2^{\text {nd }}$ and $3^{\text {rd }}$ lower molars) (Coşkun, 1991, and own observations). Alveolar pattern is not always categorical because roots are short and as a consequence alveoli are shallow.

Dimensions are given in Tables 49 and 50. Body mass of males is significantly larger than that of females (Nevo et al., 1986); in Turkish populations, the difference between the sexes is about $10 \%$.

Chromosomes. Diploid number of chromosomes
in S. ehrenbergi varies between $2 \mathrm{~N}=48$ and $2 \mathrm{~N}=$ 60 (Nevo et al., 2001; Coşkun et al., 2006). Turkish populations were studied intensively and large amount of information accumulated over the last fifteen years (Yüksel, 1984; Yüksel \& Gülkaç, 1992; Nevo et al., 1994, 1995; Ivanitskaya et al., 1997; Coşkun, 1999b, 2004a,b,c; Sözen et al., 1999). Chromosomal variation was recently reviewed by Coşkun et al. (2006) who recognised five chromosomal races (populations in their terminology), with diploid numbers ranging from $2 \mathrm{~N}=48$ to $2 \mathrm{~N}=56$, and number of austosomal arms between $\mathrm{NF}_{\mathrm{a}}=62$ and $\mathrm{NF}_{\mathrm{a}}=72$. Unfortunately, the paper by Coşkun et al. (2006) involves inconsistencies and ignores discrepancies between various authors.

The actual knowledge on chromosomal polymorphism is summarised in Fig. 247 and Appendix 10. No less than twelve chromosomal forms (cytotypes) have been recorded so far within Palestine mole rat in Turkey. These forms differ in various combinations of five different diploid numbers ( $2 \mathrm{~N}=48,52,54$, 56,58 ) and nine different fundamental numbers of autosomal arms $\left(\mathrm{NF}_{\mathrm{a}}=62,64,68,70,72,76,78,82\right)$. Differences are due to several types of chromosomal rearrangements: Robertsonian translocations, deletions of euchromatin, chromosome missings, shifts of centromeric position, and heterochromatin deletions or additions; e.g. Ivanitskaya et al. (1997) identified 7-10 rearrangements. No hybrid animals have been recorded so far in Turkey and the extent of parapatry, if at all present, is also unknown.

The most widespread chromosomal form has diploid number $2 \mathrm{~N}=52$ and fundamental number of autosomal arms $\mathrm{NF}_{\mathrm{a}}=72$. The autosomal complement consists of 11 biarmed and 14 acrocentric pairs. The X chromosome is a medium sized metacentric or sub-

|  | males |  |  | females |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | N | mean | $\min -\max$ | N | mean | $\min -\max$ |
| Head and body | 54 | 178.8 | $135-220$ | 78 | 169.4 | $130-210$ |
| Hind foot | 54 | 24.4 | $20.0-29.0$ | 75 | 23.3 | $19.0-27.0$ |
| Weight | 31 | 135.9 | $82-252$ | 46 | 139.6 | $73-186$ |
| Condylobasal length | 58 | 40.3 | $31.8-47.8$ | 78 | 38.7 | $33.0-43.1$ |
| Zygomatic breadth | 54 | 29.6 | $24.0-30.3$ | 78 | 27.8 | $26.5-32.2$ |
| Maxillary tooth-row | 57 | 7.0 | $6.2-8.2$ | 80 | 6.9 | $6.2-7.8$ |

Table 49. External and cranial dimensions of Spalax ehrenbergi from Turkey. Based on Kıvanç (1988), Coşkun \& Bilgin (1988), Coşkun (2004b), Neuhäuser (1936); Yiğit \& Çolak, (1999), specimens in SMF, ZFMK, and NMNH, and our own material.

|  | Elazig, Diyarbakir |  |  |  | Şanlı Urfa |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | males |  | females |  | males |  | females |  |
|  | N | mean | N | mean | N | mean | N | mean |
| Head and body | 14 | 166.6 | 19 | 156.1 | 10 | 183.9 | 11 | 166.9 |
| Hind foot | 14 | 22.1 | 19 | 21.8 | 10 | 23.5 | 11 | 21.5 |
| Weight | 15 | 122.3 | 17 | 110.6 | 1 | 145.0 |  |  |
| Condylobasal length | 14 | 39.9 | 19 | 38.3 | 10 | 39.1 | 11 | 36.9 |
| Zygomatic breadth | 11 | 29.2 | 19 | 27.0 | 10 | 29.3 | 10 | 26.4 |
| Maxillary tooth-row | 14 | 7.1 | 19 | 7.0 | 10 | 6.7 | 11 | 6.6 |
|  |  |  |  |  |  |  | Tars |  |
|  |  | les |  | ales |  |  |  | ales |
|  | N | mean | N | mean | N | mean | N | mean |
| Head and body | 29 | 183.0 | 44 | 177.5 | 1 | 135 | 4 | 150.8 |
| Hind foot | 30 | 25.7 | 44 | 24.4 | 1 | 25.0 |  |  |
| Weight | 16 | 150.6 | 24 | 139.1 | 1 | 53 | 3 | 85.0 |
| Condylobasal length | 33 | 40.8 | 44 | 39.6 | 1 | 32.3 | 4 | 37.4 |
| Zygomatic breadth | 33 | 29.8 | 45 | 28.4 | 1 | 24.0 | 4 | 28.3 |
| Maxillary tooth-row | 33 | 7.1 | 46 | 6.9 | 1 | 6.9 | 4 | 7.5 |

Table 50. Means for external and cranial dimensions for four geographic samples of Spalax ehrenbergi from Turkey. Based on Kıvanç (1988), Coşkun \& Bilgin (1988), Coşkun (2004b), Neuhäuser (1936); Yiğit \& Çolak (1999), specimens in SMF, ZFMK, and NMNH, and our own material.
metacentric, and the Y chromosome is a small acrocentric or subtelocentric. This cytotype was denominated as the Diyarbakır population by Coşkun et al. (2006) and was first described by Yüksel (1984) from Elazığ. Its geographic range extends from the Euphrates basin (where it also occupies the western river bank) in the west to the species' eastern border around Şırnak; the northern border is around Elazığ. Mole rats from Şanlıurfa have identical diploid number but are more polymorphic in fundamental number of autosomal arms which is either $\mathrm{NF}_{\mathrm{a}}=$ 78 (14 biarmed and 11 acrocentric pairs; Nevo et al., 1995) or $\mathrm{NF}_{\mathrm{a}}=76$ (13 biarmed and 12 acrocentric pairs; Ivanitskaya et al., 1997). These differences in the number of chromosomal arms were explained by the changing of centromeric position or pericentric inversion in a small pair of autosomes (Ivanitskaya et al., 1997). Another cytotype ( $2 \mathrm{~N}=54, \mathrm{NF}_{\mathrm{a}}$ $=72$ ) was reported from Suruç (Yüksel \& Gülkaç, 1992), i.e. within the range of the Diyarbakır race, but was not subsequently confirmed by Coşkun et al. (2006). Populations from Gaziantep, which occupy the bank of the Euphrates River opposite to the Diyarbakır form, are highly polymorphic. Three different cytotypes were reported from this small area:
$2 \mathrm{~N}=58, \mathrm{NF}_{\mathrm{a}}=78$ (Nevo et al., 1995), $2 \mathrm{~N}=56, \mathrm{NF}_{\mathrm{a}}$ $=82$ (Yüksel \& Gülkaç, 1992), and $2 \mathrm{~N}=56, \mathrm{NF}_{\mathrm{a}}$
$=78$ (Ivanitskaya et al., 1997). The differences in diploid counts with the same fundamental number of arms are likely due to the Robertsonian process (Ivanitskaya et al., 1997).

A small area between Gaziantep and the Ceyhan River is inhabited by a chromosomal race with 2 N $=52$ and a fundamental number of autosomal arms $\mathrm{NF}_{\mathrm{a}}=70$. The autosomal complement consists of 10 biarmed and 15 acrocentric pairs. The X chromosome is a small submetacentric, and the Y chromosome is a small acrocentric. This cytotype was first described by Coşkun (1999b) from 7 km to the east of Kilis and was subsequently denominated as Hatay population (Coşkun et al., 2006). Individuals from Çengenköy (the type locality of S. intermedius) are of Hatay cytotype (Coşkun et al., 2006). The westernmost portion of S. ehrenbergi range in Turkey (to the west of the Ceyhan River) is inhabited by another form with the diploid number of chromosomes 2 N $=56$ and fundamental number of autosomal arms $\mathrm{NF}_{\mathrm{a}}=68$ (Tarsus population sensu Coşkun et al., 2006). The autosomal complement consists of 7 biarmed and 20 acrocentric pairs. The X chromosome


Figure 247. Geographic distribution of chromosomal forms in Spalax ehrenbergi. Symbols correspond to diploid number counts $(2 \mathrm{~N})$; numbers refer to fundamental numbers of autosomal arms $\left(\mathrm{NF}_{\mathrm{a}}\right)$. For further details see text and Appendix 10.
is small to medium large metacentric or submetacentric, and the Y chromosome is a small acrocentric. A local population from Kozan Pekmezci, situated between the rivers of Ceyhan and Seyhan, has the same diploid number $(2 \mathrm{~N}=56)$ but differs in lower number of autosomal arms $\left(\mathrm{NF}_{\mathrm{a}}=64\right.$; 5 biarmed and 23 acrocentric pairs; Coşkun et al., 2006). Ivanitskaya et al. (1997) showed that cytotypes from Tarsus (2N $=56, \mathrm{NF}_{\mathrm{a}}=68$ ) and Gaziantep $\left(2 \mathrm{~N}=56, \mathrm{NF}_{\mathrm{a}}=78\right)$ differ in the relatively small number of chromosomal rearrangements and are thus closely related. Besides, these two cytotypes are also the most derived among Turkish populations of S. ehrenbergi studied by Ivanitskaya et al. (1997).

A small-range chromosomal form evolved along the northeastern border of S. ehrenbergi (Siirt population sensu Coşkun et al., 2006). The diploid number of chromosomes is $2 \mathrm{~N}=56$ and fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=62$. The autosomal complement consists of 4 biarmed and 23 acrocentric pairs. The X chromosome is a medium sized submetacentric, and the Y chromosome is a small acrocentric. Another form is known from a single locality in southern Hatay; diploid number of chromosomes is $2 \mathrm{~N}=48$ and fundamental number of autosomal arms is $\mathrm{NF}_{\mathrm{a}}=70$. The autosomal complement consists of 12 biarmed and 11 acrocentric pairs. The X chromo-
some is a medium sized metacentric; the Y chromosome has not been described yet (Coşkun, 2004b). This chromosomal race was reported as Yayladağ (Coşkun, 2004b) or Yayladağı population (Coşkun et al., 2006).

## Variation

The Palestinian mole rat is a highly variable species. In Israel, body size displays a latitudinal gradient. Animals living in a cooler and more productive mesic environment are larger than southern animals living in a warmer and less productive xeric environment (Nevo et al., 1986). Colour varies in Israel in accordance with varying soil type; animals living on terra rossa and basal soil are more reddish brown, while specimens from dark soils (alluvial clay, brown rendzina) and light soils (pale rendzina, sandy loams and loess) tend to be more yellowish (Heth et al., 1988a).

Phenetic variation among Turkish populations is not very pronounced. Quite surprisingly, northern populations (Elazığ, Diyarbakir) are smaller than those living further south in Hatay and in arid habitats around Şanlıurfa, thus suggesting the reverse Bergmann's response. Animals from the northern part of their range in Turkey are of approximately the same average size (mean body mass in males:


Figure 248. Dorsal view of skull in adult Spalax ehrenbergi to show variation in shape. a - a female from Haruniye (= Düziçi), Adana Turkey; $\mathbf{b}$ - an unsexed animal from the vicinity of Antakya, Turkey; c - a male from Bekaa valley, Lebanon; d - a male from Damascus, Syria. Based on specimens in ZFMK (a-c) and BMNH (d). Not to scale.
122.3-150.6 g; females: 110.6-139.1g: Table 51) as their counterparts from Israel. Body mass of four cytotypes from Israel varies between 120 g and 173 g (Nevo et al., 2001); animals on Mt. Hermon weigh up to 240 g (Mendelssohn \& Yom-Tov, 1999). Egyptian mole rats are smaller than their counterparts from Israel, but larger than those from Libya (Osborn \& Helmy, 1980).

Kıvanç (1988) recognised two geographical races in Turkey: S. e. intermedius and S. e. kirgisorum. The latter was diagnosed by smaller molar dimensions and was restricted to the area around Șanlıurfa on the eastern bank of the Euphrates River. The material we saw is insufficient to judge the reality of the existence of two morphotypes.

Coşkun (1996a) described, entirely on morphological grounds, a new subspecies Spalax nehringi nevoi from the vicinity of Gaziantep. It is beyond doubt that this taxon is within the scope of S. ehrenbergi, as defined by Musser \& Carleton (2005). Diagnostic characters, however, are not convincing and the new form has not been compared to two subspecies recognised by Kıvanç (1988). Furthermore, no discontinuity in phenetic variation has been demonstrated between nevoi and intermedius (Coşkun, 1996a).

In the times of traditional taxonomy (e.g. Ellerman \& Morrison-Scott, 1951; Topachevskii, 1976), S. ehrenbergi was divided into two subspecies: S. e. aegyptiacus Nehring, 1898 (Type loc.: Ramleh near Alexandria, Egypt) from northeastern Africa, and the nominate form from the rest of species' range. As discussed above, the extensive chromosomal variation suggests several independent species (cf. Ivanitskaya et al., 1997). Allozyme diversity at 37 gene loci was high among four Turkish cytotypes and indicated more than one species in the area. The sample from Tarsus was the most distinct while genetic distance was the lowest between populations from Şanlıurfa and Diyarbakır (Nevo et al., 1995). Reconstruction of the phylogenetic relations among different cytotypes of S. ehrenbergi and based on 25 polymorhic allozyme loci suggested basal position for Turkish samples (Nevo et al., 2001). Genetic indices (mean number of alleles per locus, proportion of polymorphic loci per population, heterozygosity per individual and genetic diversity) are mainly within the range for S. xanthodon, hence the heterozygosity at the population level is low (Nevo et al., 1995).

## Distribution

Eastern and southeastern Mediterranean coast in Africa and the Near East. Populations in Africa (Cyrenaica and Egypt) are isolated from the rest of species' range and the Palestine mole rat does not occupy Sinai (Osborn \& Helmy, 1980). The Palestine mole rat mainly follows the Mediterranean coast in the Near East where it is widespread in Israel (Mendelssohn \& Yom-Tov, 1999) and in Lebanon (Lewis et al., 1967). The eastern border is in western Jordan (Amr, 2000) and in western Syria, where the Palestine mole rat is fairly widespread (Shehab
et al., 2004). The species also populates northern Iraq as far south as the left bank of the Záb al Asfal River (Harrison \& Bates, 1991). The Palestine mole rat has so far not been recorded in Iran (Lay, 1967)
although Reed (1958) reports its occurrence "in the northern corner of Iraq within a few miles of the Iranian and Turkish borders".

Turkey is on the very northern range border of


Figure 249. Distribution of Spalax ehrenbergi in Turkey and adjacent regions. Records: $\mathbf{1}$ - Mersin; $\mathbf{2 a}-5 \mathrm{~km}$ west of Tarsus, Mersin; 2b-3 km north of Tarsus, Mersin; 2c - İbrişim, Tarsus, Mersin; $\mathbf{3}$ - Pirice nahyesi, Karataş, Adana; $\mathbf{4 a}-3 \mathrm{~km}$ west of Yakapınar, Ceyhan, Adana; 4b - 5 km south of Adana; 4c - Şeyhmurat, Adana; 5 - Pekmezci, Kozan, Adana; 6 - Anberinarki, Kadirli, Adana; 7 - Belen, Hatay; 8a - Arsuz, Hatay; 8b - Çengenköy, Arsuz, Hatay; 9 - Şenkoy,Yayladağı, Hatay;
$10 a$ - Beşarlan, Reyhanlı, Hatay; 10b - Reyhanlı, Hatay; 11a - Kırıkhan, Hatay; 11b - Muratpaşa, Kırıkhan, Hatay;
12a - Ceyhan, Adana; 12b - Çona, Osmaniye, Adana; 13a - Islahie, Gaziantep; 13b - Boğaziçi, Islahiye, Gaziantep;
14 - Fevzipaşa, Gaziantep; 15 - 4 km west of Bahçe, Adana; 16 - Türkoğlu, Kahraman Maraş; 17a - 7 km east of Kilis, Gaziantep; 17b - 15 km east of Kilis, Gaziantep; 17c - 2 km south of Elbeyli, Kilis, Gaziantep; 18a - Gaziantep; 18b - 10 km east of Gaziantep; 18c - Sarıgüllük, 6 km west of Gaziantep; 18d - 3 km north-west and 1 km east of Gaziantep; 19-1 km west of Birecik, Şanlı Urfa; 20 - Seyrantepe, Pazarcık, Kahraman Maraş; 21 - 2 km north of Gölbaşı, Adıyaman; 22 - 1 km west of Şambayat, Adıyaman; 23 - Adıaman; 24 - Mürşitpınar, Suruç, Şanlı Urfa; 25 - Suruç, Şanlı Urfa; 26 - 25 km east of Şanlı Urfa; 27 - 10 km north of Şanlı Urfa; 28 - Balgat, Harran, Şanlı Urfa; 29 - Hilvan, Adıaman; 30 - Küçükgöl, Siverek, Şanlı Urfa; 31 - Gözeli, Elazığ; 32 - 13 km west of Elazığ; 33 - Elazığ; 34 - Viranşehir, Şanlı Urfa; 35 - 15 km north of Ceylanpınar, Şanlı Urfa; 36 - Ceylanpınar, Şanlı Urfa; 37 - İstasion, Kızıltepe, Mardin; 38 - Evciler, Mazıdağı, Mardin; 39 - 4 km east of Ömerli, Mardin; 40 - Söğütlü, Nusaybin, Mardin; 41 - 10 km east of İdil, Mardin; 42 - Çukurca, Silopi, Siirt; 43 - Ormandağı, Pervari, Siirt; 44 - Yeniköprü, Bağlıca, Siirt; 45 - Suçeken, Batman, Siirt; 46 - Baykan - Kurtalan - Siirt crossroad; 47 - Yeniçağlar, Kozluk, Siirt; 48 - Yeniköy, Bismil, Diarbakır; 49 - Kulp, Diarbakır. Corresponding references: Szunyoghy (1941): 12a. Kock et al. (1972): 33. Yüksel (1984): 33. Kivanç (1988): 3, 34. Yüksel \& Gülkaç (1992): 18a, 23, 25, 26, 29. Nevo et al. (1994): 2a, 18b, 27. Coşkun (1996a): 18c. Ivanitskaya et al. (1997): 2b, 18d, 19, 32. Coşkun (1999b): 17a. Sözen et al. (1999): 17b. Yiğit et al. (2003): 16, 36. Coşkun (2004a): 45. Coşkun (2004b): 7, 8a, 9, 10a, b, 11a, b, 13a, 14. Coşkun et al. (2006):2c, $4-6,8 b, 12 b, 13 b, 15,20-22,24,28,30,31,35,37-44,46-49$. Sözen et al.(2006a): 4b, c, 17c. BMNH: 1. Our own data: 26.
the Palestine mole rat. In the west the distributional border roughly follows the River Seyhan (although S. ehrenbergi occupy a small area to the west of the river) till its confluence with the River Yenice. Further east, the range putatively follows the line confluence of the Göksu with the Seyhan - confluence of the Aksu with the Ceyhan. Afterwards, the Palestine mole rat's range spreads between the Aksu and Euphrates rivers as far north as Adıyaman. All records to the north of Adıyaman are on the eastern bank of the Euphrates and to the south of the lower flow of the River Murat. The eastern border can be tentatively defined by the line Diarbakır-Pervari-Silopi. Spalax ehrenbergi is in no place sympatric with S. xanthodon.

Palaeontology. Three names have been proposed for the Upper Pleistocene mole rats from the Near East: Spalax fritschi Nehring, 1902 (possibly a subspecies of S. ehrenbergi; Tchernov, 1968; Topachevskii, 1976), a small S. neuvillei Haas, 1951, and a large S. kebarensis Tchernov, 1968. Spalax ehrenbergi has continuously been recorded in Israel since the Late Middle Pleistocene (250,000 year ago) and was preceded by S. minutus (Early Middle Pleistocene). During the Upper Pleistocene (120,000-40,000 years ago) S. ehrenbergi was sympatric with $S$. neuvillei, and around 40,000 years ago with S. kebarensis (Tchernov, 1975). The Upper Pleistocene records of S. ehrenbergi are also known from Iraq (Palegawra Cave, 14,400 $\pm 760$ years BC; Hazard Merd Cave, 25,000 BP; Turnbull, 1975) and Lebanon (Antelias Cave near Beiruth, Palaeolithic; type of S. fritschi), but not from Turkey. With the exception of remnants of the Holocene age from Lybia (Topachevskii, 1976) there are no fossil records from northern Africa (Turnbull, 1975). That is in accordance with the putative fairly recent colonisation of Africa, which Lay \& Nadler (1972) placed in the Upper Pleistocene (70,000-35,000 year BP).

## Habitat

The Palestine mole rat is common in the open country biota of the Mediterranean and steppic regions and is limited by the 100 millimeter isohyet (Nevo, 1961). It is restricted to terra rossa in the Mediterranean part of Jordan (Amr, 2000). In Egypt, the animal occupies coastal plains with deep, sandy, loamy soils where Asphodelus microcarpus predominates
and sandy soils under Thymelaea hirsuta (Osborn \& Helmy, 1980). Desert is avoided throughout the range. In Israel, the species is common in all types of soil, including alluvial loams, terra-rossa, rendzina, loess and stationary sands and also penetrates into openings in the maquis and woodland (Nevo et al., 2001). In Iraq, Reed (1958) came across mounds in small clearings in virgin deciduous forest in the mountains and Harrison (1956b) observed abundant earth mounds in the vicinity of Ser'Amadia (Iraqi Kurdistan), on the high mountain slopes where the ground was very stony, as well as in the valleys with richer soil.

Turkish localities are from two climatic regions, the coastal Mediterranean and the dry steppic further inland. Annual precipitation is low around Şanlıurfa ( 330 mm ) and relatively high in regions under the Mediterranean climate regime ( 600 mm ); summer


Figure 250. Habitat of Spalax ehrenbergi 25 km west of Şanlı Urfa. Photo: A. Kryštufek.
precipitation is scarce everywhere ( $<5 \mathrm{~mm}$ ). Range along the Syrian border is characterised by hot summers (mean July temperature $>30^{\circ} \mathrm{C}$ ). Vegetation cover is dominated by Eryngium sp., Securigera sp., Peganum sp. and Agropyron sp. (Yiğit et al., 2003). Watson (1961) observed mole rat mounds near Mersin "just above sea level on a salt-clay bar covered with low Salicornia".

Altitude of localities ranges in Israel from 300 m below sea level to at least $2,200 \mathrm{~m}$ on Mt. Hermon (Nevo et al., 2001). Lewis et al. (1967) stated for Lebanon that "mounds abound at all elevations from sea level to the higher mountain valleys" and Reed (1958) recorded mole rats in Iraq up to $1,850 \mathrm{~m}$. The species is most likely widespread along the entire elevational gradient in Turkey; the known altitudinal range is $10-1,020 \mathrm{~m}$ a.s.l. (Nevo et al., 1995). Kıvanç (1988) gives $1,260 \mathrm{~m}$ a.s.l. as the highest elevation and observations of Watson (1961) are from "just above sea level".

Associates. Burrows of the Palestine mole rat occur in habitats occupied in Turkey by Mesocricetus auratus, Cricetulus migratorius, Meriones tristrami, M. crassus, Gerbillus dasyurus, Microtus guentheri, Apodemus witherbyi, A. mystacinus and Allactaga euphratica (Yiğit et al., 2003; own observations). This mole rat is in no place sympatric with $S$. xanthodon.

Density. Mean densities in Israel vary between $90.0 \pm 5.3$ individuals per $\mathrm{km}^{2}$ in the south and 176.8 $\pm 20.1$ per $\mathrm{km}^{2}$ in the north (mean $=105.1 \pm 4.4$ per $\mathrm{km}^{2}$; Nevo et al., 1982). Population continuity is high (89-100 \%) in central ranges, much lower (28 \%) in the periphery (Savić \& Nevo, 1990). No data are available from Turkey, where the Palestine mole rat seems less abundant than its larger counterpart $S$. xanthodon.

## Biology

Activity. The Palestine mole rat is a solitary, territorial and aggressive animal, active about 50 \% of the time all year round (Mendelssohn \& Yom-Tov, 1999). Results by Kushnirov et al. (1998) show that animals are diurnal and polyphasic during the rainy season, and nocturnal and monophasic during the dry season. Although this species is highly subterranean, in Israel mole rats can be seen frequently above ground between March and May and during
autumn months (Nevo, 1961); similar observations have been reported from elsewhere as well. On the ground surface, mole rats collect green food, search for a mate, disperse to new territories (Osborn \& Helmy, 1980), and escape from territorial fights (Mendelssohn \& Yom-Tom, 1999).

Individual mole rats occupy well-defined home ranges, which vary in size on an average $101 \mathrm{~m}^{2}$ in females to $576 \mathrm{~m}^{2}$ in males (Kushnirov et al., 1998); Savić \& Nevo (1990) reported territories of $51-121 \mathrm{~m}^{2}$ (mean $=69 \mathrm{~m}^{2}$ ). The density and distribution of mole hills do not reflect the shape of individual territories (Zuri \& Terkel, 1996).

Mole rats developed a vibrational communication system. The signals are produced by thumping the head against the tunnel ceiling in a rhythmic pattern (Heth et al., 1987). Calls used during courtship are noisy. Their main frequency is from $502.3 \pm 36.9$ to $568.0 \pm 35.6 \mathrm{~Hz}$, and the pulse repetiton rate is $23.7 \pm$ $2.8 \mathrm{~s}^{-1}$ (Heth et al., 1988b).

Burrows. Mole rats live nearly exclusively subterraneanly, consequently their underground passages are extensive. Burrowing is initiated by scratching with the fore-claws and thrusting with the head, while the majority of excavation is done by lower incisors. Loose excavated soil is packed and pushed to the surface with the head or hind legs (Osborn \& Helmy, 1980; Mendelssohn \& Yom-Tov, 1999). The burrowing animal can disappear quickly, even into dry stony ground; it took 2 minutes and 20 seconds for a specimen observed by Reed (1958) to get underground. Excavated soil forms small mounds 15-20 cm high. Fresh mounds are mainly visible during wet season while there is not much digging activity going on during dry season when the ground is hard. Overall length of passages is also less in summer (on average 19 m ) than in winter ( 39 m ; Mendelssohn \& Yom-Tov, 1999). Subterranean tunnels are about $10-40 \mathrm{~m}$ in length and $10-40 \mathrm{~cm}$ below the surface in winter, but descend as deep as 1.5 m during summer. Tunnels are branched and have nesting and sanitary chambers; the outermost tunnels are for caches with connections to peripheral feeding galleries. The nest is connected to the tunnel system by $2-3$ passages (Nevo, 1961; Osborn \& Helmy, 1980; Mendelssohn \& Yom-Tov, 1999).

Elaborate breeding mounds, 40 cm high, 160 cm long and 135 cm wide, are built prior to parturition.

The nest is centred 10 cm below the surface and surrounded by many storage chambers connected by passages (Nevo, 1961; Atallah, 1978; Osborn \& Helmy, 1980). In poorly drained areas, nesting chambers are shallower (5-6 cm deep; Lewis et al., 1967) and are located in the mound above ground in heavy soils (Mendelssohn \& Yom-Tov, 1999). Nest chamber ( 20 cm in diameter) is lined with grass.

Reproduction. Parturition occurs in Lebanon from early February at low altitudes to early April at high elevations (Lewis et al., 1967). In Israel, breeding peaks in early February and afterwards again in late March (Nevo, 1961). Reproduction starts with the rainy season (October-November) in Egypt (Osborn \& Helmy, 1980). Copulation takes place in the breeding mound and gestation lasts 28-36 days (Mendelssohn \& Yom-Tov, 1999). Females give birth once annually, some possibly breed for the second time in years of high primary production (Mendelssohn \& Yom-Tov, 1999). The most frequent number of young per litter is 2-3 in Lebanon (Lewis et al., 1967) and 3-4 in Israel (Nevo, 1961). The young gradually disperse from the mother's nest at two months old. They disperse by digging their first underground tunnel as a lateral extension of the maternal burrow system, hence, they establish their first territories adjacent to their mother's territories. After the tunnel length of a juvenile reaches about 4 m , the connection with the maternal tunnel is sealed. At high densities when young cannot establish their own territories around that of the mother's, they disperse aboveground (Rado et al., 1992). In captivity, Palestine mole rats may live up to 10 years (females) and 15 years (males; Savić \& Nevo, 1990). The age structure of 386 animals caught in nature was 19 \% of juveniles, $40 \%$ of $1-2$ years old, and $41 \%$ of 2-3 years old (Savić \& Nevo, 1990).

Food. Main food items are tubers and bulbs of Muscari sp., Narcissus tazetta, Belevalia flexuosa, Gladiolus italicus, Oxalis pes-caprea, Arisarum vulgare, Leopoidia comosa and Asphodeles microcarpus, roots of Alhagi mannifera and green parts of above ground plants (alfalfa, lettuce, Asphodeles microcarpus, Medicago sp., Urginea maritima, Hordeum sp., and Eryngium sp.; Nevo, 1961; Ali, 1978; Osborn \& Helmy, 1980). Harrison (1956b) found in two
stomachs from Kurdistan in Iraq greenish vegetable pulp, seed cases, slices of tuberous roots and the remains of a small insect. Tubers and bulbs are stored in underground chambers (Osborn \& Helmy, 1980), generally each food item in a different chamber. Up to 25 kg of potatoes and carrots were found in a single burrow system (Mendelssohn \& Yom-Tov, 1999). Captive animals take fruits, bread, onion, potatoes, carrots, beets, shelled broad beans and cheese (Atallah, 1978; Osborn \& Helmy, 1980). They are not cannibalistic (Atallah, 1978). The Palestine mole rat is considered to be one of the major pests to agriculture in Israel (G. Shenbrot, personal communication). Contrary to this, Yüzbaş \& Benli (1995) did not record noteworthy damage around Adana.

Gross energy intake is $132.8-155.9 \mathrm{~kJ}$ per day in a mesic environment and $75.0-80.3 \mathrm{~kJ}$ per day in xeric environment (Nevo, 1991).

Predation. Obuch (1994) found a single Palestine mole rat in pellets of the tawny owl Strix aluco from Hatay, and Seçkin \& Coşkun (2006) identified an individual in the pellets of the long-eared owl Asio otus from Diyarbakır province. This mole rat is also preyed upon by owls in Syria (Shehab, 2005), in Lebanon (Bate, 1945) and in Israel (Mendelssohn \& Yom-Tov, 1999). In Syria, mole rats constitute $0.8 \%$ of small mammals taken by the barn owl Tyto alba (Shehab, 2005). Lehmann (1969) found two juvenile mole rats in the nest of Circaetus gallicus in Ceylanpınar. In a high density population young compete for tunnelling space and disperse aboveground to new territories (see above) where they are easy prey for owls and diurnal raptors (Mendelssohn \& Yom-Tov, 1999). List of bird predators in Israel include Bubo bubo, Tyto alba, Strix aluco, Asio spp., Neophron percnopterus and Milvus migrans (Mendelssohn \& Yom-Tov, 1999). Domestic dogs and wild carnivores are known to destroy breeding mounds when seeking young (Lewis et al., 1967; Atallah, 1978).

During excavation of breeding mounds in a mountain valley in Lebanon, Lewis et al. (1967) found drowned mole rats killed after their tunnels had been flooded by melting snow from adjacent snow banks.

Conservation. Vulnerable in Turkey (Yiğit et al., 2006c).

## Family: Calomyscidae Vorontsov \& Potapova, 1979

Thomas (1905) regarded Calomyscus as "a member of the Cricetinae, or biserial-toothed Muridae" and concluded that "in Calomyscus we have another Cricetine Mouse preserved in the mountains of Persia, closely allied to the N. American Peromyscus, and widely different from any of the Asiatic Muridae hitherto known." As such, Calomyscus was placed in the past either into the subfamily Cricetinae (Thomas, 1905; Ellerman, 1948; Ellerman \& Mor-rison-Scott, 1951; Matthey, 1961; Bobrinskij et al., 1965; Corbet, 1978; Gromov \& Erbajeva, 1995; Roberts, 1997), or into the family Cricetidae (Gromov et al., 1963; Kumerloeve, 1975; Šidlovskij, 1976; Vorontsov et al., 1979; Gromov \& Baranova, 1981; Voroncov, 1982; Zima \& Král, 1984; Pavlinov, 1980; Pavlinov \& Rossolimo, 1987, 1998; Lebedev et al., 1998; Harrison \& Bates, 1999; Meyer \& Malikov, 2000).

For a long time, Calomyscus was persistently considered to be "not very closely related to other Palaearctic cricetine genera but closer to the American genus Peromyscus" (Corbet, 1978), a view supported by the structure of the auditory bullae (Pavlinov, 1980). Pavlinov (1980) included Calomyscus into a New World cricetid subfamily Sigmodon-
tinae Wagner, 1843, which at that time also involved Peromyscus Gloger, 1841 (now in Neotominae Merriam, 1894; Musser \& Carleton, 2005). Matthey (1961) suggested that the autosomes of Calomyscus resemble those of the Palaearctic Cricetinae, but that the heterosomes are closer to that of Peromyscus. Recent assessment of chromosomal sets in Cricetinae, Mus, Peromyscus and Calomyscus, did not confirm Matthey's interpretation and suggested that Calomyscus is a sister taxon to the Murinae-CricetinaeNeotominae clade (Romanenko et al., 2007). In the pennial morphology, Calomyscus appeared closest to Cricetulus migratorius (Hooper \& Musser, 1964). Quite unusually, Yiğit et al. (2006c) placed Calomyscus into Arvicolinae.

Some paleontologists link Calomyscus with a fossil Myocricetodontinae Lavocat, 1962, from the Miocene and Pliocene of southern Europe, southwestern Asia, and Africa. Myocricetodontinae show a resemblance to gerbils and jirds, consequently palaeontologists include them into the family Gerbillidae De Kay, 1842 (Wessels, 1998, 1999; Agustí \& Casa-novas-Vilar, 2003). The origin and initial development of Myocricetodontinae may have been on the Arabian Peninsula; since the Lower Miocene myocricetodontines are also known from Turkey (Wessels et al., 2003). The origin of Calomyscus within myocricetodontines is unclear. The only fossils of my-


Figure 251. Zagros mountains calomyscus Calomyscus bailwardi. Drawing: J. Hošek.


Figure 252. Calomyscus mystax. Photo: J. Vogeltanz.
ocricetodontines which resemble Calomyscus were found in Namibia, but Calomyscus was evidently never present in Africa (Wessels, 1998). Musser \& Carleton (2005) are sceptical as to whether a resemblance between Myocricetodontinae and Calomyscus reflects phylogenetic proximity.

Several nuclear genes retrieved a unique and isolated position of Calomyscus within Muroidea, and its early evolutionary split from Muridae and Arvicolidae (Michaux et al., 2001; Jansa \& Weksler, 2004). Its allocation into a family in its own right, as proposed by Vorontsov \& Potapova (1979), was accepted by Musser \& Carleton (2005) and is also followed here. Calomyscus, with eight currently recognized species, is the only genus of the family Calomyscidae (Musser \& Carleton, 2005).

## Genus: Calomyscus Thomas, 1905

## Taxonomy

Calomyscus was traditionally considered to be a monotypic species (Ellerman, 1948; Ellerman \& Morrison-Scott, 1951; Vereščagin, 1959; Gromov et al., 1963; Lay, 1967; Šidlovskij, 1976; Corbet, 1978; Roberts, 1997; Harrison \& Bates, 1991). Chromosomal variation, with eight different cytotypes known thus far (Graphodatsky et al., 2000; Somayeh et al., 2008), molecular evidence (Morshed \& Patton, 2002; Norris et al., 2008), and morphometrics (Lebedev et al., 1998; Norris et al., 2008) resulted in eight distinct species as recognized by Musser \& Carleton (2005). All spe-
cies, except C. bailwardi (cf. species account below), are listed below; extent of range is unresolved for a majority of them (Musser \& Carleton, 2005):
Calomyscus baluchi Thomas, 1920. Type loc.: Kelat District, northwest Baluchistan, Pakistan. Range: western Pakistan and Afghanistan.
Calomyscus elburzensis Goodwin, 1938. Type loc.: Degermatie, Kurkhud Mts., Khorasan, Iran. Range: mountains of northeastern Iran and adjacent Turkmenistan and Afghanistan.
Calomyscus grandis Schlitter and Setzer, 1973. Type loc.: 11 km east-northeast of Fasham, Tehran prov., Iran. Range: northern Iran.
Calomyscus hotsoni Thomas, 1920. Type loc.: 50 km southwest of Panjgur, Gwambuk Kaul, Baluchistan, Pakistan. Range: Baluchistan in Pakistan (Norris et al., 2008).
Calomyscus urartensis Vorontsov and Kartavtseva, 1979. Type loc.: 7 km north of Dzulfa, Nakhicevan, Azerbaijan. Range: Azerbaijan and northwestern Iran.
Calomyscus mystax Kashkarov, 1925. Type loc.: Bashi-Mugur, Nibid-Dag, Turkmenistan. Range: southwestern Turkmenistan.
Calomyscus tsolovi Peshev, 1991. Type loc.: 18 km northwest of Der'a, Thafas, Syria. Range: known only from type locality.

| Species | 2 N | $\mathrm{FN}_{\mathrm{a}}$ |
| :--- | :---: | :---: |
| C. bailwardi | 37 | 44 |
|  | 50 | 50 |
|  | 52 | 56 |
| C. baluchi | karyotype | not known |
| C. elburzensis | 44 | 58 |
|  | 44 | 60 |
|  | 30 | 44 |
| C. grandis | 44 | 46 |
| C. hotsoni | karyotype not known |  |
| C. mystax | 44 | 46 |
| C. tsolovi | karyotype not known |  |
| C. urartensis | 32 | 42 |

Table 51. Summary of taxonomic and chromosomal diversity in the genus Calomyscus. Taxonomy largely follows Musser \& Carleton (2005); chromosomal variation is summarized from Graphodatsky et al. (2000) and Somayeh et al. (2008).

Chromosomal variation, which is, for the time being, the best diagnostic trait, is summarized in Table 51. A detailed description of all cytotypes was provided by Graphodatsky et al. (2000) and taxonomic interpretation of chromosomal variability was executed by Musser \& Carleton (2005). An additional cytotype $\left(2 N=44, \mathrm{FN}_{\mathrm{a}}=60\right)$ has been reported since then from Khorasan (Somayeh et al., 2008). Being geographically marginal to $2 \mathrm{~N}=44, \mathrm{FN}_{\mathrm{a}}=58$ chromosomal form of C. elburzensis, we tentatively included it under that species. Two species (C. grandis and C. mystax) share the same cytotype, possibly a consequence of homoplasy or synplesiomorphy (Meyer \& Malikov, 2000; Musser \& Carleton, 2005).

It is not clear whether the extensive karyotypic variation in Calomyscus indicates recent speciation events and is therefore a manifestation of intraspecific polymorphism. The geographic distribution of cytotypes is still imperfectly documented. Also the chromosomal differences between populations, which are caused by centric and tandem fusions and heterochromatin changes, do not ensure post-mating reproductive isolation when a balanced meiotic system is produced. Natural hybrids between individuals characterised by different karyotypes (2N/FN ; $44 / 58 \times 30 / 44$ ) were recorded in Turkmenistan and further hybrids were produced in captivity: 32/42 $\times$ $44 / 58,32 / 42 \times 30 / 44,44 / 46 \times 44 / 58,44 / 58 \times 30 / 44$ (Graphodatsky et al., 2000).


Figure 253. Skins of Calomyscus bailwardi from Iran in dorsal and ventral view. a - an adult male from Posht Chenar, province Fars; b - a moulting subadult from Khollar, province Fars. Photo: C. Mlinar.

## Zagros mountains calomyscus Calomyscus bailwardi

Calomyscus bailwardi Thomas, 1905. Type loc.: Izeh, 120 km southeast of Ahvaz, Zagros Mts., Eastern Khuzistan Province, Iran.

## Taxonomy

Species limits of C. bailwardi are loosely defined (Musser \& Carleton, 2005) and three distinct cytotypes are pooled under this binominal (cf. Table 51 and chapter on Chromosomes below). While Graphodatsky et al. (2000) showed that two cytotypes of C. elburzensis readily hybridize both in nature and in captivity, putative hybrid zones in C. bailwardi remain entirely unknown. Besides, the karyotype of $C$. bailwardi topotypes is also not available (Musser \& Carleton, 2005).

Taxonomic identity of Turkish material is tentative. It seems quite possible that specimens from Hakkari on the one hand, and Birecik on the other (see account on Distribution), do not belong to the same species.

Vernacular name follows Musser \& Carleton (2005) who proposed calomyscus (from Greek ' $k a$ los', i.e. beautiful) to replace 'mouse-like hamsters' which was used until recently.

## Description

External characters. Small and slender mouse-like rodent, with long ears (about as long as hind foot) and with tail normally longer than head and body (mean $=103.0 \%$, range $=94.2-112.0 \%, \mathrm{~N}=9$ ). The ears are nearly naked, the eyes are of moderate size, and whiskers are long (up to 35 mm ). Pelage is soft and fine, up to 9 mm long on the back, 6 mm on the belly. The tail is well haired throughout, and hairs are becoming longer towards the tip where they form pencil (up to 12 mm long). Hind feet are long and narrow; front feet are much shorter. The thumb is reduced on front foot which hence bears four digits; hind foot is with five digits. The dorsal side of hands and feet is hairy; soles are naked except just under the heel. There are five palmar and six plantar pads. Claws are sharp but short (up to 1 mm ).

Colour. General colour above pinkish buff, dark-


Figure 254. Skull and mandible of Calomyscus bailwardi from 5 km north of Abshar, province Fars, Iran. Scale bar = 5 mm .
ened on the back by black hair tips, but clear and rich along the flanks. Head is buff, slightly paler than back. Belly is pure white to hair bases and sharply demarcated along the flanks; white hairs ascend rather high up to the checks and nearly reach the eyes. Ears are pale greyish brown, with a small white patch above the base. Upper surface of paws is pure white. Tail is bicoloured, greyish buff above and darkening terminally to blackish, interspersed with some white hairs; ventral side is pure white to dirt white (Thomas, 1905). Juveniles are greyer.

Nipples. There are six mammae (Roberts, 1997).
Penis. Glans penis in C. mystax is short and cylindrical (its width about equal to the length), with a ventral furrow and an extensive triangular terminal crater. The terminal crater encompasses a long central projection, a pair of short medial projections, and two lateral projections of medium size. Ventral side is densely covered with denticles, which become scarce on the lateral side and disappear entirely on the dorsal side (Voroncov, 1982). Voroncov (1982) figured a baculum in C. urartensis. Proximal baculum is stalk-like with broadly expanded base. Distal bacu-
lum consits of three subequal processes.
Skull is small, narrow (zygomatic width equals to 55.5 \% of condylobasal length; range = 53.5-57.3 $\%, \mathrm{~N}=11$ ), and moderately deep. Rostrum is long, narrow and deep. Narrow nasals protrude far in front of the incisors, but do not reach the orbit posteriorly. Interorbital region is broad, smooth, and slightly convex; its edges are marked although no ridges develop on the parietals. Braincase is rounded. Zygomatic arches are powerful; masseteric plate is short, its anterior edge descends anteriorly. Incisive foramens have an ovular shape and are short, terminating in front of molars. Posterior margin of hard palate is just back to $3^{\text {rd }}$ molars; pterygoid processes are bent and diverge posteriorly. Bullae are rather small. Mandible is of murine appearance, with a long articular process; coronoid process is relatively long, considerably overtopping the condyle.

Teeth. Incisors are smooth and compressed; enamel on their front surface is dull yellow. Molars are brachyodont; $1^{\text {st }}$ molar is the longest and $3^{\text {rd }}$ molar is the shortest. Being cuspidate, molars of Calomyscus resemble the pattern seen in Turkish Cricet-


Figure 255. Upper ( $\mathbf{a}, \mathbf{c}$ ) and lower molars (b, d) of Calomyscus bailwardi from 5 km north of Abshar, province Fars, Iran. Lingual side is to the left, anterior is at the top. Scale bar $=1 \mathrm{~mm}$.
inae, although there are important differences. Molars are more robust in Calomyscus, and the $3^{\text {rd }}$ molar is more reduced in size. Cuspidation is of bi-serial type, however, arrangement of cusps is asymmetrical (symmetrical in Cricetinae). In the maxilla, $1^{\text {st }}$ and $2^{\text {nd }}$ molar have two lingual and three labial cusps; the labial row is shifted forward. The antero-labial cusp is considerably reduced on $2^{\text {nd }}$ molar. Only three cusps remain visible on $3^{\text {rd }}$ molar; they obliterate early into a circular enamel rim. In the mandible, $1^{\text {st }}$ and $2^{\text {nd }}$ molars have three cusps on each side; similarly as in the upper cheek-teeth, the lingual row is placed forward and the antero-labial cusp is reduced to an enamel ridge on $2^{\text {nd }}$ molar. Third lower molar has three cusps and an antero-labial ridge of enamel.

Dimensions. Sexes are subequal in our Iranian sample. Measurements of the type are as follows: head and body length 78 mm , tail 87 mm , hind foot 20.5 mm , ear length 21.5 mm , greatest length of skull 26 mm (in our Zagros sample: mean $=25.8$ mm , range $=25.2-26.3, \mathrm{~N}=12$ ), maxillary tooth-row length $=3.3 \mathrm{~mm}$ (Thomas, 1905).

Chromosomes. Three cytotypes are ascribed to C. bailwardi (cf. Musser \& Carleton, 2005, and the

|  | N | mean | $\min -\max$ |
| :--- | :---: | :---: | :---: |
| Head and body | 12 | 85.3 | $80-90$ |
| Tail | 9 | 88.9 | $81-95$ |
| Hind foot | 12 | 19.6 | $18.4-20.8$ |
| Ear | 11 | 19.4 | $18.0-20.0$ |
| Weight | 9 | 19.4 | $17-22$ |
| Condylobasal length | 12 | 22.9 | $22.4-23.7$ |
| Zygomatic breadth | 11 | 12.7 | $12.2-13.2$ |
| Maxillary tooth-row | 12 | 3.7 | $3.5-3.8$ |

Table 52. External and cranial dimensions of Calomyscus bailwardi from the Zagros Mts., Iran. Based on our own material.
above account on taxonomy). Information below is summarized from a detailed description provided by Graphodatsky et al. (2000). Cytotype $2 \mathrm{~N}=37$, $\mathrm{FN}_{\mathrm{a}}=44$, which is known from a single male collected in the Bahtaran Province, Zagros Mts., includes four pairs of biarmed and 13 pairs of acrocentric autosomes, and a single large submetacentric element. The X chromosome is medium-sized and biarmed; its short arm is heterochromatic. The Y chromosome is the smallest element in the set. Cytotype $2 \mathrm{~N}=52$, $\mathrm{FN}_{\mathrm{a}}=56$, is known from a single female collected


Figure 256. Distribution of Calomyscus bailwardi in Turkey. Records: 1 - Birecik, Gaziantep; $\mathbf{2}$ - Hakkari province (no exact locality). Corresponding references: Yiğit et al.(2006c): 1, 2.
in the Kerman Province and consists of acrocentric and subtelocentric chromosomes; the X chromosome is as in the previous form. Cytotype $2 \mathrm{~N}=50, \mathrm{FN}_{\mathrm{a}}=$ 50, which is known from two females from the Zagros Mts., Fars Province, contains one biarmed pair and 23 acrocentric pairs of autosomes; the X chromosome is acrocentric.

## Variation

Species limits are unsatisfactorily defined which makes intraspecific comparisons tentative. See above for chromosomal variation. Corbet (1978) reports in calomyscus a "considerable variation in colour, size and proportion" varying in a mosaic pattern. For colour variation see Morshed \& Patton (2002). Interspecific size variation is slight in Calomyscus, e.g. mean (range parenthesised) maxillary tooth-row length is from $3.33 \mathrm{~mm}(3.1-3.6)$ in C. elburzensis to $3.53 \mathrm{~mm}(3.4-3.7)$ in C. mystax (Lebedev et al., 1998).

## Distribution

Allopatric ranges of eight calomyscus species extend from Azerbaijan in Transcaucasia, across much of Iran and Afghanistan as far east as northern Pakistan. The northern border is in southwestern Turkmenistan and there is one isolate in southwestern Syria (Musser \& Carleton, 2005). Calomyscus bailwardi occurs only in the Zagros Mts. in western Iran, in the provinces of Kordistan, Ilam, Western Esfahan, Eastern Khuzistan, Luristan, Fars, and Western Kerman; the actual range still has to be defined (Musser \& Carleton, 2005). Possible presence of C. bailwardi in Turkey was first mentioned by Kumerloeve (1975) and reported shortly afterwards by Mursaloğlu (1976; paper not seen but evidently an unpublished report). Paper by Mursaloğlu (1976) was ignored by nearly all students of Turkish rodents (Doğramacı, 1989a; Demirsoy, 1996; Kurtonur et al., 1996; Kryštufek \& Vohralík, 2001), but quoted recently in Yiğit et al. (2006c). Range in Turkey was given as "only known from Hakkari province" but subsequently the authors refer also to a specimen from Birecik, Gaziantep province (Yiğit et al., 2006c).

Calomyscus occupy two regions in the vicinity of Turkey. Closest record comes from the vicinity of Maku in the northwestern corner of Iran (Lay,
1967), which is only about 15 km away from Turkish province of Ağrı. This locality is within the presumed range of C. urartensis; for maps see Šidlovskij (1976) and Norris et al. (2008). Another region is the Kordestan Province in Iran, some 250 km from the Hakkari Province; material was identified as C. bailwardi (Graphodatsky et al., 2000; Norris et al., 2008).

Palaeontology. Fossil Calomyscus of the Upper Miocene-Pliocene age were found in Spain, France (Wessels, 1998; Agustí \& Casanovas-Vilar, 2003), the Island of Rhodes (identified as Calomyscus minor; Şen \& de Bruijn, 1977; van der Meulen \& van Kolfschoten, 1986), Transcaucasia (Vereščagin, 1959), and Turkey (Upper Miocene at Süleimanlı; Wessels, 1998). A sample from the middle flow of the Araks River (Transcaucasia) is from the Pliocene (Vereščagin, 1959). Myocricetodontinae were abundant in Anatolia during the Miocene (Wessels et al., 2001).

## Habitat

All species of the genus Calomyscus are adapted to live in dry mountainous country and inhabit barren rocky and scarcely vegetated mountainsides in arid steppes, semideserts and desert regions (Gromov \& Baranova, 1981; Gromov \& Erbajeva, 1995; Gromov et al., 1963; Šidlovskij, 1976). There are disagreements regarding contingency of populations. While Lay (1967) believed that habitat availability allows Calomyscus to exist throughout Iran, Graphodatsky et al. (2000) presumed that populations are distributed in a patchy, mosaic pattern. There seems to be hardly any difference regarding habitat selection among various species. The two calomyscus species in Pakistan (C. baluchi and C. hotsoni) favour mountain steppe regions and the driest rocky hillsides, but are absent from low elevation valleys. Specimens were also collected along stone walls and embankments between small fields or terraced cultivations (Roberts, 1997). Within the ranges of C. elburzensis and C. grandis in the Elborz Mts., main habitats are rocky outcrops of rock strata and numerous cracks, steep mountain slopes, steep ridges, and bare cliffs. Scant vegetation of grass clumps, nettleweed, legumes, thistle, Cousinia sp., Chichorium sp., Salvia sp., Thymus sp., Astragalus sp., Achilea sp., and occasionally thorny bushes (Paliurus aculeatus),


Figure 257. Habitat of Calomyscus bailwardi in the vicinity of Sivand, province Fars, Iran. Photo: V. Vohralík.
is scattered and in small patches ( $<0.25 \mathrm{~m}^{2}$ ). Vegetation (Astragalus sp., Artemisia sp., Vorthemia persica, Centaurea sp., Crisium sp., Zizypus sp.) is rarely abundant (Lay, 1967). In the Maku region of northwestern Iran, Lay (1967) collected C. urartensis in the scree-strewn slopes with thistles, scattered grass and wild rose bushes, and among large rocks placed in rough terraces with extremely scattered vegetation (Setania sp., Centaurea sp., Cousinia sp., Aster sp., Malva sp., Polygonum sp., Verbasculum sp.). Calomyscus tsolovi was obtained from a stone desert (Peshev, 1989). In Turkmenistan, calomyscus (C. elburzensis and/or C. mystax) is entering caves (V. Hanák, personal communication), and we collected three C. bailwardi at the entrance to a cave in southern part of the Zagros Mts.

Within the presumed range of C. bailwardi, Lay (1967) described the main habitat as a landscape of barren, dry, rocky hill and mountainsides with scant vegetation. This species also favours crevices between thorn and rock rows (with Centaurea sp, Astragalus sp., and Acantholium sp.) among grain fields. On the edge of the Isfahan Basin, which is influenced by the Zagros Mts., calomyscus inhabited low (300600 m ), narrow, elongated mountains which rose as islands from the plain with numerous small salt basins; vegetation consisted of Cousinia sp., Festuca sp., Boissera pumilo, Hordeum sp., Elymus sp., Bromus sp., and Peganum hormala. The species was also occasionally found in a lacustrine valley (Lay, 1967). Our specimens from the southern part of the Zagros Mts. were also obtained from rocky situations with boulders and sparse vegetation of grasses and
weeds, but also from scattered low trees (Acer sp., Quercus sp., Cytiscus sp.) and bushes (Amygdalus sp., Crategus sp.).

Altitude. Calomyscus bailwardi was recorded between 760 m (Lay, 1967) and 2,130 m (our own data). Vertical range in Afghanistan (presumably of C. baluchi) is $400-3,500 \mathrm{~m}$ (Hassinger, 1973), in the Elborz Mts. (range of C. elburzensis and/or C. mystax) 945-3,350 m (Lay, 1967), in Maku region, northwestern Iran (range of C. urartensis) 910-3,125 m (Lay, 1967), and in Pakistan (C. baluchi and C. hotsoni) 610-3,100 m (Roberts, 1997). Calomyscus peshevi is known only at an altitude of about 400 m (Peshev, 1989).

Associates of C. bailwardi are Tatera indica, Meriones persicus, Apodemus witherbyi, Mus sp., and Ochotona rufescens. (Lay, 1967, and our own data). The other species of calomyscus share their habitat with Meriones persicus, Apodemus sp., Cricetulus migratorius, Chionomys nivalis, and Hemiechinus auritus on the Elborz Mts. (Lay, 1967), Meriones persicus in Maku (Lay, 1967), and Gerbillus nanus in Pakistan (Roberts, 1997).

Density. Out of 21 small mammals we collected in the southern Zagros Mts., 12 (= 57 \%) were C. bailwardi. Abundant in Afghanistan (Hassinger, 1973) and locally in Pakistan; in a report by Roberts (1997) "fifty percent of the traps ... in one night were visited by these rodents [Calomyscus]"

## Biology

Information is scattered, largely anecdotal, and frequently contradictory. Besides, taxonomic identity is not clear in the majority of sources. We subsequently summarized all relevant information available to us. Similarly as in the above text, we indicate putative specific affiliation whenever appropriate.

Activity. Calomyscus is reported to be "quite gregarious" (Roberts, 1997) and to be "highly social" (Nowak, 1999). Roberts (1997) further states that calomyscus "is a very agile mouse, able to jump among tumbled boulders with considerable agility and also climb." Observations in captivity suggest calomyscus to be very susceptible to temperature what restricts its activity to afternoon and early morning in cold weather; despite this, there is no hibernation and activity goes on year-round (Roberts, 1997). Calomyscus urartensis is nocturnal
(Šidlovskij, 1976), while C. mystax emerges out of burrows also during the daytime in spring and autumn, however, summer activity is strictly nocturnal (Gromov \& Erbajeva, 1995).

Burrows. Šidlovskij (1976) reports, presumably for $C$. urartensis, nesting among rocks and in crevices. The single nest found in the Elborz Mts. of Iran was "built in a narrow horizontal crevice in rock strata on a rocky outcrop at $11,000 \mathrm{ft}$. [ $=3,350 \mathrm{~m}$ ]" and consisted of a ball of fine grass and sheep wool (Lay, 1967). In Pakistan, Roberts (1997) trapped calomyscus in burrows excavated by Meriones persicus.

Reproduction. In captive calomyscus, pregnancy lasted 29-31 days and post-partum mating was never observed. Animals bred throughout the year. Litter size was $1-5$ (mean $=2.8, \mathrm{~N}=39$ litters). Number of litters per female was high: one female delivered 15 litters with a total 41 young during 28 months, another female produced 12 litters with a total 36 young during 22 months. Sex ratio of newborn cubs was balanced ( 48 males : 46 females); their body mass was $1.53-2.95 \mathrm{~g}$ (mean $=2.15 \mathrm{~g}$ ), mean head and body length was 37 mm and mean tail length was 37 mm . They were blind and naked, but already had vibrissae. Postnatal development was slow: eyes opened at the age of 17 days and solid food was taken when young attained 22 days. Young animals were grey; moult into an adult brown colour started around the age of two months and completed at the age of $80-135$ days. First females breed when 4 months old, males when 5 months old. In captivity, longevity of $>4$ years was common which is quite exceptional for such a small rodent (Volf \& Volf, 1993); the highest recorded was 9 years and 3 months (Volf, 2003).

Despite considering the information provided by Volf \& Volf (1993) as entirely reliable, we quote deviations found in other sources anyway: eyes open 13 days after birth (Roberts, 1997; Nowak, 1999) and adult colouration and size are attained in 6-8 month-old animals (Nowak, 1999). Roberts
(1997), on the contrary, reported a rapid development since he found young to be of three quarters of the mother's size while still suckling. Information from the nature is rather scarce. In Iran, Lay (1967) found lactating females in August and December, recorded uterine swellings and placental scars ( $2 \times 2,3 \times 4,3 \times$ 7 ; mean $\approx 5$ ) from August to December, and trapped half-grown individuals in August. Our material captured between 23 April and 3 May in the southern Zagros Mts. contains one juvenile (body mass of 7 g ) and two nearly full-grown individuals in grey juvenile pelage (body mass of 15 and 16 g , respectively). Reproductive period for $C$. mystax lasts from end of March till early June, with two annual litters (Gromov et al., 1963). Hassinger (1973) captured two pregnant females in July in Afghanistan, each with 3 embryos; another female from Baluchistan produced two cubs on 6 April (Roberts, 1997). Roberts (1997) reported breeding during winter-time in Pakistan. Litter size in C. mystax is $3-5$, and the number of embryos can be up to 7 (Gromov \& Erbajeva, 1995).

Food consists mainly of seeds, fruits, buds, and leaves. According to Nowak (1999), calomyscus readily eat animal matter, and are cannibalistic in captivity (Roberts, 1997).

In Iran, Lay (1967) found cracked grass (Bromus sp.) seeds and occasional thistle buds under overhanging rocks. Stomach contents in his specimens contained grass seeds. Calomyscus mystax lives mainly on seeds of grasses and weeds, less so on leaves and flowers (Gromov \& Erbajeva, 1995), and staple diet of $C$. urartensis is xerophyte plants, seeds and fruits (Šidlovskij, 1976). Captive specimens eat chopped vegetables and millet seeds, and also drink water (Roberts, 1997).

Predation. Roberts (1997) provided a list of possible predators in Pakistan: the pallid scops owl (Otus brucei), stone marten (Martes foina), marbled polecat (Vormela peregusna), rat snake (Sphalerosophis atriceps), and Levantine viper (Vipera lebetina).

## Family: Hystricidae G. Fischer, 1817

The Old-World porcupines (family Hystricidae) are perhaps the most divergent group in the suborder Hystricomorpha Brandt, 1855 (Woods \& Kilpatrick, 2005). Three genera and 11 species occupy deserts, savannahs, and forests of the Mediterranean Europe, southern Asia, and throughout Africa. One species inhabits Anatolia.

## Genus: Hystrix Linnaeus, 1758

A genus of about eight species in three subgenera; range includes Italy (where it was possibly introduced), Africa, and southern Asia. The Indian crested porcupine $H$. indica is in the subgenus Hystrix, together with H. cristata Linnaeus, 1758, and H. africaeaustralis Peters, 1852; for a revision see Corbet \& Jones (1965). Hystrix indica is clearly distinct from H. cristata (for morphometric comparison


Figure 258. Indian porcupine Hystrix indica. Drawing: J. Hošek.
see Angelici et al., 2003) by having a predominately brown crest (white in H. cristata), a conspicuous patch of short, white spines on the rump (dark in $H$. cristata), less inflated nasal region (Corbet, 1978), and shorter and narrower nasals, which are most often less than half the occipitonasal length (Ellerman, 1948).

Dental formula is $1 / 1,0 / 0,1 / 1,3 / 3=20$.

## Indian crested porcupine - Hystrix indica

Hystrix cristata var. indica Kerr, 1792. Type loc.: India.
Hystrix hirsutirostris mersinae Müller, 1911. Type loc.: Mersin, Turkey.

## Taxonomy

The Indian crested porcupine was first reported as H. cristata for the Near East (Tristram, 1866) and for Turkey (Danford \& Alston, 1877, 1880). Although it was subsequently demonstrated that this name relates to crested porcupines of Africa and Italy (Ellerman \& Morrison-Scott, 1951), cristata was occasionally used by Russian authors (Bobrinskij et al., 1965), and is still frequently applied for Turkish porcupines in literature dealing with various morphological aspects of the animal (e.g. Atalar \& Ylmaz, 2005; Aydin, 2003, 2004, 2005; Ozdemir, 2005; Ozdemir et al., 2005; Timurkaan et al., 2006; Yilmaz, 1998).

Ellerman (1948) classified porcupines from southwestern Asia as H. leucurus Sykes, 1831 (Type loc.: Deccan, India), and Ellerman \& MorrisonScott (1951) were probably the first to use the current name of $H$. indica. The Indian crested porcupine is nearly uniformly reported as $H$. indica by students of the mammals of southwestern Asia in general (Bodenheimer, 1958; Hatt, 1959; Lay, 1967; Lewis et al., 1967; Šidlovskij, 1976; Atallah, 1977, 1978; Kadhim et al., 1977; Corbet, 1978; Pavlinov \& Rossolimo, 1987, 1998; Nadachowski et al., 1990; Harrison \& Bates, 1991; Qumsiyeh, 1996; Kadhim, 1997; Mendelssohn \& Yom-Tov, 1999; Amr, 2000; Bukhnikashvili, 2002; Ferguson, 2002; Amr et al., 2004) and of Turkey in particular (Misonne, 1957; Osborn, 1964; Corbet \& Morris, 1967; Kumer-
loeve, 1975; Turan, 1984; Kinzelbach, 1986; Doğramacı, 1989a; Demirsoy, 1996; Kurtonur et al., 1996; Yiğit \& Çolak, 1997; Kryštufek \& Vohralík, 2001; Yiğit et al., 2003, 2006c; Arslan, 2006, 2008). Hystrix leucurus was mainly adopted by Russian authors (Vereščagin, 1959; Vinogradov \& Gromov, 1984; Gromov \& Erbajeva, 1995), but rarely by others (Mohr, 1965; Kumerloeve, 1967a,b). Turkish porcupines were occasionally also referred to as $H$. hirsutirostris (Müller, 1911, 1919, 1920; Gülen, 1952; Kosswig, 1955), which is now mainly used as a valid subspecific name to denote the Transcaucasian populations (see under Variation).

## Description

External characters. A heavy plantigrade rodent with short and hidden tail (about 20 \% of head and body length; range $=14-28 \%, N=9$ ). Body is much


Figure 259. Indian porcupine Hystrix indica from Jordan. Photo: J. Vogeltanz.


Figure 260. Cadaver of Hystrix indica, found 8 km south of Bucakkışla, Taurus Mts. Photo: A. Kryštufek.


Figure 261. Skin of Hystrix indica from Menzil, Gorgan, north-western Iran (BMNH). Photo: B. Kryštufek.
larger posteriorly then anteriorly. Head is heavy, short and deep, with a convex profile. Rhinarium is hairy, and slit-like nostrils are about 27 mm long; vibrissae are stiff and long (up to 230 mm ). Eyes are small (diameter about 13 mm ); ears are low and rounded. Front foot is short and broad, with four well developed digits; slightly curved claws are heavy and blunt, up to 11.5 mm long and 6 mm wide. Naked palms are almost entirely occupied by three large pads. Hind foot is narrower and has five digits; claws are about 11 mm long and 5 mm wide. Palmar surface has six indistinct pads. Palm and hind foot are figured in Gülen (1952).

Head, shoulders, limbs and underparts are covered with coarse grooved bristles up to 230 mm long and about 2 mm wide. Hair is short on the head (5 mm ) and shoulders ( 45 mm ); neck has a conspicuous crest of up to 350 mm long coarse bristles. The head,
nape, and front back are covered with long quills; stout quills along the sides and the posterior half of the body are up to 380 mm long. The long quills are cylindrical in the proximal half, flattened and furrowed on the distal end (Chernova \& Kuznetsov, 2001). Coarse hair among the spines and quills is up to 95 mm long. End of the tail bears short rattle quills, which are hollow cylinders with a narrow flattened base, flat apex, and expanded ( 7.5 mm wide) hollow portion.

Colour. Head, ventral body, and extremities are blackish brown. Whiskers are black. The crest on the neck is drab brown, and there is white band across the throat. Quills are blackish horn-colour, with 1-3 whitish annulations and a long whitish terminal area. The black quilted region is conspicuously spotted and streaked with white, the effect most pronounced in the posterior part of the body. Rattle quills are mainly whitish.

Nipples. Number of nipples varies between one and three pairs (Mendelssohn \& Yom-Tov, 1999). Three pectoral pairs are seemingly the prevailing condition (Harrison \& Bates, 1991) but only one pair is functional (Thomé \& Thomé, 1980). Nipples are located along the lower flanks, and not under the belly (Roberts, 1997).

BACULUM "is a robust rod, with the base broadened, narrowing to the tip, which is not expanded. The shaft is concave below the base, flattening distally and smoothly convex above" (Harrison \& Bates, 1991).

Skull is deep and wide, particularly so in its facial portion; dorsal profile is slightly convex. The majority of dorsal portion is covered by enlarged nasals and interparietals; the braincaise appears relatively small. The combined breadth of nasals exceeds their length. Rostrum narrows in its anterior part; much enlarged infraorbital foramen is about the same size as the orbit. Zygomatic arches are powerful. Hard palate does not extend behind $3{ }^{\text {rd }}$ molars; its posterior margin is evenly concave. Interpterygoid fossa is wide; bullae are relatively small. In occipital region, the brain-case is truncate; paroccipital process and parietal crest are well developed. Foramen magnum is wider than the height. Mandible is relatively slender; angular process is nearly absent and coronoid process is small.

Teeth. Incisors are robust; upper incisor is wider $(6.5 \mathrm{~mm})$ than the lower one ( 5.5 mm ). Enamel on


Figure 262. Skull and mandible of Hystrix indica, based on a specimen from 8 km south of Bucakkışla. Scale bar $=20 \mathrm{~mm}$.
the front surface is yellow, darker in upper incisors. Cheek-teeth are rather large, with high, flat crowns. Roots are imperfectly developed. Crowns of maxillary cheek-teeth are elliptical, longer than wide, with three re-entrant folds on the labial side and one fold in the lingual side. Mandibular cheek-teeth are essentially of the same shape but of reversed enamel pattern; they are narrower and thus longer relative to width. Re-entrant angles become isolated with advanced age as narrow islands.

Dimensions. Sexes are apparently subequal. In male/female couples (see Activity), females are usually heavier; values given for four pairs from Lebanon are (male/female; in kg): 16.8/19.4, 17.6/19.05, 21.9/20.25, 10/10.95 (Thomé \& Thomé, 1980). Information on body mass is scarce, however. Among the Israeli population the range is $10-15 \mathrm{~kg}$ (mean $=13.9 \mathrm{~kg}$; Server \& Mendelssohn, 1991), while the maximum body mass ( 18.5 kg ) reported was for a male (Mendelssohn \& Yom-Tov, 1999). A female from Iraq weighed 11.3 kg , and a male from India 13.6 kg (specimens in BMNH).

Morphometrics of porcupines from Turkey is also poorly documented; cf. Tables 53-55 for a summary of information available to us. Arslan (2008) reported means (in mm) for two Turkish specimens (to-
tal length 888, tail length 146 , hind foot 96 , ear 43 , condylobasal length of skull 136.5, zygomatic width 82.5, maxillary tooth-row 34.0) and Gülen (1952) provided measurements of his captive adult individ-


Figure 263. Upper (a, c) and lower molars (b, d) in Hystrix indica. Note age-dependent variation in enamel abrasion. Lingual side is to the left, anterior is at the top. $\mathbf{a}, \mathbf{b}-8$ km south-west of Bucakkışla, Turkey; c, d - Menzil, Iran (BMNH). Scale bar = 10 mm .

| Origin | Turkey | $\begin{gathered} \text { Iran } \\ \text { female } \end{gathered}$ | India |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sex |  |  | females |  |  |  |  | males |  |  |
| Head and body | 650 | 725 | 700 | 740 | 713 | 750 | 642 | 790 | 633 | 720 |
| Tail | 150 | 175 | 100 | 210 | 142 | 130 | 93 |  | 140 | 130 |
| Hind foot | 98 | 95 | 98 | 96 | 95 | 105 | 85 | 107 | 89 | 108 |
| Ear | 41 | 45 | 40 | 47 | 43 | 47 | 35 | 44 | 45 | 42 |

Table 53. External dimensions (in mm) of Hystrix indica from Turkey (our own material), Menzil (north-western Iran; $\mathrm{BMNH})$, and India (BMNH).

| Origin <br> Sex |  |  | Turkey | Iraq <br> female | Iran <br> female | Yemen <br> male |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Condylobasal length | 135.0 | 138.6 | 133.8 | $107.2^{*}$ | 143.0 | 144.6 | 147.0 |
| Zygomatic breadth | 73,7 | 82.0 | 80.4 |  | 77.8 | 82.4 | 76.1 |
| Maxillary tooth-row | 30,2 | 32.3 | 32.7 | 24.3 | 33.0 | 35.5 | 33.1 |

Table 54. Cranial dimensions (in mm) of Hystrix indica from Turkey (left to right: Mersin [type of mersinae]; Bucakkışla; Finike; Xanthus) and adjacent regions in south-western Asia. Based on specimens in BMNH, ZMB, and our own material. Asterisk denotes a juvenile specimen.

| Origin | Israel |  |  | E Mediterranean <br> Sex |  | males $(\mathrm{N}=5-7)$ |  | females $(\mathrm{N}=4-5)$ | pooled $(\mathrm{N}=17)$ |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | mean | min-max | mean | min-max | mean | min-max |  |  |  |
| Head and body | 666 | $390-850$ | 675 | $560-713$ | 764 | $660-790$ |  |  |  |
| Tail | 143 | $120-165$ | 141 | $81-170$ | 167 | $105-240$ |  |  |  |
| Hind foot | 100 | $94-113$ | 106 | $74-120$ | 96 | $80-105$ |  |  |  |
| Ear | 40 | $35-46$ | 40 | $32-48$ | 35 | $30-46$ |  |  |  |
| Weight | 8.2 | $5.9-11.3$ | 9.9 | $7-11$ |  |  |  |  |  |
| Condylobasal length | 134.3 | $130.7-138.5$ | 136.0 | $130.3-139.6$ | 138.8 | $121.5-145.9$ |  |  |  |
| Zygomatic breadth | 80.3 | $80.0-84.3$ | 78.5 | $70.9-84.0$ | 76.6 | $72.2-80.9$ |  |  |  |
| Maxillary tooth-row | 32.0 | $30.0-34.7$ | 31.0 | $28.9-32.4$ | 30.8 | $24.2-32.8$ |  |  |  |

Table 55. External and cranial dimensions (in mm; body mass in kg ) of Hystrix indica from Israel (Mendelssohn \& Yom-Tov, 1999), and the Eastern Mediterranean region (Atallah, 1977).
ual origination from Haruniye near Adana (head and body length 625, tail length 120).

Chromosomes. Arslan (2006) karyotyped two females from Turkey and reported the diploid number of chromosomes $2 \mathrm{~N}=66$, and the fundamental number of autosomal arms $\mathrm{NF}_{\mathrm{a}}=112$. The X is metacentric and the largest chromosome in a set. Identical diploid number was already reported for an individual identified as H. cristata. As a matter of fact, H. cristata from Italy and East Africa have a lower diploid number $(2 \mathrm{~N}=60)$ and variable number of autosomal arms $\left(\mathrm{NF}_{\mathrm{a}}=114\right.$ and 116) (Zima \& Král, 1984).

## Variation

Mohr (1965) recognized 10 subspecies (under $H$. leucurus) and listed six for southwestern Asia:
H. i. hirsutirostris Brandt, 1835. Type loc.: Talysh, Transcaucasia.
H. i. satunini Müller, 1911. Type loc.: Geok Tepe, east of the Caspian Sea, southern Turkmenistan.
H. i. mersinae Müller, 1911. Type loc.: Mersin, Turkey.
H. i. aharonii Müller, 1911. Type loc.: Emmaus, west of Jerusalem, Israel.
H. i. schmidtzi Müller, 1911. Type loc.: Ain Dcheier, northwest of Dead Sea, Jordan Valley, West Bank, Israel.


Figure 264. Skulls of Hystrix indica in dorsal view. Note variation in shape. a - Finike, Antalya, Turkey (BMNH); b - Xanthus, Turkey (young animal; BMNH); c - Menzil, Iran (BMNH); d - Jebel Abdul Azir, Syria (type of mesopotamica; redrawn from Müller, 1920). Scale bar $=50 \mathrm{~mm}$.
H. i. mesopotamica Müller, 1920. Type loc.: Jebel Abdul Azir, northeastern Syria.

Müller $(1911,1920)$ evidently failed to distinguish between individual variation, which is considerable in porcupines; Fig. 264), and geographic variation. Ellerman \& Morrison-Scott (1951) were sceptical as to whether "this porcupine can be divided into subspecies in a satisfactory manner" and retained only hirsutirostris as a distinct subspecies (occurring in Transcaucasia); all other names were synonymised with the nominotypical subspecies. Gept-
ner (1952) provided diagnostic characters distinguishing between indica from Central Asia and Trancaucasian hirsutirostris. The upper ramus of the zygomatic process of maxilla (malar process) is evidently more robust in H. i. indica (Fig. 265). Noteworthy, a fossil porcupine from the Neogene Siwalik beds in the sub-Himalayan range resembles in this respect the extant subspecies hirsutirostris (Fig. 265c). From the anterior view, the infraorbital foramen is triangular or oval (width > height) in H. i. indica, and circular (width $\approx$ height) in H. i. hirsutirostris (Fig. 266). Chernova \& Kuznetsov (2001) found differences in the length of quills between H. i. leucurus (= indica) and H. i. hirsutirostris; long quills: 155165 mm in the former, $120-380 \mathrm{~mm}$ in the later; short rattle quills: $80 \pm 5 \mathrm{~mm}$ in ssp. indica, $110 \pm 10 \mathrm{~mm}$ in ssp. hirsutirostris.


Figure 265. Zygomatic arch in two subspecies of Hystrix indica. a - H. i. indica from Menzil, Iran (BMNH); b-H. i. hirsutirostris (redrawn from Geptner, 1952); c - fossil Hystrix from the the Neogene Siwalik beds (redrawn from Black, 1972). Anterior is to the left. mp - malar process. Not to scale.


Figure 266. Infraorbital foramen (if; in frontal view) in two subspecies of Hystrix indica. a - H. i. indica from Bucakkışla, Turkey; a-H. i. hirsutirostris (modified from Geptner, 1952). Not to scale.

The skulls of Turkish specimens (including the type of Hystrix hirsutirostris mersinae) we saw belong to H. i. indica, a subspecies which occurs throughout Arabian Peninsula (Harrison \& Bates, 1991).

## Distribution

Range encompasses Transcaucasia (Georgia, Armenia, Azerbaijan; Šidlovskij, 1976; Bukhnikashvili, 2004), Asia Minor, eastern Mediterranean coast in Lebanon and Israel (Lewis et al. 1967; Atallah, 1978; Mendelssohn \& Yom-Tov, 1999), northern Sinai (Saleh \& Basuony, 1998), Arabia (Harrison \& Bates, 1991), Iran (Lay, 1967), Afghanistan (Hassinger, 1973), Turkmenistan, Kirgistan, Tadžikistan, Uzbekistan, southern Kazakhstan (Bobrinskij et al., 1965; Gromov \& Baranova, 1981), Pakistan (Roberts, 1997), Kashmir, Nepal, and India (Woods \& Kilpatrick, 2005). The northern border is just south of Lakes Aral and Balkash (Bobrinskij et al., 1965). Saltz \& Alkon (1989) suggested that the northern limit is posed by the minimum amount of time available for night foraging which is seven hours.

On the islands, the Indian crested porcupine occurs only in Sri Lanka (Woods \& Kilpatrick, 2005). Earlier reports for the Aegean Islands (Rhodes by Danford \& Alston, 1877, and Lesbos and Ikaria, Wettstein, 1941) are evidently erroneous (Ondrias, 1966).

In Turkey, the range covers the coastal areas along
the Aegean and the Mediterranean Sea, and southeastern Anatolia as far east as Siirt and Bitlis. In Transcaucasia, there are several population isolates along the Arax River (Šidlovskij, 1976) the animal, however, is evidently absent from the Van area. Kosswig (1955) plotted records also for northwestern Anatolia, but these are discredited by Yiğit et al. (2006c). Therefore the northern border along the Aegen coast possibly coincides with the line Bergama - Demircı.

Palaeontology. The oldest fossil record of Hystricidae is from the Miocene and is ascribed to the genus Atherurus F. Cuvier, 1829. Atherurus has two extant species in Asia and Africa, respectively. Miocene forms were low-crowned but Late Miocene and Early Pliocene fossils from China already show a tendency towards hypsodonty (Weers, 2005). Neogene porcupines from Turkey (Çobar Pınar and Bayirköy) are similar to H. primigenia (Wagner, 1848) (Șen \& Kovatchev, 1987), originally described from Pikermi in Greece and contemporarily fairly widespread in southern Europe (Bonis et al., 1992)

Five Hystrix species were distinguished in the Pleistocene of Asia, and three of them are from the low-crowned subgenus Acanthion Cuvier, 1823. A large member of the genus Hystrix, H. refossa Gervais, 1852, includes also H. angressi Frenkel, 1970, from the Pleistocene of Israel (Weers, 2005). Emergence of $H$. indica is uncertain. Gromov \& Baranova (1981) reported it since the Middle Pleistocene, and Black (1972) identified two individuals from the Neogene Siwalik beds in the sub-Himalayan range as ‘Hystrix cf. H. leucurus'. Early Pleistocene porcupines from Israel are also classified as $H$. cf. indica (Goren-Inbar et al., 2008). Tchernov (1988, 1994) reported the presence of $H$. indica in Israel for the last 160,000 years but did not assign the material from the early Middle Pleistocene to a species level (Tchernov, 1975, 1992). Unidentified porcupines (Hystrix sp.) are reported also for Gelibolu peninsula, European Turkey (from the Miocene), and from the Island of Rhodes (Lower Villanyian, i.e. Pliocene; Meulen \& Kolfschoten, 1986). A PleistoceneHolocene size reduction was noted in $H$. indica in Israel (Bar-Oz et al., 2004).

Kosswig (1955) presumed that H. indica colonized Anatolia fairly recently, more specifically at "the end of last glacial epoch". Such a scenario is highly unlikely keeping in mind the evidence from

Israel. Hystrix occurred in the Caspian coast of Iran about 11,500-8,600 years before present (Turnbull, 1975).

## Habitat

The Indian crested porcupine is ecologically adapt-
able, and is found in various habitats: sand-hill and sand-dune desert areas, steppic regions, dry rocky hillside, moist temperate deciduous forests, irrigated forest plantations (e.g. in the Indus Plain; Roberts, 1997), juniper forests, shrubby vegetation, agricultural areas, and so forth. The porcupine is more plen-


Figure 267. Distribution of Hystrix indica in Turkey and adjacent regions. Records: 1 - Kınık (= Xanthus), Bergama, İzmir; 2 - Demircı, Manisa; 3 - Salihli, Manisa; 4 - Ödemiş, İzmir; 5 - Tire, İzmir; 6a - Bayındır, İzmir; 6b - Ovacık, İzmir; 7 - near Smyrna (= İzmir); 8 - Samsun Dağı National Park, above Doğanbey, İzmir; 9 - Aydın; 10a - Beşparmak Mts., above Kapıkırı (= Herakleia), Muğla; 10b - Labranda (=Labraunda), ca 15 km north of Milas, Muğla; $\mathbf{1 1}$ - between Bafa Gölü (= Çamiiçi Gölü) and the sea, Aydın;12 - Köyçeğiz, Muğla; 13 - Geok-Tepe (= Gök Tepe, north of Söğütlüdere), Muğla; $\mathbf{1 4}$ - Çiğllkara, Antalya; 15 - Finike, Antalya; 16 - Antalya; 17 - Alanya; 18 - Kılbasan, Karaman; 19 - 8 km south of Bucakkışla, Karaman, ca 800 m a.s.l.; 20 - Bozyazı, Mersin; 21 - Gülnar, Mersin; 22 - Silifke, Mersin; 23 - Elvanlı, Mersin; 24 - Mersin; 25 - Zebil (=Sebil), Bolkar Dağları, Mersin; 26a - Gülek Boğazı, Bolkar Dağları, Mersin; 26b - Gülek Yayla, Mersin; 27 - Pozantı, Adana; 28a - Seyhan Baraji, Adana; 28b - University Campus, Adana, ca 150 m a.s.l.; 29 - Ömer Gölü, Yumurtalık, Adana; 30 - Ceyhan, Adana; 31 - Kadirli, Adana; 32 - Osmaniye, Adana; 33 - Haruniye (=Düziçi), Adana; 34 - Andırın, Kahraman Maraş; 35 - Ahır Dağı, Kahraman Maraş; 36 - Pazarcık, Kahraman Maraş; 37 - Turkoğlu, Kahraman Maraş; 38 - Fevzipaşa, Gaziantep; 39 - Islahiye, Gaziantep; 40 - Hassa, Hatay; 41 - 15 km south of İskenderun, Antakya; 42 - Bedirge, Uluçınar, Hatay; 43a - Samandağ, Hatay; 43b - Mağaracık (= Seleucia Pieria), Antakya; 44 - Yayladağı, Hatay; 45a - Antakya, Hatay; 45b - Hüyük of Yeşilova, 7 km north-east of Antakya; 46 - 10 km east of Kilis; 47 - Nizip, Gaziantep; 48 - Adıyaman; 49 - Samsat, Adıyaman; 50 - Kahta, Adıyaman; 51 - Bozova, Adıyaman; 52 - Halfeti, Şanlı Urfa; 53 - Birecik, Şanlı Urfa; 54 - Şanlı Urfa; 55 - Harran, Şanlı Urfa; 56 - Ceylanpınar, Şanlı Urfa; 57 - Diarbakır; 58 - Siirt; 59 - Bitlis. Corresponding references: Danford \& Alston (1877): 7, 25. Müller (1911): 1, 13, 24. Misonne (1957): 55. Kumerloeve (1967a): 3, 4, 5, 9, 12, 16, 17, 21, 22, 23, 26a, 26b, 27, 28a, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 42, 43a, 44, 45a, 47, 48, 49, 50, 51, 52, 53, 54, 57, 58, 59. Kinzelbach (1986): 8, 10a, 10b, 11, 41, 43b, 45b. Winden \& Bosman (1988): 29. Yiğit et al. (2003): 2, 6a, 6b, 14, 18, 46, 56. Arslan (2008): 20, 30. BMNH: 15. Own data: 19, 28b.
tiful in areas with broken rocky hillsides. In Israel, where the porcupine ranges throughout the country, it is more abundant in the Mediterranean zone than in the desert (Mendelssohn \& Yom-Tov, 1999). Lay (1967) provides details for Iran. On the northern slopes of the eastern Elbroz Mts., porcupines were observed and collected on a dry rocky hillside above the stream bed overgrown with Stellaria sp., Erysimum sp., Thymus sp., Centaurea sp., Marrabium sp., Dracocephallum sp., Astragalus sp., Pisun sp., Cousinia sp., and Acantholium sp. In the southern Zagros Mts., porcupines occupied scree slopes with sparse grass and weeds and occasional green-leafed vines and Prunus spartoides. In the Turkmen plains, the species lives in a mosaic of fields and moist deciduous forests of oaks, beech and hornbeam as well as on arid plains and undulating hills covered by 0.3-0.6 m high disjunct clumps of various Chenopodiaceae (Salicornia sp., Salsola sp., Halostochys sp., Gamanthus sp., Alhagi sp.). In the subtropical lowlands of southwestern Iran, porcupines live along the River Karkheh in fallow areas within Tamarisk-Populus euphraticus "jungle" (Lay, 1967). In Iraq, the Indian crested porcupine is found mostly in the Euphrates and Tigris valleys, while it is absent from the marshy areas and deserts, and is very rare in the mountains (Kadhim, 1997); Hatt (1959) also reported its occurrence in ruins. Kadhim (1997) trapped all his animals ( $\mathrm{N}=75$ ) near river and stream banks. In Transcaucasia, porcupines live in forested areas in the lowlands and foothills (Šidlovskij, 1976).

Range of $H$. indica in Turkey is within the Mediterranean climate and vegetation at lower elevations (mainly $<700 \mathrm{~m}$ a.s.l.), with a mean annual temperature $11-14^{\circ} \mathrm{C}$, and receiving at least $300-400 \mathrm{~mm}$ of precipitation annually (Gülen, 1952; Kumerloeve, 1967a). Actual precipitation is $650-700 \mathrm{~mm}$ along the Aegean coast, $300-530 \mathrm{~mm}$ in the coastal foothills of the Taurus Mts., and 330-800 mm in southeastern Anatolia (Yiğit et al., 2003). Main habitat in the coastal zone is a mosaic of arable and fallow land, dry barren slopes, and sclerophylous shrubs and woodland with Pinus brutia, P. nigra, Cedrus libani, Juniperus excelsa, J. oxycedrus, Cistus creticus, Rhus coriaria, Olea europaea, Pistacia lentiscus, P. terebinthus, and Quercus coccifera. At higher elevations, the woodland is a mixture of deciduous oaks (Quercus cerris, Q. pubescins) and pine (Pinus ni-
gra). In southeastern Anatolia, the steppic habitats are typically dominated by various grasses and herbs: Cyperus longus, Carex otrubae, Bolbochoenus maritimus, Scilla biflora, Hordeum sp., Eryngium sp., Securigera sp., Peganum sp., and Agropyron sp. (Yiğit et al., 2003). In Hatay and the periphery of Adana porcupines occur around villages (Gülen, 1952).

Altitude. In Anatolia, the altitudinal range is from close to the sea coast and lowlands up to 1,400-1,450 m at Gülek Boğazi in the Cilician Taurus (Kumerloeve, 1967a) and about 1,500 m (5,000 ft) elsewhere on the Taurus Mts. (Danford \& Alston, 1877). Highest records from the rest of the range are 1,000 m in Lebanon (Thomé \& Thomé, 1980), 1,4001,450 in Arabia (Harrison \& Bates, 1991), 1,800 m in Transcaucasia (Gromov \& Erbajeva, 1995), $2,400 \mathrm{~m}$ in central Tadzikistan (Gromov \& Erbajeva, 1995), 2,750 m in Baluchistan (Roberts, 1997), and 3,900 m in Pamir (Gromov \& Baranova, 1981). Range in Iran is from 30 m in the Khuzistan Plain up to $1,150 \mathrm{~m}$ at Sama in northern Elbroz Mts. (Lay, 1967).

Associates. In Israel, porcupine burrows may be occupied by mongooses, badgers, caracals, and owls (Mendelssohn \& Yom-Tov, 1999).

Density. Mean density is 4 porcupines per $\mathrm{km}^{2}$ in the Mediterranean zone of Israel (Server \& Mendelssohn, 1991). In the Negev highlands, densities are higher in agricultural areas ( 7.5 per $\mathrm{km}^{2}$ ) than in natural habitats (2.1 per km²; Alkon, 1999).

No information is available for Turkey, the authors, however, found the Indian crested porcupine to be common around İzmir and "in the Taurus, from


Figure 268. Habitat of Hystrix indica around Bucakkışla in the Taurus Mountains. Photo A. Kryštufek.
the plain to 5000 feet" (Danford \& Alston, 1877), common in the Samsun Dağı National Park above Doğanbey, İzmir, not rare in the area of Labranda, north of Milas (Kinzelbach, 1986), and common around Finike (Corbet \& Morris, 1967). According to Atallah (1978), porcupines are uncommon, although widespread in the Eastern Mediterranean region. For Iran, Lay (1967) reported them to be common in forested areas along the Caspian coast in Mazanderan and Gorgan provinces, on the Turkmen and Khuzistan plains, and in the Zagors Mts.

## Biology

Activity. A nocturnal animal, resting during the day in a burrow or a small cave (Atallah, 1978). Couples remain only in underground shelters at daytime, while solitary males also use surface shelters (dense shrub etc.; Server \& Mendelssohn, 1991). Porcupines emerge from their burrows from 20 minutes (in summer) to 2 hours (in winter) after sunset and return at sunrise in summer but up to 2 hours after sunrise in winter (Mendelssohn \& Yom-Tov, 1999). Saltz \& Alkon (1989) reported in Israel mean home range size of $1.5 \mathrm{~km}^{2}$, and movements of 2.8 km per night. Walking speed is about 2 km per hour. Home ranges were smaller in agricultural areas ( 0.375 and $0.487 \mathrm{~km}^{2}$ for two animals respectively) than in natural environment $\left(1,215 \mathrm{~km}^{2}\right)$ and solitary males traveled a larger distance per night ( $2,310 \mathrm{~m}$ ) than couples (1,684 m; Server \& Mendelssohn, 1991). Home ranges are relatively stable (Saltz \& Alkon, 1992). Adult porcupines are active on the surface for about 7 hours; activity is higher during summer ( 9.2 hours) than in winter (6.7 hours); from October to March, porcupines optimize winter activity for minimal exposure to moonlight (Alkon \& Saltz, 1988).

Adult porcupines generally live in pairs (Mendelssohn \& Yom-Tov, 1999).

Burrows. Porcupines spend the day in permanent burrows or in caves. Burrows are frequently excavated on slopes beneath rocks which serve as roofs. The tunnel of one or more openings expands into a chamber at its far end. Tunnels have 30-40 cm in a diameter and are 15 m long or more (up to 20 m ; Roberts, 1997). No lining is used in the chamber (Mendelssohn \& Yom-Tov, 1999). From Turkey Arslan (2008) reported five burrows in Ceyhan and

Bozyazı which were in a forested area near the river. Entrance was on average 40 cm in diameter and mean length of burrows was 4.5 m . Saleh \& Basuony (1998) described a den from Sinai with a diameter of about 50 cm . In Iran, porcupines den in similar situations as elsewhere: "beneath boulders, in cracks between exposed horizontal rock strata", in burrows and caves (Lay, 1967). In Anatolia, dens were mainly found in dense impenetrable bushes and along forest edges; they were sheltered from cold northern winds (Gülen, 1952). Porcupines also frequently seek shelter in caves (e.g. Corbet and Morris, 1967).

Reproduction. Kadhim (1997) found in Iraq a female biased sex ratio ( $=58.7 \%, \mathrm{~N}=75$ ) while a balanced ratio was reported from Israel ( $=51 \%, \mathrm{~N}=$ 113; Mendelssohn \& Yom-Tov, 1999). Females attain sexual maturity at two years old (Thomé \& Thomé, 1980); Mendelssohn \& Yom-Tov (1999) reported sexual maturity to be attained at about one year when porcupines weigh about 10 kg . There are two litters annually (Thomé \& Thomé, 1980; Kadhim, 1997) and pregnancy lasts for about three months (Thomé \& Thomé, 1980). In Iraq, pregnant females were collected from April to September (Kadhim, 1997) and young are born in Israel between February and August (Mendelssohn \& Yom-Tov, 1999). Number of embryos is 1-3 in Iraq (mean = 2.3; Kadhim, 1997), while nine litters from Lebanon contained $2-4$ cubs (mean $=3.0$; Thomé \& Thomé, 1980). Mean weight of newborns is 255325 g. Young are precocial, with their eyes open and body covered with soft hair; they are able to walk (Thomé \& Thomé, 1980). Maximum longevity in captivity was 14 years (Mendelssohn \& YomTov, 1999), although $H$. cristata lived 21 years in the Hamburg Zoo and more than 20 years in the London Zoo (Mohr, 1965).

Food. The Indian crested porcupine is an adaptable, generalist herbivore, exploiting a variety of above-ground and subsurface plant tissues. Maintenance energy requirements of a 13 kg porcupine average 1.3 kg of fresh potatoes or 1.1 kg of Erodium crassifolium, which is important natural forage. Such requirements can be compensated within about 7 hours feeding time (Alkon, 1999). Subterranean organs of 18 species of geophytes and hemicryptophytes (mainly Bellevalia desortorum, Erodium crassifolium, Malabaila secacul, Zozimia absinthii-
folia, Scorzonera papposa, Leontice leontopetalum, Scorzonera judaica, Bellevalia eigii, and Tulipa systola) are utilized in Israel; these plants are largely restricted to relatively mesic sites receiving annually about 400 mm of precipitation. Porcupines feed on $80-90 \%$ of the above plant species and destroy $20-$ 30 \% of them (Alkon, 1999). While searching for below-ground tubers and roots, porcupines dig similar sized, discrete, elongated pits (mean surface of $257 \mathrm{~cm}^{3}$ in the Negev Desert; Shachak et al., 1991), and in this way impact up to $4 \%$ of soil surface (Alkon, 1999).

Kadhim (1997) found plant matter (roots, tubers, buds, small branches, leaves, wild fruits, and seeds), in 75 porcupine stomachs from Iraq. This plant matter formed $98-100 \%$ of the content; 38 stomachs (= $51 \%$ ) also contained insects (mainly beetles). Remnants of bones were found in 19 samples, and belonged to a house mouse (Mus sp.) in two samples; the rest were probably lizards (Kadhim, 1997). Porcupines are known to occasionally gnaw bones (Mendelssohn \& Yom-Tov, 1999). Arslan (2008) found only roots in two stomachs from Turkey, and Gülen (1952) reported that captive animals were particularly fond of oak roots. Captive specimens readily take cabbage and other leafy vegetation (Lewis et al., 1967). Food is not stored.

Porcupines cause damage to agriculture throughout the range, e.g. to tuberous root crops (potatoes, beets, groundnuts Arachis hypogea, turnips, and carrots) in Pakistan (Brooks et al., 1988; Roberts, 1997) and to watermelons in Sinai (Saleh \& Basuony, 1998). They eat the bark on fruit trees (Alk on, 1999) and also break small peach trees in order to reach the fruit (Saleh \& Basuony, 1998).

Porcupines do not need to drink and normally get all the water from their food (Mendelssohn \& Yom-Tov, 1999).

Predation. In the Near East the porcupines are
preyed upon by leopards, hyenas and perhaps wolves (Qumsiyeh, 1996), reportedly also by the red fox (Vulpes vulpes), jackal (Canis aureus), and mongoose (Herpestes auropunctatus; Kadhim, 1997). When threatened, they erect their quills and run quickly, then suddenly stop running, so that the attacker runs into their spines (Mendelssohn \& Yom-Tov, 1999). They also charge backwards towards their enemies and can thrust quills deep into their bodies (Qumsiyeh, 1996). When alerted, they can rattle quills together, vibrating to produce a hisslike rattle, which is a warning sound for predators. (Saleh \& Basuony, 1998).

Conservation. Although H. indica is seemingly common in Turkey (cf. under Density), one should keep in mind the extreme scarcity of reliable information on the one hand, and the worrying status in the adjacent regions on the other. Lewis et al. (1967) concluded that "There is little indication for the Indian porcupine to be common in Lebanon nor is it particularly well known by local residents." The porcupine was still common in Iraq during the early $20^{\text {th }}$ century (Hatt, 1955), however, Kadhim (1997) reported a sharp decline since the mid-1970s. It is a species of conservation concern in Turkey (Yiğit et al., 2006c) and Armenia (Anonymus, 1987).

The Indian crested porcupine is hunted for flesh in many parts of its range, e.g. in the Eastern Mediterranean region (Atallah, 1978; Qumsiyeh, 1996), Iraq (Kadhim, 1997), and Pakistan (Roberts, 1997). The Bedouin in Israel believe in the therapeutic nature of various parts of the porcupine body (Mendelssohn \& Yom-Tov, 1999). Because of damage to agriculture and forest plantations, it is killed in the Eastern Mediterranean region (Atallah, 1978; Qumsiyeh, 1996), Israel (Alkon, 1999), and Pakistan, where bounties are paid for animals killed (Roberts, 1997).

## Family: Myocastoridae Ameghino, 1904

The family Myocastoridae includes a single monospecific genus (Myocastor Kerr, 1792) (Woods \& Kilpatrick, 2005). Myocastor was earlier in the family Capromyidae Smith, 1842 (e.g. Hall, 1981; Zima \& Král, 1984).

Dental formula is $1 / 1,0 / 0,1 / 1,3 / 3=20$.

## Coypu or Nutria - Myocastor coypus

Mus coypu Molina, 1782. Type loc.: Rio Maipo, Santiago Province, Chile.

## Description

External characters. Large and robust rat-like rodent, with a heavy triangular head, small eyes and short, rounded ears, which are hidden in fur. Tail is cylindrical in cross-section and shorter than head and body (about 72-82 \%). The hind feet are much longer than front feet; there are five clawed digits on hind feet (the first four being webbed by skin), and four on front feet. Upper pelage of coarse guard hairs, which nearly conceals the soft and thick underfur, is coarser on the back than on the belly. The tail is scaly and thinly haired throughout, except for the base.

Colour. Dorsal side is yellowish brown to reddish brown, the belly is pale yellow, and the tail is dark brown. Colour varieties, ranging from white to black,
were selected in captive-bred stocks, and are occasionally also seen in feral animals.

Nipples. Females have four pairs of pectoral nipples situated high on the sides of the body (Nowak, 1999).

Skull is large and powerful. Massive rostrum is compressed laterally; nasals are wide and relatively short, not reaching the orbit posteriorly. Incisive foramens are triangular and shorter than half of diastema length. Infraorbital foramen is much enlarged, but is smaller than the orbit. Zygomatic arches are heavy and well expanded; zygomatic breadth is equal to about 65 \% of condylobasal length. Interorbital region is wide with a short and blunt postorbital process. Brain-case is relatively small, with very powerful paroccipital process and well pronounced parietal crest; foramen magnum is only slightly wider than height. Hard palate does not extend behind $3^{\text {rd }}$ molars; its posterior margin is evenly concave. Interpterygoid fossa is wide and bullae are small. Mandible is relatively slender, with much prolonged angular process, and short but heavy articular process; the coronoid process is entirely absent.

Teeth. Incisors are robust and of approximately the same width (about 6.5 mm ) in the upper and lower jaw; enamel on their front surface is dull orange, paler on lower incisors. Cheek-teeth are highcrowned with short roots, rather large and with flat crowns. In both rows, the maxillary and the mandibular, $2^{\text {nd }}$ upper molar is the largest and premolars are the smallest. Crowns of maxillary cheek-teeth are


Figure 269. Coypu Myocastor coypus. Drawing: J. Hošek.


Figure 270. Stuffed coypu Myocastor coypus from Turkish Thrace (TUE). Photo: A. Kryštufek.
with two re-entrant folds on both sides; mandibular cheek-teeth have one labial and three lingual re-entrant angles. Re-entrant folds become isolated as narrow islands with advanced age.

Dimensions. In a sample from Florida, males appear slightly, although insignificantly, heavier (mean $=5.52 \mathrm{~kg}$, range $=4.25-8.0 \mathrm{~kg}, \mathrm{~N}=145$ ) than females (mean $=5.38 \mathrm{~kg}$, range $=4.0-7.5 \mathrm{~kg}, \mathrm{~N}=114$; Brown, 1975); secondary sexual dimorphism is not
evident from skull measurements of coypus introduced to Russia (Rossolimo, 1958). For external dimensions of specimens from Turkey see Table 56: values for tail length in Mursaloğlu (1973) are evidently erroneous (140-180 mm) and are not reported here. For morphometrics of populations from Israel see Table 57. An adult male from Thrace has a condylobasal skull length of 110.4 mm , zygomatic width of 71.6 mm , and maxillary tooth-row length of 33.3


Figure 271. Skull and mandible of Myocastor coypus, based on an adult male from Pazarkule near Edirne (TUE).
Scale bar $=25 \mathrm{~mm}$.


Figure 272. Upper (a) and lower cheek-teeth (b) of Myocastor coypus (same specimen as on Fig. 271). Lingual side is to the left, anterior is at the top. Scale bar = 10 mm .
mm . Skull dimensions in an adult specimen from Burgas in Bulgaria are: condylobasal skull length of 117 mm and maxillary tooth-row length 29.4 mm (Peshev et al., 2004).

|  | N | mean | min-max |
| :--- | :---: | :---: | :---: |
| Head and body | 3 | 529 | $485-550$ |
| Tail | 3 | 403 | $385-440$ |
| Hind foot | 3 | 131 | $124-140$ |
| Ear | 3 | 29 | $25-37$ |
| Weight | 2 |  | $4.35 / 5.8$ |
| Condylobasal length | 5 | 108.2 | $100.1-117.7$ |
| Zygomatic breadth | 5 | 70.5 | $65.9-80.3$ |
| Maxillary tooth-row | 4 | 28.3 | $26.6-28.6$ |

Table 57. External and cranial dimensions (in mm; body mass in kg ) of Myocastor coypus from Israel. Modified from Mendelssohn \& Yom-Tov (1999).

Chromosomes. Karyotyping was mainly performed on captive individuals. Diploid number is 2 N $=42$ and fundamental number of chromosomal arms is $\mathrm{FN}_{\mathrm{a}}=80$. All the autosomes and the X chromosome are bi-armed; the Y chromosome is acrocentric (Zima \& Král, 1984).

## Variation

Five subspecies are distinguished within the coypu's native range. Animals introduced to Europe are descendants of M. c. bonariensis (Commerson, 1805) (Type loc.: Isla Ella, Delta des Rio Paraná) from northern Argentina (Reggiani, 1999).

## Distribution

Native to South America: southern Brasilia, Bolivia, Paraguay, Uruguay, Peru, sub-tropical Argentina, and Chile (Reggiani, 1999). The Coypu was introduced to North America, Europe, temperate Asia (including Japan), the Near East, and Africa. Feral populations originate from such deliberate introductions, from animals which escaped from fur farms, or both.

The coypu inhabits Turkey in two widely separated regions: in the European part (Thrace) and in east-

|  | Thrace |  |  |  |  | North-eastern Anatolia |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Sex | male* | $?$ | male | female | female* | female* | male | female |  |
| Head and body | 340 | 440 | 535 | 555 | 330 | 330 | 460 | 440 |  |
| Tail | 290 | 295 | 440 | 400 |  |  |  |  |  |
| Hind foot | 100 | 114 | 134 | 133 | 56 | 55 | 84 | 84 |  |
| Ear | 20 | 21 | 28 | 29 | 14 | 13 | 17 | 17 |  |
| Weight | 2.0 |  | 7.1 | 8.0 |  |  |  |  |  |

Table 56. External dimensions of Myocastor coypus from Turkish Thrace (Özkan \& Kurtonur, 1994) and north-eastern Anatolia (Mursaloğlu, 1973). Asterisk denotes juveniles.


Figure 273. Distribution of Myocastor coypus in Turkey. Records: 1 - Değirmenyeni köy, Edirne; 2 - Kapikule, Edirne; 3a - Pazarkule, Edirne; 3b - Karaagaç, Edirne; 3c - Sögütlük, Edirne; 3d - Yildirim, Edirne; 3e - Bosanöy, Edirne; 4 - Elçili, Edirne; 5 - Kiremitçisalih, Edirne; 6 - Enez, Edirne; 7 - River Arpa Çayi, Kars; 8 -River Kara Su, Aralık, İğdır. Corresponding referrences: Mursaloğlu (1973): 8. Kumerloeve (1975): 7. Özkan \& Kurtonur (1994): 1. Özkan (1999): 2, 3a-e, 4, 5, 6.
ern Anatolia along the border with Armenia, Azerbaijan, and Iran (Kumerloeve, 1975; Doğramacı, 1989a; Demirsoy, 1999; Kurtonur et al., 1996; Yiğit et al. 2006c). The Thracian population has been known since 1984 (Özkan \& Kurtonur, 1994), and putatively originated from colonies in adjacent Bulgaria. The first nutrias appeared in Bulgaria before 1953 and are known currently from various colonies which are widely scattered across the country (Reggiani, 1999): Mandrenskoto ezero, Reserve Arkutino, around Burgas, the Sredecka River, and humid parts along the Black Sea coast (e.g. estuary of the Batova River and Šabla and Durankulak Lakes; Peshev et al., 2004). Nutrias occur along the entire Meriç River within its Turkish borders, between Kapikule in the north and Enez in the south. They are also present in the Tunca River, a tributary of the Meriç (Özkan, 1999b). Further west, the species is absent from Thrace in Greece, but populates the lower flow of the River Axios in Greek Macedonia (Reggiani, 1999).

The population in eastern Anatolia doubtlessly originated from introductions to Transcaucasia which started in 1932 (Bukhnikashvili \& Kandaurov, 1998). The only reports thus far are by Mursaloğlu (1973) from the Kara Su River near Aralık and by Kumerloeve (1975) from the Arpa Çayi River. In Transcaucasia, the coypu established permanent populations in Azerbaijan and Georgia, more specifically in the lowlands along the Kura, Arax, and Rioni rivers, on the Lenkoran Plain, in the Lake Ajgerlič, and in the Colchic Plain along the Mtkvari River (Šidlovskij, 1976; Bukhnikashvili \& Kandaurov, 1998). For a detailed map in Georgia, see Bukhnikashvili (2004).

To the south of Turkey, the coypu is absent from the large rivers of Iraq (Kadhim et al., 1977), but an isolated occurrence is documented for Israel. The coypu was introduced to Israel in the early 1950s for the economic benefit provided by the fur, which, however, proved to be worthless in the warm climate. Farms were therefore shut down and animals
released. Nutrias are now present throughout the Mediterranean areas of Israel wherever there are suitable aquatic habitats (Mendelssohn \& Yom-Tov, 1999). To the east of Anatolia, the coypu spread from Transcaucasia and southern Tadžikistan into Iran and Afghanistan (Gromov \& Erbajeva, 1995).

Palaeontology. The geological range of Myocastoridae is Late Oligocene to Recent in South America (Nowak, 1999); Myocastor is known since the Upper Pliocene (Stubbe, 1982).

## Habitat

As a semi-aquatic rodent, the coypu inhabits marshes, edges of lakes, slow streams and rivers, and occasionally also brackish and salt water (Nowak, 1999). A wide array of aquatic habitats are utilised in Israel: streams, fish ponds, water reserves, and even small ditches (Mendelssohn \& Yom-Tov, 1999). In eastern Georgia, nutrias live in riparian forests (Bukhnikashvili \& Kandaurov, 1999).

In Turkey, the coypu inhabits banks of deep lowland rivers (Mursaloğlu, 1973; Özkan, 1999). Habitat in Thrace is characterized by mild winters with mean January temperature of $2.2^{\circ} \mathrm{C}$. The Meriç River, which is presumably the preferred habitat, features many islets while its banks are densely reeded with numerous willows and poplar trees; the adjacent land is cultivated (Özkan, 1999b).

Altitude of localities in Turkish Thrace is about 40 m a.s.l. (Özkan, 1999b). Altitudinal range in Georgia is from sea level up to 400 m (Bukhnikashvili \& Kandaurov, 1999).

Density estimates vary from 0.1 coypu per ha, to


Figure 274. Habitat of Myocastor coypus on the River Tunca, Turkish Thrace. Photo: V. Vohralík.
24.7 per ha (Nowak, 1999). The coypu often reaches remarkable population densities outside its native range (Reggiani, 1999). Twenty coypus introduced to Louisiana in 1938 multiplied to an estimated 20 million feral animals by the late 1950s (Nowak, 1999). Seasonal fluctuations are considerable (about 25 -fold) and are generally ascribed to freezing weather in the Northern Hemisphere (Reggiani, 1999). In Thrace, the coypu is believed to be rare along the Tunca River, less so along the Meriç River (Özkan, 1999b).

## Biology

Activity. Although coypus are predominantly nocturnal animals, they are also frequently seen during the daytime. Much time is spent swimming and feeding. During swimming, hind legs alternate to propel the animal while the front legs are held close to the body; the tail serves as a rudder. Coypus move through the grass and reeds within a radius of about 180 m of their dens, using runways. Home ranges measure from 2.47 ha for females to 5.68 ha for males. Coypus live in pairs or in small groups of several related females and their offspring (Nowak, 1999).

Burrows. Coypus shelter in holes of other animal or construct their own burrows along the shores of various water bodies. Dens are either simple tunnels (diameter of about 20 cm ) or complex systems with passages extending 15 m or more. Nesting chamber contains a crude nest of vegetation (Nowak, 1999). In areas with rich swamp vegetation, nutrias build huge nests of reeds and similar plant matter (Mendelssohn \& Yom-Tov, 1999).

Reproduction. Females are polyestrous and produce annually two or three litters, each with $1-13$ precocial cubs (mean = 4.6-5.8; Stubbe, 1982). The gestation period is 127-138 days (Stubbe, 1982). Breeding occurs year-round and juveniles from early litters attain sexual maturity in the same year. Life expectancy in wild animals is usually $2-3$ years (up to 4 years); captive individuals lived for over six years, and occasionally survive up to 12 years (Stubbe, 1982; Nowak, 1999).

Two females, collected in Turkish Thrace on 25 December and 7 January respectively, were pregnant (Özkan, 1999b); each of them had four embryos (Özkan \& Kurtonur, 1994; Özkan, 1999b). Body mass of embryos (130-145 g; Özkan \& Kurtonur,
1994) suggests that delivery was close; newborns weigh 175-332 g (Stubbe, 1982).

Food. The diet is mainly vegetarian and the coypu consumes a wide range of plants in Europe: Agropyron repens, Agrostis spp., Alnus glutinosa, Angelica sylvestris, Apium nodiflorum, Azolla filiculoides, Baldellia ranunculoides, Berula erecta, Caltha palustris, Calystegia sepium, Carex spp., Centaurea nemoralis, Cicuta virosa, Cirsium spp., Cladium mariscus, Crategus monogyna, Dactylis glomerata, Eleocharis palustris, Elodea canadensis, Epilobium hirsutum, Eriophorum angustifolium, Eupatorium cannabinum, Festuca spp., Filipendula ulmaria, Glyceria maxima, Hedera helix, Hippuris vulgaris, Holcus lanatus, Hydrocharis morsus-ranae, Iris pseudacorus, Juncus spp., Lemna spp., Menyanthes trifoliata, Myriophillum spp., Nuphar lutea, Phragmites communis, Poa trivialis, Potamogeton spp., Potentilla palustris, Rorippa nasturtium-aquaticum, Rubus spp., Rumex spp., Salix spp., Scirpus spp., Solium perenne, Sonchus palustris, Sparganium ramosum, Stachys palustris, Stratiotes aldoides, and Typha spp. (Stubbe, 1982). Roots are the most important food (Nowak, 1999), however, preferences for a certain type of food vary seasonally (Stubbe, 1982). By eating Phragmites rhizomes, the coypu can convert the beds into open-water areas. It also pulls up Typha and Juncus, eating the submerged parts and roots and leaving the rest floating (Davis, 1956). Occasionally snails and other invertebrates are also eaten (Mendelssohn \& Yom-Tov, 1999). No information on diet is available from Turkey.


Figure 275. Eurasian beaver Castor fiber. Drawing: J. Hošek.

## Family: Castoridae Hemprich, 1820

A Holarctic family of two extant species, both in the genus Castor Linnaeus, 1758. One species survived in the Near East into prehistoric times but is now extirpated.

## Eurasian beaver - Castor fiber

Castor fiber Linnaeus, 1758. Type loc.: Sweden.
The beaver is a large semiaquatic rodent. General form is heavy; head is powerful, ears are short, eyes are small; fore feet are considerably shorter than hind feet, which are webbed. Tail is wide and flattened dorso-ventrally. Fur is very dense, uniformly clayish buff, less yellowish on the belly. The skull is low, robust and heavily-built, with widely expanded zygomatic arches. Mandible is powerful, with expanded angular process. Incisors are heavy, covered with dark yellowish brown enamel. Cheek teeth (one premolar and three molars) are large, with flat crowns which show pattern of enamel folds. Dimensions (in mm ) are as follows: length of head and body $=830$ 1020 , length of tail $=300-345$, length of hind foot $=170-200$, length of ear $=30-41$, body mass $=17-$ 35 kg , condylobasal length of skull $=121.0-149.4$, zygomatic width $=84.4-110.0$, length of maxillary tooth-row = 29.6-35.0 (Miller, 1912; Ognev, 1947; Kryštufek et al., 2006).

Beavers occupy habitats with year-round access to water and plant food: swamps, lakes, rivers and streams. Permanent water level and banks are essential as they allow digging for burrows. Beavers are strictly vegetarian and during the winter period depend on woody vegetation. Due to their tree cutting and dam construction, they have a major impact on the surrounding environment (Tattersall, 1999; Kryštufek et al., 2006).

Eurasian beavers once occurred throughout Palaearctic Eurasia, but were brought close to extinction by the early $20^{\text {th }}$ century when only about 1,200 individuals survived. Populations recovered afterwards and increased to currently almost 500,000 beavers, the majority of which are in Europe (Tattersall, 1999).

## Beavers in Turkey

Pleistocene. The oldest evidence regarding the occurrence of beavers in Turkey is from the Middle Pleistocene of Emirkaya II near Seydișehir in Central Anatolia (Şen et al., 1991; Montuire et al., 1994). Beaver bones were also excavated from a strata older than 35,000 years in Bisitun in the eastern Tigris drainage in Iran (Legge \& Rowley-Conwy, 1986).

Prehistoric and early historic period. Evidence regarding the beaver's presence in the Near East during the prehistoric period is abundant and reliable; for reviews see Boessneck (1974), Turnbull (1975), Legge \& Rowley-Conwy (1986) and Becker (2005). In Turkey, beavers occurred at Pınarbaşı in the Konya plain during the early Neolithic at about 10,000 years ago (Asouti, 2003) and in Domuztepe around 7,000 years ago (Campbell \& Carter, 2008). The majority of available information is about 3,000-5,000 years old: Alisar Hüyük on the River Delice Irmağı (tributary of the Kızıl Irmak River) (Boessneck, 1974; Legge \& Rowley-Conwy, 1986); Korucutepe on the upper Euphrates (Boessneck, 1974), Besik-Yassitepe near Troy (Becker, 2005), Norsuntepe near Elazığ (Boessneck, 1974), and Sirkeli Höyük near Adana (Becker, 2005). Yakar (2004) lists the beaver as one of the game species hunted by Early Bronze Anatolian farmers.

Contemporary evidence is also available for Iran, Iraq and Syria. In Iran, beavers occurred in Shanidar on the Greater Zab River between 12,000 and 10,600 years ago and in Tepe Sarab near Bisitun Cave about 8,900 years ago (Legge \& RowleyConwy, 1986). Subsequent Iranian sites are younger or not dated: Bastam, Akçay, 85 km south of Makou (Boessneck, 1974), Tamtama at Lake Urmiya and Belt Cave, close to the southern shore of the Caspian Sea (Legge \& Rowley-Conwy, 1986). The oldest Syrian records are from a period 8,000-15,000 years before present: Tell Sheikh Hamad, Sheik Hassan, Jerf al Ahmar (Becker, 2005), and Tell Abu Hureyra, 50 km downstream to Tell Hadidi (Legge \& Rowley-Conwy, 1986). Other finds are 6,000 years old at most: Mulla Matar, Tell Bderi, Tell-esSweyhat (Becker, 2005), and Tell Hadidi (Legge \& Rowley-Conwy, 1986). Iraqi records are of the Neolithic age or undated: Shanidar Cave, Palegawra, and Zawi Chemi Shanidar (Legge \& RowleyConwy, 1986).

Indirect evidence from the Tigris-Euphrates basin is reviewed by Legge \& Rowley-Conwy (1986), and incorporates a 2,800-3,000 year-old beaver carving on a stela from Tell Halaf, a 2,700 year-old Assyrian medical text reporting castoreum, and a Zoroastrian religius text from the $7^{\text {th }}$ century.
$19^{\mathrm{TH}}$ and $20^{\mathrm{TH}}$ CENTURY. The only information on the beaver in Turkey during the $19^{\text {th }}$ century is from Danfort \& Alston (1880) "Very trustworthy authorities at Kaisariyeh [Kayseri] told Danford that in the marshes between that place and Indjesu there existed an animal like an Otter, but which had a broad hairless tail. This description points directly to the Beaver, an animal which still exists in the Euphrates near Aleppo, and in the rivers of the Caucasus. The species is included in Smarda's list of the Mammals of Mesopotamia, and, though 'with some doubt,' in Mr. Blanford’s Fauna of Persia." Additional reports from the $19^{\text {th }}$ century are available for Syria. A report to the Royal Geographical Society concerning the Euphrates expedition of 1835-7 claims that "The existence of the beaver, either in the Euphrates or its affluents, has been ascertained." Specifically, one beaver was reportedly captured by the expedition and one of the expedition members saw a beaver skin near the town of Day res-Zor (Legge \& RowleyConwy, 1986). Legge \& Rowley-Conwy (1986) also refer to a report by Layard from 1853, who claimed that the beaver had formerly been abundant on the Kabour River, but had been hunted to near extinction by the time of his travels; Layard reportedly saw several beavers himself.

In the $20^{\text {th }}$ century, the beaver was reported for Turkey by Kumerloeve (1967b, 1975) for the River Ceyhan in 1949 (30 km to the north of the town of Ceyhan) and in 1973, from the vicinity of Yumurtalik between the rivers Ceyhan and Seyhan (in 1972), and in Körsulu Çayi near Kahraman Maraş (1959). All reports were based on verbal communication by local people and Kumerloeve himself never saw a beaver. More recently Turan (1984) listed the beaver for Turkey on the account of Kumerloeve (1975), and Demirsoy (1996) mapped the beaver’s putative presence in southern Central Anatolia and south-eastern Anatolia. Yiğit et al. (2006c) stated that "In the past, there were some records for this species from Habur, River Karasaz, Sultansazlığı, River Körsulu (Kahramanmaraş), and some branches of Kızılırmak

River (around Kayseri)" but concluded that the beaver "is most probably extinct" in Turkey.

In the last decade Professor Michael Stubbe from the Martin-Luther University (Halle, Germany) undertook a field survey in Anatolia dedicated to verification of the reported occurrence of the beaver. This survey failed to find any positive signs of its presence (Stubbe, personal communication).

The conclusion by Legge \& Rowley-Conwy (1986) is hence still fully valid: "the beaver was part of the fauna in mountain regions of the Near East
.. into historic times. ... Survival into the more recent past is problematic ..." because all the travellers' accounts contain uncertainties. Similar are conclusions by other authorities, namely that the reports from the $19^{\text {th }}$ and $20^{\text {th }}$ century are "far from satisfactory" (Harrison 1972) and therefore "lack credibility" (Becker, 2005). Although the period when the beaver was extirpated in the Near East in general and in Turkey in particular, cannot be estimated with any degree of certainty, it is beyond doubt that the animal is not present in the region any longer.

## Appendices

## Appendix 1

Records of Cricetulus migratorius (see also Fig. 11)
1 - Tunca River, near Edirne; 2 - Sinanköy, Lalapaşa, Edirne; 3 - Şeytandere, 2 km east of Kırklareli; 4a Umurcaköy, Lüleburgaz, Kırklareli; 4b - Yörükdere, Lüleburgaz, Kırklareli; 5 - Velika, Kırklareli; 6 - Tevfikiye, Edirne; 7a - 5 km east of Keşan, Edirne; 7b - Keşan Yerlisu köy, Edirne; 8 - Naip köy, Barbaros, Tekirdağ; 9 - 3 km north of Tekirdağ; 10 - Yenikonak, Bursa;11 - Karlıdere, Soğukpınar, Bursa; 12a - Ulu Daĝ, Bursa, 1,800 m a.s.l.; 12b - Ulu Dağ, Bursa 2,000 and 2,150 m a.s.l.; 13 - Izmit; 14 - Gökçekısık köyü, Eskişehir; 15 - Uluçayır köyü, Eskişehir; 16 - Eskişehir; 17 - Abant Gölü, Bolu; 18 - Karaça-Su (=Karacasu), Bolu; 19a - Emir Lake, near Ankara; 19b - Gölbaşı, Ankara; 19c - Çankaya, Ankara; 19d - Mühiye köy, Çankaya, Ankara; 19e - Yıldıztepe, Çankaya, Ankara; 20 - Yakupaptal köyü yaylasi, Elmadağ, Ankara, 1,540 m a.s.l.; 21a - Bayrak tepe, Çubuk barajı, Ankara; 21b - Çubuk barajı, Ankara; 22a - Çamkoru, Kızılcahamam, Ankara; 22b - Kızılcahamam, Ankara, 1,050 and 1,350 m a.s.l.; 23 - Balamba köyü, Bartin, Zonguldak; 24 - Korkorlu köy, Çiçekdağı, Kırşehir; 25 - Dıkmen, Kırıkkale; 26 - Cangri (= Çankırı); 27a - Tosya, Kastamonu; 27b - 5 km south-east of Tosya, Kastamonu; 27c - Suluca köy, Tosya, Kastamonu; 28 - Bürnük, Kastamonu; 29 - Dikmen, Sinop; 30 - Samsun; 31 - 20 km west of Kayseri; 32 - Kaysarieh (= Kayseri); 33 - Güneşli nahiyesi, Kayseri; 34-10 km south-west of Pınarbaşı, Kayseri; 35 - Gücük, Şarkişla, Sivas, 1,400 m a.s.l.; 36 Yıldızeli, Sivas; 37 - Zara, Sivas; 38 - Çambaşı, Ordu; 39-10 km south-east of Tunceli; 40 - Ovacik, Tunceli; 41 - 4 km south-east of Güzyurdu, Gümüşhane, c. 2,300 m a.s.l.; 42 - Aşkale, Erzurum; 43 - 16 km west od Bayburt, Gümüşhane; 44 - Baibort (=Bayburt); 45a - Havaalanı (= airport), Trabzon; 45b - Trabzon; 46a - Coşandere (=Khotz), Trabzon; 46b - Taşköprü yayla, Meryem Ana, Trabzon; 47 - Cimil, Başköy, Ikizdere, Rize, 2,140 m a.s.l.; 48 - Erzurum; 49 - Güzelyayla, Erzurum 2,260 and 2,310 m a.s.l.; 50 - Tortoum (=Tortum), Erzurum; 51-1 km east of Erence, Erzurum; 52 - Yonçalı köy, Karaköse, Ağrı; 53-3 km north of Sirbasan, Kars, 2,200 m a.s.l.; 54 - Sarıkamış, Kars; 55 - Çoban köy, Göle, Kars; 56a - Kutul Geçidi, Ardanuç, Artvin; 56b - Kutul yayla, Ardanuç, Artvin, 2,200 m a.s.l.; 56c - Karagözoğlu yayla, Ardanuç, Artvin, 2,250 m a.s.l.; 57-10 km east of Ardahan, Kars; 58 - 5 km east of Kars; 59 - Nahçıvan köy, Dıgor, Kars; 60 - Gaziler, Kazkoparan, Tuzluca, Kars; 61 - Aralık, Kars; 62 - Bendimahi, Muradiye, Van; 63 - Güzel dere köy, Özalp, Van; 64 - Van; 65 - 10 km south of Van; 66 - Gürpınar, Van; 67 - Mordağ, Ÿksekova, Hakkarı; 68 - Nemrut Gölü, Bitlis, 2,300 m a.s.l.; 69 - 3 km south of Tatvan, Bitlis; 70 - Ceylanpınar, Şanlıurfa; 71 - Diarbakır; 72 Gezin köyü, Elazığ; 73 - Buzluk, Harput, Elazığ; 74-10 km south of Elazığ; 75 - 5 km south of Alişam, 30 km east of Elazığ; 76 - Karadut, Nemrud Dağı, Adıyaman; 77 - Darende, Malatya; 78 - 23 km west of Darende, Malatya; 79 - Ahır Dağı, Kahraman Maraş, 900-1,000 m a.s.l.; 80a - Türkoğlu, Kahramanmaraş; 80b - Sarılar köy, Türkoğlu, Kahraman Maraş; 81 - Toprakkale, Adana; 82a - 10 km east of Kilis; 82b - Telhabeş köyü, Kilis; 83 - Topboğazı Geçidi, Belen, Hatay; $\mathbf{8 4}$ - Amik Gölü, Hatay; $\mathbf{8 5}$ - Adana; $\mathbf{8 6}$ - Demir Kaziköy, Ala Dağları, Adana; $\mathbf{8 7}$ - Pozanti, Adana; $\mathbf{8 8}$ - Madenköy, Ulukışla, Niğde; $\mathbf{8 9}$ - Cehennem Dere (= 16 km south of Namrunkale), Mersin; 90 - Fundukpunar (= Fındıkpınari), Mersin; 91 - Mersin; 92 - Ereĝli, Konya; 93 - Balli, Mersin, 1,600 m a.s.l.; 94 - 5 km south of Yellibeli Geçidi, Karaman, ca 1,900m a.s.l.; 95 - Bucakkışla, Karaman; 96 - Karaman; 97 - Kılbasan, Karaman; 98 - Madenşehri köy, Kara Dağ, Karaman; 99 - Yaprakhisar, Ihlara, Aksaray; 100 - Divanlar, Konya; 101 - Yapalı köyü, Cihanbeyli, Konya, ca 1,000 m a.s.l.; 102a - Inevi (Cihanbeyli), Konaya; 102b - 6 km north of Cihanbeyli, Konya; 102c - 5 km west of Cihanbeyli, Konya; 103 Çubuk, Kadınhanı, Konya; 104a - 4 km north-east of Beyşehir; 104b - Budak, Beyşehir, Konya; 105 - Ağalar, Ilgın, Konya; 106 - Karabulut, Akșehir Gölü, Konya, 990 m a.s.l.; 107 - Doğanköy, Eber Gölü, Afyon 995 m a.s.l.; 108 - Seyitler baraji, Çobanlar, Afyon; 109 - Pazarköy, 22 km south-east Eğirdir, Isparta; 110 - Çendik, Suludere, Burdur; 111 - Antalya; 112 - Mancarlı Daĝ (= 25 km north of Finike), Antalya; 113 - Çığlıkara, Antalya; 114 - Sütleğen, Antalya; 115 - Çardak, Denizli; 116 - Honaz Dağ, Denizli; 117 - 3 km south-east of Muğla; 118a - Murad Dag (= Murat Daĝı), Kütahya; 118b - Ilıcalar, Murat Dağı, Kütahya; 119 - Uşak; 120 - Demircı, Manisa; 121 - 5 km north-west of Bergama, İzmir, ca 200 m a.s.l.; 122 - Bayındır, İzmir; 123 Bozdağ, İzmir; 124 - Smyrna (= İzmir). Corresponding references: Danford \& Alston (1880): 32, 48. Tho-
mas (1905): 44, 50. Thomas (1917): 46a. Aharoni (1932): 91. Neuhäuser (1936a): 16, 26, 27a, 29, 64, 90, 92, 95, 96, 102a, 118a, 124. Lehmann (1957): 85. Kahmann (1964): 1, 29, 30. Osborn (1965): 7a, 12a, 19a, 19b, 19c, 19d, 19e, 28, 89, 112. Steiner \& Vauk (1966): 104a. Felten et al. (1971b): 18, 109, 113, 114, 116, 119, 123. Sickenberg (1971): 100. Kurtonur (1972): 2, 4a, 6. Kock et al. (1972): 75. Morlok (1978): 37. Doğramacı (1989b): 3, 4b, 7b, 8, 9, 11, 12b, 13, 14, 15, 19 b, 19c, 19d, 19e, 20, 21a, 21b, 22a, 22b, 23, 24, 25, 27b, 27c, 30, 31, 33, 34, 39, 40, 42, 43, 45a, 46b, 47, 49, 52, 55, 56a, 56b, 56c, 57, 58, 59, 60, 61, 63, 66, 67, 68, 72, 74, 78, 79, 80b, 82b, 88, 98, 102b, 102c, 108, 117, 118b. Nadachowski et al. (1990): 81. Doğramaci \& Kefelioğlu (1991b): 38. Obuch (1994): 54, 62, 69, 76, 83, 86, 99. Yiğit et al. (2003): 5, 10, 36, 65, 70, 77, 80a, 82a, 97, 115, 120, 122. Seçkin \& Coşkun (2006): 71. Arslan \& Alkan (2008): 103, 104b, 105. ZFMK: 45b, 87, 111. Our own data: 35, 41, 51, 53, 73, 93, 94, 101, 106, 107, 110, 121.

## Appendix 2

## Records of Apodemus witherbyi (see also Fig. 72)

1 - Ulu Dağ, Bursa, 1, 400 and 1,700 m a.s.l.; 2 - Sapanca, Izmit, 500 ft. a.s.l.; 3 - Abant Gölü, Bolu, 1,000 m a.s.l.; 4-7 km west (by road) of Alaplı, Zonguldak; 5 - Çaırköy, Zonguldak; 6 - 8 km north-west of Yenice, Zonguldak, ca 100 m a.s.l.; 7 - 5 km north of Safranbolu, Zonguldak, ca 500 m a.s.l.; 8 - Bürnük, Kastamonu; 9 - 2 km east of Seyfe, Amasya, 1,100-1,400 m a.s.l.; 10 - Gücük, Sarkıșla, Sivas, 1,400 m a.s.l.; 11 4 km east of Șerefiye, Sivas, 1,620 m a.s.l.; 12 - Tamdere, Giresun, 1,550 m a.s.l.; 13 - Trabzon; 14 - Khotz (=Çosandere), Trabzon; $15-4 \mathrm{~km}$ south-east of Güzyurdu, Gümüşhane, ca 2,300 m a.s.l.; $\mathbf{1 6}-2 \mathrm{~km}$ south-east of Derebük, Erzican; 17 - Çamlik, Rize, 1,380 m a.s.l.; 18 - Ovitdağı Geçidi, Rize, 2,450 m a.s.l.; 19 - Kabaca, 8 km south of Murgul, Artvin, ca 800 m a.s.l.; 20 - Damar, 4 km south east of Murgul, Artvin, ca 1,000 m a.s.l.; 21 - Cankurtaran Geçidi, Artvin, 1,050 m a.s.l.; 22 - Borçka, Artvin; 23 - Yavuzköy, Şavşat, Artvin, ca 1,500 m a.s.l.; 24a - Yalnızçam Geçidi, Artvin, ca 2,500 m a.s.l.; 24b - 5 km west of Bağdaşan, Kars, ca 2,600 m; 25 - 3 km north of Sirbasan, Kars, ca 2,200 m a.s.l.; $26-3 \mathrm{~km}$ west of Handere, Kars, ca 2,600 m a.s.l.; 27 - 3 km south of Sarıkamış, Kars, ca 2,400 m a.s.l.; 28 - Çayırtepe, Erzurum, 1,950 m a.s.l.; 29 - Erence, Erzurum; 30 - 10 km south-west of Aydoğlu, Ağrı, 1,600 m a.s.l.; 31 - Doğubayazıt, Ağrı; 32 - Tatvan; 33 - 6 mi southwest of Tatvan, Bitlis, 5,800-6,000 ft a.s.l.; 34 - Erdemit, Van, 4,600 ft a.s.l.; 35 - Hakkâri; 36 - 4 mi north of Urfa; 37 - Birecik, Şanlı Urfa; 38 - Belen Pass, Hatay; 39 - Tanır, Kahraman Maraş, ca 1,200 m a.s.l.; 40 - Feke, Adana, ca 600 m a.s.l.; 41 - Çukurova University Campus, Adana, 100-150 m a.s.l.; 42 above Burucek, Tarsus, Mersin, 1,350 m a.s.l.; 43 - Zebil (=Sebil), Bulgar Dagh (=Bolkar Dağları), Mersin; 44 - Madenköy, Ulukışla, Niğde; 45 - Pozantı, Adana, 900 m; 46 - Yazlik, north of Darılık, Ala Dağları, Adana; 47 - Ercyes, Kayseri, 1,850 m a.s.l. 48 - Talas, Kayseri; 49 - 3 km north-west of Akköy, Yeşilhisar, Kayseri, 1,350 m a.s.l.; 50 - Göre, Nevşehir, 1,250 m a.s.l.; 51 - Gücük, Sarkışla, Sivas, 1,400 m a.s.l.; 52 - 6 km south of Kırşehir; 53 - Ballı, Mersin (= İçel), 1,450-1,600 m a.s.l.; 54 - Balkusan, Konya, ca 1,600 m a.s.l.; 55 - Yellibeli Geçidi, Karaman, ca 1,850 m a.s.l.; 56 - Lake Emir, Ankara; $57-10$ km north-east of Sivrihisar, Ankara; 58 - Karabulut, Akşehir Gölü, Konya, 990 m a.s.l.; 59 - Doğanköy, Eber Golü, Afyon, 995 m a.s.l.; 60 - 12 km south-east of Eğirdir, Isparta; 61 - Burdur, Isparta; 62 - Cığlıkara, ca 25 km south-east of Elmali, Antalya, 1,300-1,700 m a.s.l.; 63 - Göksuyu river, 10 km south-east of Kütahya; 64 - 4 km south of Akçaköy, Aydın, 190 m a.s.l.; 65 - İzmir; 66 - 10 km north-east of Bardakçı, Manisa, ca 600 m a.s.l.; 67 - Bergama, İzmir; 68 10 km south-east of Çırpılar, Kaz Dağları, Çanakkale, ca 1,000 m a.s.l.; 69 - Behram, Ayvacık, Çanakkale; 70 - Island of Bozcaada. Greek islands: 71 - 5 km south of Antimachi, Kos; 72 - Kamiros, Rhodes; 73 - Kattavia, Rhodes. Corresponding references: Barret-Hamilton (1900): 43. Filippucci et al. (1996): 1, 3, 6, 7, 60, 62, 63, 67. Özkan (1999a): 70. Macholán et al. (2001): 9, 15, 20, 24a, 25, 31, 35, 61. Frynta et al. (2001): 19, 24b. Çolak (2003): 44. Kryštufek \& Mozetič Francky (2005): 72, 73. Kryštufek \& Vohralík (2008): $1,3,4,5,6,7,9,10,11,12,15,16,17,18,19,20,21,23,24 a, 24$ b, 25, 26, 27, 28, 29, 30, 39, 40, 41, 45, 46, $47,49,50,51,52,53,54,55,57,58,59,61,62,64,66,68,69,72,73$. ZFMK: 13, 22, 32, 37, 38, 42. NMNH:

8, 14, 48, 65. FMNH: 2, 33, 34, 36, 56. Our own data: 71. Diamonds in south-eastern Anatolia point on "Apodemus sylvaticus tauricus" by Doğramacı (1974): I - Erganı, Diyarbakır; II - Diyarbakır, bank of the River Tigris; III - Şemdinli, Hakkari.

## Appendix 3

Records of Apodemus mystacinus (see also Fig. 91)
1 - Behram, Ayvacık, Çanakkale; 2 - 10 km south-east of Çırpılar, Kaz Dağları, Çanakkale; 3 - Yenikonak, Bursa; 4 - Ulu Dağ, Bursa; 5 - Soğukpınar, Bursa; 6 - Bozüyük, Bilecik; 7 - Gökçekısık, Eskişehir; 8 - 5 km south of Bolu; 9 - Akçakoca, Bolu; 10a - Zonguldak; 10b - 4 km south-west of Zonguldak; 11a - Çaycuma, Zoguldak; 11b - Çayır, Zonguldak; 12 - 5 km north of Safranbolu, Zonguldak; 13 - Kızılcahamam, Ankara; 14 - Bayrak tepe, Çubuk barajı, Ankara; 15 - Kaleyakası mevkii, Tosya, Kastamonu; 16 - Borabay Lake, 20 km west of Taşova, Amasya; 17 - 2 km east of Seyfe, Amasya; 18a - Amasya; 18b - 4 km west of Amasya; 19 - Yıldızeli, Sivas; 20 - Topçam, Ordu; 21 - Düroğlu, 13 km south (by road) of Giresun; 22 - Trabzon; 23a Scalita (=Altındere), Trabzon; 23b - Sumela (=Meryem Ana), Trabzon; 23c - Maçka, Trabzon; 24 - Ikizdere, Rize; 25 - Damar, Murgul, Artvin; 26 - Borçka, Artvin; 27 - Artvin; 28a - Karanlıkmeşe, Ardanuç, Artvin, $1,225 \mathrm{~m}$ a.s.l.; 28b - Ardanuç, Artvin; 29 - 10 km south-west of Aydoğdu, Ağrı, ca 1,600 m a.s.l.; $\mathbf{3 0}$ - 10 km south of Van; 31 - Şemdinli, Hakkâri, 1,350 m a.s.l.; 32 - Nemrut gölü, Nemrut Dağı, Bitlis, 2,280 m a.s.l.; 33 Tatvan, Bitlis; 34-10 km south of Bitlis; 35 - Ovacik, Tuncelı, 1.500 m a.s.l.; 36 - 10 km south-east of Tunceli; 37 - Darende, Maltya; 38 - Buzluk, Harput, Elazığ; 39 - Hazar gölü, Elazığ, 1,300 m a.s.l.; 40 - Alişam, 30 km east of Elazığ; 41 - Karadut, Nemrud Dağı, Adıyaman; 42 - Akrecgi geçidi, Mardin, 1075 m a.s.l.; 43 - Ceylanpınar, Şanlı Urfa; 44 - Göksun, Kahraman Maraş; 45-6 km north-east of Osmaniye, Adana; 46 Nur Dağı Geçidi, Bahçe, Adana; 47-10 km north-west of Gaziantep; 48 - near Kilis, Gaziantep; 49 - Yukarı Karafakılı, Hassa, Hatay; 50 - Kırıkhan, Hatay; 51a - Belen Pass (=Topboğazı Geçidi), Hatay; 51b - Şebük, Belen, Hatay; 51c - Soguk Oluk (=Soğukoluk), Belen, Hatay; 52 - Iskenderun, Hatay; 53 - Talas, Kayseri; 54 - Erciyes Dağı, Kayseri; 55 - Feke, Adana; 56 - Yazlik, Darılı, Adana; $57-7$ km north-west of Niğde; 58 - Yaprakhisar, Ihlara, Aksaray; 59a - Pozanti, Adana; 59b - 10 km west of Pozanti; 60 - Madenköy, Niğde; 61 - Cehennem Dere (= 16 km south of Namrunkale), Mersin; 62 - Zebil, (=Sebil), Bolkar Dağ, Mersin; 63 Mersin; 64a - 20 km east of Silifke, Mersin; 64b - Korykos, Silifke , Içel (= Mersin); 64c - Limonlu, Erdemli, Mersin; 65 - Silifke, Mersin; 66a - Kara Dağ, ca 80 km south-east of Konya, Karaman; 66b - Kılbasan, Karaman; 67 - Bucakkışla, Karaman; 68 - 26 km east of Ermenek, Konya; 69 - Ermenek, Konya; 70 - 2 km west of Kaş Yayla, 39 km north-east of Demirtaş, Antalya; 71 - Incekum, 26 km north-west of Alanya, Antalya; 72 Güzelsu, Antalya; 73 - Akseki, Antalya; 74a - 15 km south-west of Beyşehir, Konya; 74b - Beyşehir, Konya; $75 \mathbf{a}$ - Beşbahce, ca 30 km south of Eğidir, Isparta; 75b - Parazköy, 22 km southe-east of Eğidir, Isparta; 76a Insuyu Mağarası, 12 km south of Burdur; 76b - Burdur; 77 - near Karain Mağarası, ca 30 km NNW Antalya; 78 - Antalya; 79a - Elmalı, Antalya; 79b - Çam Kuyusu, near Elmali, Antalya; 80 - Yalniz, ca 25 km north of Finike, Antalya; 81-7-12 km west of Finike, Antalya; $\mathbf{8 2}$ - Cığllkara, ca 25 km south-east of Elmali, Antalya; 83 - Kaş, Antalya; 84a - the pass 50 km south-west of Elmali (= Sinekcibeli Geçidl), Antalya; 84b - Sütleğen, Antalya; 85 - Ikizce (north of Kalkan) Antalya; 86 - Fethiye, Muğla; 87 - 2 km north of Aşağigürlek, Bozbel, Muğla; 88 - Daylan, Köyceğis, Muğla; 89 - Beldibi köy, Marmaris, Muğla; 90a - Murad Dağ (=Murat Dağı), Kütahya; 90b - Ilicalar, Murat Dağı,Gediz, Kütahya, 1,450 m a.s.l.; 91 - Ulubey, Uşak; 92 - Buharkent (=Burhaniye), Aydin; 93 - 3 km north of Pamukkale, Denizli; 94 - Honaz Dağ, Denizli; 95 a - 7 km south of Eskiçine, Aydı; 95b - ca 10 km north of Yatağan, Muğla; 96-4 km south of Akcaköy, Aydın; 97a - Efes, Selçuk, İzmir; 97b - 10 km north of Kuşadası, İzmir 98 - Ovacık, İzmir; 99 - Demircı, Manisa; 100a - Smyrna (=İzmir); 100b - Pınarbaşı köy, Bornova, İzmir; 100c - 2 km north of Bornova, İzmir; 100d - Kemalpaşa, İzmir; 100e Yamanlar Dağı, İzmir; 101 - 10 km south of Karaburun, İzmir; 102 - Akhisar, Manisa; 103 - Demircı, Manisa. Greek Islands: 104 - Crete; 105 - Karpathos; 106 - Rhodes; 107 - Kos; 108 - Ikaria; 109 - Samos; 110 - Chi-
os; 111 - Lesbos. Corresponding references: Danford \& Alston (1877): 62. Thomas (1903): 100a. Neuhäuser (1936a): 5, 10a, 23a, b, 27, 63, 66a, 67, 69, 79a, 90a. Osborn (1965): 16, 18a, 52, 53, 61, 91. Steiner \& Vauk (1966): 74a, Lehmann (1966): 26, 51a, 59a, 65. Corbet \& Morris (1967): 80. Lehmann (1969): 33. Kock et al. (1972): 40. Felten et al. (1973): 4, 45, 46, 60, 64a, 68, 70, 71, 72, 75a, b, 76a, 81, 82, 84a, b, 86, 88, 93, 94, 95a, b, 97b, 100c, 101. Doğramacı (1974): 8, 10b, 13, 14, 15, 18b, 24, 28a, 31, 32, 34, 35, 36, 39, 42, 47, 48, 51b, 89, 90b, 97a, 100b. Storch (1977): 104 - 111. Morlok (1978): 22. Obuch (1994): 41, 58. Zima \& Macholán (1995): 2, 11a, 12. Vohralík et al. (2002): 17, 25, 49, 55, 56, 83. Yiğit et al. (2003): 3, 7, 19, 30, 37, 43, 66b, 98, 99, 103. Çolak et al. (2004): 6, 9, 28b, 44, 50, 73, 74b, 76b, 92, 100d, 102. Michaux et al. (2005) : 78. Kryštufek \& Janžekovič (2005): 1, 11b, 20, 23c, 38, 54, 57, 64b, c, 85, 96. BMNH: 59b. ZFMK: 51c. SMF: 77, 79b. Our own material: 18a, 21, 29, 87, 100 e.

## Appendix 4

Records of Rattus rattus (see also Fig. 103)
Records in Turkey: 1 - Island of Bozcaada; 2 - Island of Gökçeada; 3 - Tevfikiye, Edirne; $\mathbf{4}$ - Karasatı, Keşan, Edirne; 5 - Ormanlı, Tekirdağ; 6 - Kumbağ, Tekırdağ; 7 - Kırklareli; 8a - Demirköy, Kırklareli; 8b Velika, Demirköy, Kırklareli; 9 - Çamlıkoy, Tekırdağ; 10 - Podima, İstanbul; 11 - Selimpaşa, İstanbul; 12 Terkos, İstanbul; 13 - İstanbul; 14 - Abant, Bolu; 15 - Akçakoca, Bolu; 16 - Kocaman (= Koraman), Zonguldak; 17a - Bolu; 17b - Karacasu, Bolu; 18 - Zonguldak; 19 - Gerede, Bolu; 20 - Ankara; 21 - Tosya, Kastamonu; 22 - Bektaşağa, Sinop; 23 - Yıldızeli, Sivas; 24 - Trabzon; 25 - Sumela, (= Meryem Ana), Trabzon; 26 - Rize; 27 - Kurayiseba (= Ikizdere), Rize; 28 - Aralık, Iğdır; 29 - 10 km south of Van; 30 - Diarbakır; 31 - Ceylanpınar, Şanlı Urfa; 32 - Darende, Malatya; 33 - Şanlı Urfa; 34 - Akçakale, Şanlı Urfa; 35 - 10 km east of Kilis; 36 - Türrkoğlu, Kahramanmaraş; 37 - Haruniye (=Düziçi), Adana; 38 - Toprakkale, Adana; 39 Iskenderun, Hatay; 40 - Ömer Gölü, Yumurtalık, Adana; 41 - Adana; 42 - Tarsus, Mersin; 43 - Mersin; 44 Kılbasan, Karaman; 45 - Inçekum ( $=26$ km north-west of Alanya), Antalya; 46 - Akseki, Antalya; 47 - Eğirdir, Isparta; 48 - Antalya; 49 - Çığlıkara, Antalya; 50 - Yalniz, near Finike, Antalya; 51 - Kaş, Antalya; 52 - Fethiye, Muğla; 53 - Çardak, Denizli; 54 - Bayındır, İzmir; 55 - Ovacık, İzmir; 56 - İzmir; 57 - Demircı, Manisa; 58 - Burhaniye, Balıkesir; 59 - Evgene Köyü, Ivrindi, Balıkesir; $\mathbf{6 0}$ - Savaştepe, Balıkesir; 61 - Kocaavşar, Balya, Balıkesir; 62 - Deve Yatağı, Bigadiç, Balıkesir; 63 - Gönen, Balıkesir; 64 - Yenikonak, Bursa; 65 - Olymp (= Ulu Dağ), Bursa; 66 - Gökçekısık, Eskişehir. Records in Cyprus: 67a - Cedar valley, Nicosia, 1,090 m a.s.l.; b - 2 km south of Klepini, Kyrenia; c - Armenian Monastery, Kyrenia; d - 10 km north of Pano Panaya, Nicosia; $\mathbf{e}$ - Pouzis river, 14 km east of Mazotos, Larnaca; $\mathbf{f}$ - Ayios Amvrosios, Kyrenia; $\mathbf{g}$ - Dhigenis rock, Nea Paphos, Paphos; h - Yermasoyia Reservoir, Limassol; i - Paphos; $\mathbf{j}$ - north-west of Neo Chorio, Akmaz Peninsula, 305 m a.s.l.; $\mathbf{k}$ - east of Troodotissa Monastery, Central Troodos Mts., 1340 m a.s.l.; $\mathbf{1}-5 \mathrm{~km}$ south of Dhierona, 610 m a.s.l.; $\mathbf{m}$ - south of Palaichori, Eastern Troodos Mts., $990 \mathrm{~m} ; \mathbf{n}$ - north of Ardana, Kyrenia Mts, 290 m a.s.l.; o - Kyrenia; p - Smyes, Akmas penninsula; r-12 mi west of Limassol; s - Agios Epikratos, distr. Kyrenia; t - Aspleokremno, Mt. Troodos, 4600 ft a.s.l.; u - near Ktina; $\mathbf{v}$ - Moni Profitis Elias (near Lythrodontas), Troodos Mts; w-Trimithousa, 5 km north of Paphos; $\mathbf{x}-3 \mathrm{~km}$ south of Evdokimon, Limassol; y - 4 km south of Kornos, Larnaca; $\mathbf{z}$ - Dhenia (=Deneia), 25 km west of Nicosia. Greek islands: 68 - Crete, 69 - Karpathos, 70 - Rhodes, 71 - Astipalea, 72 - Kos, 73 - Ikaria, 74 - Samos; 75 - Chios, 76 - Lesbos. Corresponding references: Bennet (1835): 24. Neuhäuser (1936a): 17a, 18, 19, 21, 26, 27, 41, 43, 48, 65. Misonne (1957): 34. Osborn (1965): 16, 22, 39, 56. Lehmann (1966): 37. Felten et al. (1971b): 15, 17b, 45, 52. Kurtonur (1972): 3, 4, 5, 6, 7, 9, 10, 11, 12, 13. Spitzenberger (1978a): 67a-h. Winden \& Bosman (1988): 40. Nadachowski et al. (1990): 20, 38, 67i. Yiğit et al. (1998b): 8a, 46. Özkan \& Kryštufek (1999): 1, 2. Amori \& Cristaldi (1999): 68-76. Yiğit et al. (2003): 8b, 14, 23, 25, 28, 29, 31, 32, 35, 36, 44, 49, 53, 54, 55, 57, 64, 66. Yiğit et al. (2006c): 63. Seçkin \& Coşkun (2006): 30. Landová et al. (2006): 67j-n. BMNH: 50, 67o-u. SMF: 47, 51, 58, 59, 60, 61, 62. NMNH: 42, 67v-z. Our own data: 33.

## Appendix 5

Records of Mus domesticus (see also Fig. 129)
1 - Island of Gökçeada; 2 - Island of Bozcaada; 3 - Tevfikiye, İpsala, Edirne; 4 - Ormanli, Tekirdağ; 5 Dalamandra, Silivri, İstanbul; 6 - Akalan, İstanbul; 7 - Selimpaşa, İstanbul; 8 - Halkali, İstanbul; 9 - Manyas Gölü (= Kuş Gölü), Balıkesir; 10 - Bozüyük, Bilecik; 11 - Kütahya; 12 - Düzce, Bolu; 13 - Abant Gölü, Bolu; 14 - Bolu; 15 - Zonguldak; 16 - Çayirköy, Zonguldak; 17 - Bartin, Zonguldak; 18 - Gerede, Bolu; 19 - Saraköy, Ankara; 20a - Ankara; 20b - Gölbaşı, Ankara; 21 - Balâ, Ankara; 22 - Tosya, Kastamonu; 23 - Dikmen, Sinop; 24 - Kurupelit, Samsun; 25 - Fatsa, Ordu; 26 - Topçam, Ordu, 850 m; 27 - Kesap, Giresun; 28 - Yomra, Trabzon; 29 - Kurayiseba (= Ikizdere), Rize; 30 - Rize; 31 - Ardeşen , Rize; 32 - Hopa, Artvin; 33 - Borçka, Artvin; 34 - Ardanuç, Artvin; 35 - Posof, Kars; 36 - Sarkamiş, Kars; 37 - 3 km north of Sırbasan, Kars, ca 2,200 m a.s.l.; 38 - Erzurum; 39 - Doğubayazıt, Ağrı; 40 - Van; 41 - Şırnak, Siirt; 42 - Nusaybin, Mardin; 43 - Ceylanpınar, Şanlı Urfa; 44 - Alişam, 30 km east of Elazığ; 45 - Elazığ; 46 - Akçakale, Şanlı Urfa, 340 m a.s.l.; 47 - Harran, Şanlı Urfa, 350 m a.s.l.; 48 - Karkamıș (=Kargamış), Barak, Gaziantep; 49 - Kilis, Gaziantep; 50a - Reyhanlı, Hatay; 50b - Amik Gölü, Hatay; 51 - Yukarı Karafakılı, Hassa, Hatay, ca 600 m a.s.l.; 52 - Yumurtalık, Adana; 53 - Osmaniye, Adana; 54 - Türkoğlu, Kahraman Maraş; 55 - Kahraman Maraş; 56 Göksun, Kahraman Maraş; 57 - Aygörmez Köyü, north-west of Pınarbaşı, Kayseri; 58 - Kayseri; 59 - Yozgat; 60 - Çukurova University Campus, Adana, 100-150 m a.s.l.; 61 - below Tepeköy, 7 km north-west (by road) of Niğde, 1,800 m a.s.l.; 62 - Cehennem Dere ( $=16 \mathrm{~km}$ south of Namrunkale), Mersin; 63 - Tarsus, Mersin; 64 - Mersin; 65 - Kızkalesi, Korykos, Mersin; 66 - Ballı, Mersin 1,450 m a.s.l.; 67 - Balkusan, Konya, ca 1,600 m a.s.l.; 68 - Inçekum, (= 26 km north-west of Alanya), Antalya; 69 - Inevi (=Cihanbeyli); 70 - Akșehir Gölü, Konya; 71 - Selimiye, Antalya; 72 - Eğirdir, Isparta; 73 - Gönen, Isparta; 74 - Burdur; 75 - Antalya; 76 - Elmalı, Antalya; 77 - Üzümlü, Muğla; 78 - Denizli; 79 - Uşak; 80 - Ödemis, Bozdağ, İzmir; 81 - Smyrna (=İzmir). Cyprus: 82a - Geri; 82b - Agios Sozomenos (ca 5 km south of Geri); $\mathbf{8 3}$ - Pyrgos; $\mathbf{8 4}$ - Limassol; 85 - Akrotiri, Limassol; 86 - Kourio, Episkopi, Limassol; 87a - Kissonerga (= ca 5 km north of Paphos); 87b Pafos (= Paphos). Greek islands: $\mathbf{8 8}$ - Crete; $\mathbf{8 9}$-Karpathos; 90 - Rhodes; 91 -Astipalea; $\mathbf{9 2}$-Kos; $\mathbf{9 3}$ - Ikaria; 94 - Samos; 95 - Chios. Corresponding references: Neuhäuser (1936a): 11, 14, 15, 17, 18, 20a, 22, 23, 29, 30, 64, 69, 75, 76, 81. Osborn (1965): 62. Lehmann (1966): 33, 36, 38. Felten et al. (1971b): 68, 71, 72, 77, 78, 79, 80. Kurtonur (1972): 3, 4, 5, 6, 7, 8. Kock et al. (1972): 44, 45. Macholán (1999a): 88-95. Özkan \& Kryštufek (1999): 2. Gündüz et al. (2000): 24, 57, 58. Bonhomme et al. (2004): 87a. Gözcelioğlu et al. (2005): 12, 13, 19, 20b, 21. Cucchi et al. (2006): 82a, 82b, 83, 84, 85, 87b. Çolak et al. (2006): 10, 25, 27, 28, 31, 32, 34, 35, 40, 41, 42, 43, 48, 49, 50a, 52, 54, 56, 63, 73, 74. Yiğit et al. ( 2006a): 39. BMNH: 59. ZFMK: 9, 50b, 53, 55, 70. Our own data: 1, 16, 26, 37, 46, 47, 51, 60, 61, 65, 66, 67, 86.

## Appendix 6

Records of Mus macedonicus (see also Fig. 135)
1 - University Campus, Edirne; 2 - Sinanköy, Lalapaşa, Edirne; 3 - 2 km south-east of Karakasim, Edirne, 40 m a.s.l.; 4 - Umurcabeyköy, Lüleburgaz, Kırklareli; 5 - Demirköy, Kırklareli; 6 - Büyükkarıştıran, Kırklareli; 7 - Halkali, Altinşehir, İstanbul; 8 - Terkos, İstanbul; 9 - Gökçeali, Çatalca, İstanbul; 10 - Dalamandra, Silivri, İstanbul; 11 - Kumbağ, Tekirdağ; 12 - Inecik, Tekirdağ; 13 - Tevfikiye, Edirne; 14 - Korudağ, Keşan, Edirne; 15 - Bigalı, Eceabat, Çanakkale; 16 - Island of Gökçeada; 17 - Island of Bozcaada; 18 - Behram, Ayvacık, Çanakkale; 19 - Ayvalık, Çanakkale; 20 - Gönen, Balıkesir; 21 - 10 km north-east of Bardakçı, Manisa, ca 600 m a.s.l.; 22 - Muratdere, Bilecik; 23 - Kocaeli; 24 - Gökçekısık, Eskişehir; 25 - Düzce, Bolu; 26 - Bolu; 27 - Sarayköy, Ankara; 28a - Gölbaşı, Ankara; 28b - Lake Emir, Ankara; 29 - Balâ, Ankara; 30 Şereflikoçhısar, Ankara; 31 - Göre, Nevşehir, ca 1,250 m a.s.l.; 32a - Kırşehir; 32b - 6 km south of Kırşehir, 1000 m a.s.l.; 33 - Sungurlu, Çorum; 34 - Kürtler, Samsun; 35 - Kurupelit, Samsun; 36 - Samsun; 37 - Tokat;

38 - 3 km north-west of Akköy, Yeşilhisar, Kayseri, 1,350 m a.s.l.; 39 - Kayseri; 40 - Bünyan, Kayseri; 41 - Gücük, Sarkışla, Sivas, 1,400 m a.s.l.; 42 - Hafik, Sivas; 43 - Koyulhisar, Sivas; 44 - Trabzon; 45 - Erzurum; 46 - Horasan, Erzurum; 47 - Aralık, Kars; 48 - Muş; 49 - Celyanpınar; 50 - Akçakale, Şanlı Urfa, 340 m; 51 - Malatya; 52 - Nizip, Gaziantep; 53 - Karkamıș (= Kargamiş), Barak, Gaziantep; 54 - Türkoğlu, Kahraman Maraş; 55 - Reyhanlı, Hatay; 56a - Madenboyu, Hatay; 56b - Amik Gölü; 57 - Çevlik (Mağaracık), Hatay; 58 - Çukurova University Campus, Adana , 100-150 m a.s.l.; 59 - Pozantı, Adana; 60 - Tarsus, Mersin, 150 m a.s.l.; 61 - Sebil, Çamlıyayla, Mersin; 62a - Kızkalesi, Korykos, Mersin; $62 b$ - Limonlu, Mersin; 63 - Kılbasan, Karaman; 64 - Alanya; 65 - Konya; 66 - Beyşehir, Konya; 67 - Akburun, Beyşehir, Konya; 68 Karabulut, Akșehir Gölü, Konya, 990 m a.s.l.; 69 - Dazkırı, Afyon; 70a - Burdur; 70b - Suludere, Burdur; 71 - Antalya; 72 - Finike, 73 - Cığlıkara, ca 25 km south-east of Elmali, Antalya, ca 1,600 m a.s.l.; Antalya; 74 Dalaman, Muğla; 75 - Datça, Muğla; 76 - Kusadası, Aydın; 77 - 4 km south of Akçaköy, Aydın, 190 m a.s.l.; 78 - Ödemiş, İzmir; 79 - Bayındır, İzmir; 80 - Kemalpaşa, İzmir. Greek islands: 81 - Rhodes; 82 - Samos; 83 - Chios; 84 - Lesbos. Corresponding references: Kurtonur (1972): 2, 4, 7, 8, 9, 10, 11, 12, 13, $14,15$. Macholán (1996c): 82, 84. Kryštufek \& Macholán (1998): 21, 68, 70a,b. Özkan \& Kryštufek (1999): 16. Macholán (1999b): 83. Gündüz et al. (2000): 35, 39. Orth et al. (2002): 36. Kryštufek \& Mozetič Francky (2005): 81. Gözcelioğlu et al. (2005): 26, 27, 28a, 29, 30. Çolak et al. (2006): 5, 6, 20, 22, 23, 24, 25, 32a, 33, 37, 40, 42, 46, 47, 48, 51, 52, 53, 54, 55, 56a, 61, 63, 65, 66, 69, 74, 78, 79, 80. Macholán et al. (2007): 28b, 43, 50, 57, 58, 60, 67, 75. Macholán et al. (2008): 71, 72. BMNH: 44, 45, 71, 72. ZFMK: 19, 49, 56b, 59, 76. Our own data: 1, 3, 17, 18, 21, 31, 32b, 38, 41, 50, 58, 62a,b, 64, 68, 70a,b, 73, 77.

## Appendix 7

Records of Meriones tristrami (see also Fig. 175)
1 - Oğlakçı, Eskişehir; 2 - Gökçekısık, Eskişehir; 3 - Ankara; 4 - Bala, Ankara; 5 - Tosya, Kastamonu; 6 - Dodurga, Çorum; 7 - Doğantepe, Amasya; 8 - Kulpy (=Tuzluca), İğdır; 9 - Aralık, Ïğdır; 10 - Doğubayazıt, Ağrı; 11 - Kulp, Diyarbakır; 12 - University Campus, Diyarbakır; 13 - Diyarbakır; 14 - Ceylanpınar, Şanlı Urfa; 15 - Çaylık köyü, Harran, Şanlı Urfa; 16 - Çermik, Diyarbakır; 17 - Karadut, Nemrud Dağı, Adıyaman; 18 - 5 km south of Alişam, 30 km east of Elaziğ; 19 - Darende, Malatya; 20 - Gürpınar köyü, Darende, Malatya; 21 - Birecik, Gaziantep; 22 - Nizip, Gaziantep; 23 - 25 km south of Gaziantep; 24 - 30 km south of Gaziantep; 25-15 km north-east of Kilis; 26 - Türkoğlu, Kahraman Maraş; 27 - Haruniye (= Düziçi), Adana; 28 - Kırıkhan, Hatay; 29 - Belen, Hatay; 30 - Bedirge, Amik Gölü, Hatay; 31 - Antiochia (=Hatay); 32 Büyüktuzhisar, Kayseri; 33 - Talas, Kayseri; 34 - Gülșehir, Nevşehir; 35 - Yeşilhisar, Kayseri; 36 - Kemerhisar, Niğde; 37 - Demir Kaziköy, Ala Dağları, Adana; 38 - Pozanti, Adana; 39 - Adana; 40 - Tarsus, Mersin; 41 - Mersin; 42 - Yaprakhisar, Ihlara, Aksaray; 43 - Ereğli, Konya; 44 - İnevi (= Cihanbeyli), Konya; 45 - Yapali köyü, Cihanbeyli, Konya; 46 - Divanlar, 40 km north-east of Konya; 47 - Kara Dağ, ca 80 km south-east of Konya, Karaman; 48 - Bozdağ, Konya; 49 - 15 km south-east of Beyşehir, Konya; 50 - Akșehir, Konya; 51 - Gömü, Afyon; 52 - Sivaslı, Uşak; 53 - Çardak, Denizli; 54 - Denizli; 55 - Demircı, Manisa; 56 - Ödemiş, İzmir; 57 - Bayındır, İzmir; 58 - Kemalpaşa, İzmir; 59 - Smyrna (= İzmir); 60 - Island of Kos, Greece. Corresponding references: Thomas (1903): 59. Thomas (1919): 47. Heptner (1934): 8. Neuhäuser (1936a): 3, 5, 41, 43, 44, 50. Pieper (1965): 60. Osborn (1965): 33, 40. Lehmann (1966a): 13, 27, 29, 30, 31, 35, 38, 39. Lehmann (1969): 14. Steiner \& Vauk (1969): 49. Sickenberg (1971): 46. Felten et al. (1971b): 54. Kock et al. (1972): 18. Morlok (1978): 21, 28. Obuch (1994): 17, 37, 42. Yiğit et al. (1995): 1, 2, 4, 7, 9, 19, 32, 34, 36, 48, 51, 53. Kefelioğlu (1997): 6, 20, 45, 52, 56, 58. Yiğit \& Çolak (1998a): 15, 22, 25. Coşkun (1999a): 11, 12, 16. Yiğit et al. (2003): 26, 55, 57. Yiğit et al. (2006c): 10. Our own data: 23, 24.

## Appendix 8

## Records of Spalax xanthodon (see also Fig. 239)

1 - Island of Bozcaada; 2 - Island of Gökçeada; 3 - Dardanos, Intepe, Çanakkale; 4 - Havran, Balikesir; 5 Biga, Çanakkale; 6 - Denizkent, Gönen, Balıkesir; 7 - Gönen, Balıkesir; 8 - Manyas, Balıkesir; 9 - Karacabey, Bursa; 10 - Ulu Dağ, Bursa; 11 - Yalova, İzmit; 12 - Karamürsel havaalanı, İzmit; 13 - Kepirler, Bilecik; 14 - 5 km east of İnegöl, Bursa; 15a - 10 km south-west of Bilecik; 15b - 14 km north of Bozüyük, Bilecik; 16 İnhisar, Bilecik; 17 - 3 km north of İnönü, Eskişehir; 18 - İkizce yaylası, Ilıca, Kütahya; 19 - 5 km west of Kütahya; 20a - 5 km west of Geyve, Sakarya; 20b - 5 km north of Taraklii, Sakarya; 21a - 3 km south of Gölpazari, Bilecik; 21b - 15 km west of Gölpazari, Bilecik; 22 - Yenipazar, Bilecik; 23 - Eshischehir (= Eskişehir); 24 - Gökçekısık, Eskişehir; 25 - Nallıhan, Ankara; 26 - Abant Gölü, Bolu; 27 - Bolu; 28 - Gerede, Bolu; 29 - Keltepe (= Kel Tepe), Karaağaç, Zonguldak; 30-11 km south of Eskipazar, Çankırı; 31a - 2 km south of Seben, Bolu; 31b - Seben, Bolu; 31c - Ayman Yaylası, Bolu; 32 - 5 km east of Nallıhan, Ankara; 33 - Sarıkavak, Peçenek, Ankara; 34 - 2 km south of Beypazari, Ankara; 35 - Beypazarı, Ankara; 36 - Güdül, Ankara; 37 Kızılcahamam, Ankara; 38 - Ayaş, Ankara; 39 - Polatlı, Ankara; 40 - 15 km north of Ankara; 41a - Ankara; 41b - Gölbaşı, Ankara; 41c - Elmandağ, Ankara; 42 - 35 km south of Ankara; 43 - Haymana, Ankara; 44a Bâla, Ankara; 44b - Elmadağ, Ankara; 45 - Saraköy, Ankara; 46 - Kalecik, Ankara; 47 - Kırıkkale; 48 - Keskin, Kırıkkale; 49-15 km west of Eflâni, Zonguldak; 50-12, 15 and 17 km south of Pınarbaşı, Zonguldak; 51 - Taşpınar, Araç, Kastamonu; 52 - 5 and 10 km east of Azdavay, Kastamonu; 53 - Ağlı, Kastamonu; 54 - 5 and 10 km south of Küre, Kastamonu; $55-2 \mathrm{~km}$ south of Seydiler, Kastamonu; 56a - 3 km south of Taşköprü, Kastamonu; 56b-2 km west of Taşköprü, Kastamonu 57-30 km west of Taşköprü, Kastamonu; 58-4 and 6 km west of Daday, Kastamonu; 59-10 km west of Kastamonu; $\mathbf{6 0}$ - 12 km north of Tosya, Kastamonu; 61 Tosya, Kastamonu; 62 - 40 and 45 km south of Taşköprü, Kastamonu; 63 - Kanghri (=Çankırı); 64 - KargınAlaca, Çorum; 65 - south-east of Çiçekdağı, Kirşehir; 66 - Merzifon, Amasya; $67-10 \mathrm{~km}$ south of Havza, Samsun; 68 - Kavak, Samsun; 69 - Alayurt köyü, Ladik, Samsun; 70a - Akyazı, Amasya 70b - 2 km west of Erbaa, Tokat; 71 - Akdağmadeni, Yozgat; 72 - Yılızdeli, Sivas; 73 - Tekke mahallesi, Sivas; 74 - 10 km south of Sivas; 75 - 3 km west od Suşehri, Sivas; 76 - İmranlı, Sivas; 77 - Gemecik, Erzincan; 78 - Refahiye, Erzincan; 79 - Eğribel Geçidi, Giresun; 80 - Alucra, Giresun; 81a - Fındıkbel Geçıdi, Alucra, Giresun; 81b - 35 km north-east of Gümüşhane; 82 - Yollarüstü, Üzümlü, Erzincan; 83 - Demirözü, Bayburt; $\mathbf{8 4}$ - Çilçil mevkii, Bayburt, Gümüşhane; 85 - Ovid Dağı, Rize; 86 - Cinis Köyü, Kandilli, Erzurum; 87 - Erzurum; 88 - 20 km east of Erzurum; 89 - Pasinler, Erzurum; 90 - 5 km west of Bağdaşan, Kars; 91 - 10 km west of Ardahan; 92 - 14 km west of Sarıkamış, Kars; 93 - Sarıkamış, Kars; 94 - Benliahmet, Selim, Kars; 95a - Kasikoporan (= Gaz Koparan, now Göle), Kars; 95 b - near Göl (= Göle), Kars; 95c - Boğatepe, Göle, Kars; 95d - Göle, Kars; $\mathbf{9 6 a}$ - 3 km south of Suzus, Kars; 96b - Suzus, Kars; $97-3$ km west of Arpaçay, Kars; 98a - 8 km south-east of Kars; 98b - 10 km west of Kars; 99 - Selim, Kars; 100 - Aralık, İğdır; 101 - Küpkıran, Hamur, Ağrı; 102 Yanalyol, Taşilçay, Ağrı; 103 - 1 km east of Çaldıran, Van; 104 - Bendimahi, Muradiye, Van; 105 - Altındere, Ercis, Van; 106-10 km south of Van; 107-20 km west of Muş; 108 - Şerefmeydanı, Bingöl; 109 - 5 km northwest of Bingöl; 110 - Kuruca, 17 km west of Bingöl; 111 - 2 km north-west of Palu, Elazığ; 112 - Taşören, Kovancılar, Elazığ; 113 - Gömemiş, ca 16 km north-east of Tunceli; 114 - Sarıtosun, Ovacık, Tunceli; 115 - Nişantaşı, Tunceli; 116 - Yeniköy, Pertek, Elazığ; 117 - Arguvan, Malatya; 118 - Yazıhan, Malatya; 119 Darende, Maltya; 120a - Malatya; 120b - Sultansuyu - Hara, Malatya; 121 - 12 km east of Malatya; 122 - Karadut, Nemrud Dağı, Adıyaman; 123a - Gürün, Sivas; 123b - Göksun, Kahraman Maraş; 124 - near Akören, Bünyan, Kayseri; 125 - south of Sarıkaya, Yozgat; 126 - between Boğazlıyan, Yozgat and Felahiye, Kayseri; 127 - Kayseri; 128 - 13 km west of Kayseri; 129 - north-east of Incesu, Kayseri; 130 - Himmetdede, Kayseri; 131 - near Topaklı, Nevşehir; 132 - ca 10 km west of Avanos, Nevşehir; 133 - west of Ürgüp, Nevşehir; 134 - south-east of Gülşehir, Nevşehir; 135 - Çeltikli, Ankara; 136 - Kulu, Konya; 137 - Cihanbeyli, Konya; 138 -Yapalı köyü, Cihanbeyli, Konya; 139-35 km west of Aksaray; 140 - 12 km east of Aksaray; 141 - Yaprakhisar, Ihlara, Aksaray; 142 - 30 km west of Ulukışla, Konya; 143 - Ulukışla, Niğde; 144 - Bulgar-Maden (=

Madenköy), Bolkar Dağları, Niğde; 145 - Demir Kaziköy, Ala Dağları, Adana; 146a - Gülek, Mersin; 146b 10 km south-west of Tekir, Mersin; 147a - Sebil, Mersin; 147b - Çamlıyayla, Mersin; 148 - Kırkkuyu Yaylasi, Anamur, Mersin; 149a - Balkusan, Konya; 149b - 20 km south-east of Akseki, Antalya; 150 - Karaman; 151 - Kılbasan, Karaman; 152 - Karapınar, Konya; 153a - Beyşehir, Konya; 153b - Yeşildağ, Beyşehir, Konya; 153c - 10 km north of Beyşehir, Konya; 154 - 6 km north of Beyşehir; 155 - Kıreli, Beyşehir, Konya; 156 10 km south-east of Akşehir; 157 - Akşehir, Konya; 158 - Yunak, Konya; 159 - 10 km west of Afyon; 160 - Yalvaç, Isparta; 161 - Gelendost, Isparta; 162 - Yılanlı, Aksu, Isparta; 163 - Pazarköy, 22 km sout-east of Eğirdir, Isparta; 164 - Çiğlıkara, 25 km south-east of Elmalı, Antalya; 165 - near Elmalı, Antalya; 166 - Mundan Ovasi, above Fethiye, Muğla; 167 - 5 km south of Burdur; 168 - 10 km west of Burdur; 169 - Çardak, Denizli; 170 - 15 miles north-east of Eushak (=Uşak); 171 - Murad-dagh (=Murat Dağı), Uşak; 172 - Demircı, Manisa; 173 - Selçuk, İzmir; 174 - Ovacık, İzmir; 175 - Bozdağ, Ödemiş, İzmir; 176 - Bayındır, İzmir; 177a - Burnabad (=Bornova), İzmir; 177b - 5 km south of İzmir; 178 - near Maltepe, Menemen, İzmir. Greece: 179 - Polychnitos, Island of Lesbos. Corresponding references: Satunin (1898): 95a. Méhely (1913): 95b, 144, 177a. Matschie (1919): 23. Hinton (1920): 63, 171. Ellerman (1948): 41a, 87, 170. Szunyoghy (1941): 120a, b. Watson (1961): 152, 165, 166. Steiner \& Vauk (1966): 154. Felten et al. (1973): 10, 26, 27, 163, 164, 175. Giagia et al. (1982): 4, 173, 179. Kivanç (1988): 3, 11, 12, 18, 64, 66, 69, 70a, 73, 80, 81a, 84, 86, 105, 108, 128, 146a, 147a, 148, 178. Gülkaç \& Yüksel (1989): 117, 118. Obuch (1994): 93, 104, 122, 141, 145. Nevo et al. (1995):19, 67, 74, 75, 92, 150,177b. Coşkun (1996b): 113. Ivanitskaya et al. (1997): 121. Özkan (1999): 1, 2. Sözen et al. (1999): 40, 42, 156, 159, 167, 168, 176. Sözen et al. (2000a): 88, 91, 96a. Sözen et al. (2000b): 139, 140, 142, 143, 146b, 147b. Yüksel \& Gülkaç (2001): 65, 124 -126, 129 134. Tez et al. (2001): 123a, 127. Coşkun (2003): 89, 94, 95c, 97, 98a, 101-103. Yiğit et al. (2003): 24, 61, 100, 106, 119, 151, 169, 172, 174. Coşkun (2004a): 108-112, 114-116. Sözen (2004): 29, 30, 31a, $32-34$. Kankılıç et al. (2007b): 25, 35-39, 41b, 43-46, 136, 137, 153a, 157, 158. Matur \& Sözen (2005): 13-17, 20 - 22. Yiğit et al. (2006d): 5-9. Sözen et al. (2006): 49 - 60, 62. Sözen et al. (2006a): 70b, 81b, 123b, 149b. Kankılıç et al. (2007a): 71, 95d. Kankılıç et al. (2007b): 28, 31b, c, 41c, 47, 48, 68, 71, 72, 76-79, 82, 83, 85, 95d, 96b, 98b, 99, 135, 153b, c, 155, 160-162. Our own data: 90, 138, 149a.

## Appendix 9

Karyotypes of Spalax xanthodon. 2N - diploid number of chromosomes; NF - fundamental number of chromosomal arms; M - number of biarmed autosome pairs; A - number of acrocentric autosome pairs; X and Y - heterochromosomes ( m - metacentric, sm - submetacentric, st - subtelocentric, a - acrocentric, * - chromosomal set involves one heteromorphic pair of chromosomes). Karyotypes are arranged according to increasing diploid number. The following $2 \mathrm{~N}=60$ cytotypes were not included into table (all from Nevo et al., 1995): 58 km N Pinarbashi and 30km W Malatya (designated as 60E), 25km SE Denizli (60W), and Karaman (60C). See also Fig. 236.

$\left.\begin{array}{llllllllll}\hline \text { Cytotype } & \text { 2N NF } & \text { M } & \text { A } & \text { X } & \text { Y Localities } & \text { Source } \\ \hline & 54 & 74 & 9 & 17 & \text { sm } & \text { st S of Sarıkaya, Yozgat; S of Boğazlıyan, Yozgat } & \text { Yüksel \& Gülkaç, 2001 } \\ \hline & 54 & 74 & 9 & 17 & \text { sm } & \text { a } & \text { 24 km W Solhan; Bingöl; 17 km W Bingöl; Taşören, } & \text { Coşkun, 2004c } \\ & & & & & & & \text { Kovancılar, Elazığ; 2 km NW Palu, Elazığ; Yeniköy, Elazığ; } \\ \text { Nişantaşı, Tunceli; Kocakoç, Gömemiş, Tunceli }\end{array}\right]$

| Cytotype | 2N | NF | M | A | X |  | Localities | Source |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Malatya B | 6080 | 80 | 9 | 20 s | sm |  | Malatya | Yüksel, 1984 |
|  | 6080 | 80 | 9 | 20 s | sm |  | Yazıhan, Malatya | Gülkaç \& Yüksel, 1989 |
|  | 60 | 80 | 9 | 20 s | sm |  | S Çiçedağı, Kırşehir; S Gülşehir, Nevşehir ; W Avanos, Nevşehir ; SE Incesu, Kayseri; E Bünyan, Kayseri; Himmetdede, Kayseri | Yüksel \& Gülkaç, 2001 |
|  | 60 | 80 | 9 | 20 s | sm |  | Batıkent, Ankara; Sarayköy, Ankara | Sözen, 2004 |
|  | 608 | 80 | 9 | 20 s | sm |  | SE of Çiçekdağı, Kirşehir; nr. Topaklı, Nevşehir; SE of Gülşehir, Nevşehir; W of Ürgüp, Nevşehir; NE of Incesu, Kayseri; nr. Akören, Bünyan, Kayseri; ca 10 km W Avanos, Nevşehir; Himmetdede, Kayseri | Yüksel \& Gülkaç, 2001 |
|  | 6080 | 80 | 9 | 20 s | sm |  | Akdağmadeni, Yozgat | Kankılıç et al., 2007a |
|  | 608 | 80 | 9 | 20 s | sm |  | Ankara; Haymana, Polatlı, Bâla, Kalecik, Ayaş, Güdül, Beypazarı, Nallıhan, Gölbaşı, Sarayköy \& Elmandağ, Ankara; Kulu, Cihanbeyli \& Yunak, Konya; Refahiye \& Gemecik, Erzincan; Yıldızeli \& İmranlı, Sivas | Kankılıç et al., 2007b |
| Ankara | 60 | 82 | 10 | 19 s | sm |  | Arguvan, Malatya | Gülkaç, \& Yüksel, 1989 |
|  | 60 | 82 | 10 | 19 s | sm |  | Ankara (centrum); 15 km N \& 35 km S Ankara; 10 km E \& 95 km SW Afyon | Sözen et al., 1999 |
| Burdur | 60 | 84 | 11 | 18 s | sm | a 5 | 5 km E \& 10 km S Burdur | Sözen et al., 1999 |
| Kütahya | 62 |  |  |  |  |  | 5 km W Kütahya; 35 km E Afyon; 45 km N Konya; 30 km S Ankara; 20 km W Kayseri; 10 km S Havza; 10 km S Sivas; 3 km W Suşheri | Nevo et al., 1995 |

## Appendix 10

Karyotypes of Spalax ehrenbergi from Anatolia. 2N - diploid number of chromosomes; NFa - fundamental number of autosomal arms; M - number of biarmed autosomes; A - number of acrocentric autosomes. Karyotypes are arranged according to increasing diploid number. In cases of no contradiction among results only the author first to report the karyotype is listed. Names of cytotypes, when applied, follow Cosskun et al. (2006). See also Fig. 247.

| Cytotype | Locality | 2N | NFa | M | A | Source |
| :--- | :--- | :---: | :---: | :---: | :---: | :--- |
| Yayladağı | Yayladağı | 48 | 70 | 24 | 22 | Coşkun, 2004b |
| Hatay | Kilis | 52 | 70 | 20 | 30 | Coşkun, 1999b |
| Hatay | Hatay | 52 | 70 | 20 | 30 | Coşkun, 2004b |
| Diyarbakır | Şırnak | 52 | 72 | 22 | 28 | Coşkun, 1998 |
| Diyarbakır | Birecik | 52 | 72 | 22 | 28 | Ivanitskaya et al., 1997 |
| Diyarbakır | Hilvan | 52 | 72 | 22 | 28 | Yüksel \& Gülkaç, 1992 |
| Diyarbakır | Diyarbakır | 52 | 72 | 22 | 28 | Ivanitskaya et al., 1997 |
| Diyarbakır | Siverek | 52 | 72 | 22 | 28 | Ivanitskaya et al., 1997 |
| Diyarbakır | Adiyaman | 52 | 72 | 22 | 28 | Ivanitskaya et al., 1997 |
| Diyarbakır | Elazığ | 52 | 72 | 22 | 28 | Yüksel, 1984 |
| Diyarbakır | Şanlıurfa | 52 | 78 | 28 | 22 | Nevo et al., 1995 |
| Diyarbakır | Şanlıurfa | 52 | 76 | 26 | 24 | Ivanitskaya et al., 1997 |
|  | Suruç | 54 | 72 | 20 | 32 | Yüksel \& Gülkaç, 1992 |
| Siirt | Siirt | 56 | 62 | 8 | 46 | Coşkun, 2004a |
| Tarsus | Kozan Pekmezci | 56 | 64 | 10 | 46 | Coşkun et al., 2006 |
| Tarsus | 5 km N of Tarsus | 56 | 68 | 14 | 40 | Nevo et al., 1995 |
| Tarsus | 3 km N of Tarsus | 56 | 68 | 14 | 40 | Ivanitskaya et al., 1997 |
| Tarsus | Anberinarkı | 56 | 68 | 14 | 40 | Coşkun et al., 2006 |
| Tarsus | Yakapınar | 56 | 68 | 14 | 40 | Coşkun et al., 2006 |
| Tarsus | 5 km S of Adana | 56 | 68 | 14 | 40 | Sözen et al., 2006b |
| Tarsus | Şeyhmurat, Adana | 56 | 68 | 14 | 40 | Sözen et al., 2006b |
| Tarsus | İbrişim | 56 | 68 | 14 | 40 | Coşkun et al., 2006 |
| Tarsus | Şeyhmurat | 56 | 68 | 14 | 40 | Coşkun et al., 2006 |
|  | Gaziantep | 56 | 78 | 24 | 30 | Ivanitskaya et al., 1997 |
|  | Gaziantep | 56 | 82 | 28 | 26 | Yüksel \& Gülkaç, 1992 |
|  | Gaziantep | 58 | 78 | 24 | 22 | Nevo et al., 1995 |

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## Erratum

## To Kryštufek \& Vohralík (2005)

The skin of Microtus socialis was reproduced twice in Plate XV/1 in Kryštufek \& Vohralík (2005, p. 279) while the dorsal view of a skin of Microtus dogramacii was not shown. This is now corrected in Fig. 276 (below).


Figure 276. Skins in dorsal view of Microtus socialis (a) from Aşkale, Erzurum, and Microtus dogramacii (b) from Boyali köyü, Suluova, Amasya (Ondokuz Mayıs University, Samsun). Photo: C. Mlinar.

# Sesalci Turčije in Cipra <br> Rodentia II: Cricetinae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae, Castoridae 

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## POVZETEK

S tretjim zvezkom sesalcev Turčije in Cipra zaključujeva obdelavo te živalske skupine v severovzhodnem delu Sredozemlja. V prvem zvezku (2001) sva predstavila taksonomski seznam 141 vrst obravnavanega območja in žužkojede sesalce (tedaj Insectivora, danes Erinaceomorpha in Soricomorpha). V vmesnem obdobju se je število vrst povečalo na 154, kar naju je navedlo k pripravi revidiranega seznama. Štiri vrste so bile na novo opisane in poimenovane (Spermophilus taurensis, Microtus anatolicus, Microtus dogramacii, Mus cypriacus), ostale vrste pa so bile znane iz sosednjih območij in prvič navedene za Turčijo, ali pa so novejše raziskave pokazale, da vrste iz leta 2001 dejansko vključujejo dve različni vrsti. Drugi zvezek (2005) je povzel del glodavcev (veverice, skakače, polhe in voluharice).

Pričujoči zvezek obravnava tri vrste hrčkov (Cricetinae), 13 vrst miši in podgan (Murinae), vrsto bodičastih miši (Deomyinae), osem vrst tekačic (Gerbillinae), tri vrste slepih kužet (Spalacidae), vrsto mišjih hrčkov (Callomyscidae), vrsto ježevca (Hystricidae), nutrijo (Myocastoridae) in bobra (Castoridae). Pri vsaki vrsti sva revidirala taksonomski status, natačno kartirala njeno razširjenost in zbrala podatke o fosilni zgodovini in načinu življenja. Taksonomska revizija je temeljila na pregledu 36 tipskih primerkih z ozemlja Turčije, Cipra in sosedstva.

Hrčki so zastopani z dvema rodovoma. Najbolj razširjen je mali sivi hrček (Cricetulus migratorius), ki je prisoten v Trakiji in Anatoliji. Morfološko razlikovanje zlatih hrčkov (rod Mesocricetus) je dokaj težavno zaradi variabilnosti v barvi in morfologiji lobanje. Zlati hrček (M. auratus) naseljuje majhno območje ob turško-sirijski meji, zaradi svoje redkosti in uničevanja življenjskega okolja pa velja za ogroženo vrsto. Turški hrček (M. brandti) živi v orednji in vzhodni Anatoliji in zahodnem Iranu, obrobno pa tudi v Transkavkaziji.

Miši in podgane so z vrstami najbogatejša skupina tako v Turčiji, kot na Cipru. Pritlikava miš (Micromys minutus), dimasta miš (Apodemus agrarius) in navadna belonoga miš (Apodemus sylvaticus) živijo samo v Trakiji. Za slednjo sicer obstajajo navedbe tudi za severozahodno Anatolijo, kar pa je potrebno ponovno preveriti. V bogatem materialu belonogih miši, ki nama je bil na voljo iz Anatolije, vrste A. sylvaticus namreč nisva identificirala. Rumenogrla miš (Apodemus flavicollis) je prisotna tako v Trakiji, kot tudi v Anatoliji. Med obema fragmentoma obstajajo pomembne morfološke in genetske razlike, ki so domnevno posledica geološke zgodovine bosporskih ožin, ki so tekom ledenodobnih klimatskih nihanj delovale kot pomemben biogeografskegi filter. Stepska belonoga miš (Apodemus witherbyi; v seznamu iz leta 2001 označena kot A. iconicus) je splošno razširjena v Anatoliji, živi pa tudi na nekaterih otokih v vzhodnem delu Egejskega morja. Uralska belonoga miš (Apodemus uralensis) je vezana na črnomorsko obalo Anatolije, kjer pa je najpogostejša vrsta rodu Apodemus. Vzhodna kraška miš (Apodemus mystacinus) naseljuje pretežno večino Anatolije, morda z izjemo osrednjega dela visoke planote in skrajnega vzhoda. Obe podgani (rod Rattus) sta alohtoni vrsti. Črna podgana ( $R$. rattus) je izjemno pogosta na Cipru, v večjem delu Anatolije pa je sinantropna žival. Razširjenost sive podgane ( $R$. norvegicus) je slabo dokumentirana, za Ciper pa sploh ni na voljo zanesljivih podatkov. Nesokija (Nesokia indica), ki živi pretežno podzemski način življenja, doseže v Turčiji skrajni severozahodni rob razširjenosti. Znana je z vsega dveh nahajališč ob sirijski meji v medrečju Eufrata in Tigrisa. Hišne miši (rod Mus) so zastopane s tremi vrstami. Vrsta Mus domesticus je pretežno sinantropna, makedonska hišna miš (M. macedonicus) pa živi izključno v odprtih habitatih in ne vdira v človekova bivališča. Obe vrsti sta splošno razširjeni v

Trakiji in Anatoliji. Ciprska hišna miš (M. cypriacus) izvira iz M. macedonicus, od katere se je odcepila pred približno pol milijona let. Evoluirala je v otoški osami na Cipru, ki je sicer ločen od obale najmanj pet milijonov let.

Sistematski položaj dveh izoliranih populacij bodičastih miši (rod Acomys) ni jasen, večina avtorjev pa ju obravnava kot samostojni vrsti. Utemeljujeva, da gre v obeh primerih za egiptovsko bodičasto miš (A. cahirinus). Ker sta izolirani populacija dobro opredeljeni, tako morfološko kot citološko, ju obravnavava kot samostojni podvrsti: A. c. nesiotes (Ciper) in A. c. cilicicus (okolica mesta Silifke na sredozemski obali Anatolije).

Tekačice so, z izjemo ene vrste (Meriones tristra$m i$ ), prisotne le na obrobju azijske Turčije: Tatera indica v medrečju Eufrata in Tigrisa vzdolž sirijske meje, Meriones vinogradovi, M. dahli in M. persicus v vzhodni Anatoliji, Meriones crassus, M. lybicus in Dipodillus dasyurus pa vzdolž meje s Sirijo. Navedba M. vinogradovi za Mezopotamijo ostaja še naprej nejasna. Primerki, ki jih je X. Misonne zbral sredi 20. stoletja v severni Siriji, so pravilno določeni, vseeno pa v prihodnjih desetletjih prisotnost te tekačice v Mezopotamiji ni bila potrjena.

Sistematika slepih kužet je povsem neurejena, zato sva se poslužila konzervativne sistematike Topačevskega in prepoznala tri alopatrične vrste iz rodu Spalax. Od teh vrst je ena (S. leucodon) ome-
jena samo na evropski del Turčije, druga (S. xanthognatus; doslej napačno imenovan S. nehringi) je endemična za Anatolijo, tretja (S. ehrenbergi) pa seže v jugovzhodno Anatolijo do Elazığa na severu. Vse vrste imajo izjemno variabilen kariotip saj diploidno število kromosomov pri S. xanthognatus variira med 38 in 60, pri S. ehrenbergi pa med 48 in 58.

Status mišjih hrčkov je enako malo jasen, kot pa to velja za slepa kužeta. Doslej je bila za Turčijo navedena ena sama vrsta (Calomyscus bailwardi), ki je znana z dveh nahajališč: Hakkari in južno od mesta Gaziantep. Ker sistematika rodu Calomyscus temelji na morfologiji kromosomov, kariotip materiala iz Turčije pa ni znan, je tudi vrstna pripadnost anatolske populacije negotova.

Azijska vrsta ježevca (Hystrix indica) živi v južni Anatoliji do jezera Van na vzhodu in vzdolž egejske obale do Bergame na severu. Vrsta je morda redka in potrebuje varstvene ukrepe. Nutrija (Myocastor coypus) je zanešena iz Južne Amerike. Kolonije so znane iz Trakije (vzdolž Marice) in iz skrajnega vzhoda Anatolije vzdolž meje z Iranom. Bober (Castor fiber) je preživel v Anatoliji in sosednjih območjih Bližnjega in Srednjega vzhoda v zgodovinsko obdobje. Čeprav posredni podatki o njegovi prisotnosti segajo v sredino 20. stoletja, so problematične že navedbe iz 19. stoletja. Danes ni nobenega dvoma, da je vrsta ne tem območju iztrebljena.

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