Cambridge University Press
978-0-521-76066-9 - Evolution of the House Mouse
Edited by Miloš Macholán, Stuart J. E. Baird, Pavel Munclinger and Jaroslav Piálek
Excerpt
More information

## 1

# The house mouse and its relatives: systematics and taxonomy

JEAN-CHRISTOPHE AUFFRAY AND
JANICE BRITTON-DAVIDIAN

## Introduction

A quarter of a century before the advent of biochemical tools for taxonomic approaches, Schwarz and Schwarz (1943) published a pioneering survey of the systematics of the house mouse. All taxa were then considered as subspecies of the house mouse (*Mus musculus*). In other words, there was only one species within the subgenus *Mus*. It was a relatively large-scale study, but the taxonomic criteria were obviously based solely on external morphology and distribution of species. It is nowadays well established that the subgenus *Mus* exhibits high interspecific morphological conservatism and that all species share an important part of their intra-specific variation. Most, if not all, classical external criteria such as coat colour, length of head, body, tail, ear, or foot, are poorly discriminating between species, and, except for very few (e.g. the zygomatic index for *M. musculus*; Orsini *et al.*, 1983), none has a general and specific diagnostic value. When only one or two species occur sympatrically, some characters may be diagnostic, such as the length of the tail, which is useful to distinguish *Mus musculus domesticus*, one of the longest-tailed mice, from all sympatric species. Thus, there is only a poor correspondence between the 15 subspecies of *Mus musculus* described by Schwarz and Schwarz (1943) and the species that are now diagnosed by taxonomists.

Biochemical and molecular tools have considerably clarified our knowledge of the taxonomy within the subgenus *Mus*. The revision began with the deciphering of the *Mus musculus* complex of species in Europe (Selander *et al.*, 1969), though the two subspecies *M. m. musculus* and *M. m. domesticus* had already been recognized by their respective tail lengths. This was followed by the establishment of *Mus spretus* as a valid species by Britton *et al.* (1976) and the recognition of the other European species, *M. macedonicus* and *M. spicilegus*. By the late 1990s, 9 of the 14 taxa known today had been clearly identified, with criteria that left no doubt as to their species status: *musculus*, *spretus*, *spicilegus*, *macedonicus*, *cervicolor*, *caroli*, *cookii*,

*Evolution of the House Mouse*, ed. Miloš Macholán, Stuart J. E. Baird, Pavel Munclinger, and Jaroslav Piálek. Published by Cambridge University Press.

Cambridge University Press
978-0-521-76066-9 - Evolution of the House Mouse
Edited by Miloš Macholán, Stuart J. E. Baird, Pavel Munclinger and Jaroslav Piálek
Excerpt
More information

*booduga*, and *terricolor*. It was only in 2003 that a second wave of amazing reviews or descriptions of new species began, which led to an increase by more than half of the number of species diagnosed by taxonomists in the subgenus *Mus*: *M. famulus* (Chevret *et al*., 2003), *M. fragilicauda* (Auffray *et al*., 2003), *M. cypriacus* (Cucchi *et al*., 2006), *M. nitidulus* (Shimada *et al*., 2007), and *M. lepidoides* (Shimada *et al*., 2010). Several subspecies were also recognized, not only in the *Mus musculus* complex but also within *M. macedonicus* (Orth *et al*., 2002a) and *M. spicilegus* (Kryštufek and Macholán, 1998). Our knowledge of *Mus* taxonomy has thus increased much faster than for mammals in general, for which the number of new species described between 1993 and 2008 is estimated at ≈10% (Ceballos and Ehrlich, 2009). Most of these new *Mus* species were cryptic, which means that the distribution areas of the formerly described species were actually occupied by more than one species. When the number of *Mus* species that have been correctly assigned to a specific name is cumulated since Schwarz and Schwarz's 1943 seminal paper, a clear exponential curve is produced (not shown here). Considering the high number of taxa (species and subspecies) that have recently been described, it is likely that the total diversity of the genus *Mus* has not yet been fully uncovered. In particular, Southeast Asia, which has provided four of the five new species, appears as the key geographic area where more new species may be found.

This review of *Mus* taxonomy follows those of Schwarz and Schwarz (1943), Marshall (1977), Marshall and Sage (1981), Corbet (1990), Musser and Carleton (1993, 2005) and Tucker (2007). Since the latter two were published, three new species have been described, justifying a taxonomic update. After a few considerations on the four subgenera composing the genus, we have chosen to focus on the species of the subgenus *Mus* and to summarize the knowledge as it stands today on the taxonomy and distribution of the 14 recognized species that are classified following the species groups (SG) proposed by Suzuki *et al*. (2004) and Shimada *et al*. (2010) (see also Suzuki and Aplin, Chapter 2 in this volume).

## Taxonomic position of the subgenus *Mus*

The genus *Mus* is a monophyletic clade comprising four subgenera – *Mus*, *Coelomys*, *Pyromys*, and *Nannomys* – totalling 41 extant species as of today. Members of this genus can be distinguished from other genera belonging to the same murine subfamily by a suite of morphological characters (Chevret *et al*., 2005; Tucker, 2007). The geographical distribution of the genus encompasses all of Eurasia and sub-Saharan Africa, and its presence elsewhere results from human-mediated introductions during the last millennia. The highest taxonomic diversity occurs in Asia (19 species/3 subgenera), where this genus likely originated (see Suzuki *et al*., 2004; Chevret *et al*., 2005; Suzuki and Aplin, Chapter 2 in this volume). Whereas the monophyly of the four subgenera is supported by a series of molecular and morphological analyses (Chevret *et al.*, 2003, 2005), the relationship between them remained elusive until the advent of comparative cytogenomics. Using a cross-species chromosome-painting approach, Veyrunes *et al.* (2006) were able to resolve unambiguously the sister-clade relationships within the genus. The subgenus *Coelomys* was the first to diverge, followed by *Nannomys* as a sister group to the *Mus Pyromys* clade. In addition, this study confirmed that diversification within the genus, which occurred 6.7–8 million years ago (Mya) (Chevret *et al.*, 2005), took place very rapidly (within 1 Myr) and was accompanied by a burst of chromosomal change. Although there has been some debate on the taxonomic rank of the four subgenera (Bonhomme *et al.*, 1984; She *et al.*, 1990), a recent reappraisal has argued in favour of maintaining the present taxonomic designation, as the extent of their divergence is no larger than that within other genera such as *Apodemus* (Chevret *et al.*, 2005).

The four subgenera differ in species richness, range, and biological features (Tucker, 2007). The two Asian subgenera, *Pyromys* and *Coelomys*, comprise five and four species, respectively. From an ancestral Eurasian distribution, the subgenus *Mus* is now present worldwide owing to the commensal association of *M. musculus* with humans. Compared to the other subgenera, the subgenus *Mus* is remarkable for its chromosomal uniformity, with all members exhibiting a 2n = 40 acrocentric chromosome karyotype. Only two taxa deviate from this pattern: the western European house mouse, *M. m. domesticus*, some populations of which have accumulated centric fusions (Hauffe *et al.*, Chapter 16 in this volume), and the Indian pygmy mouse, *M. terricolor*, in which several centric fusions and pericentric inversions have been observed (see below). The subgenus *Nannomys*, the African pygmy mouse, is the most speciose with 18 recorded species (Musser and Carleton, 2005). This subgenus is noteworthy for its highly conserved morphology, which contrasts with an extensive karyotypic diversity (Matthey, 1966; Jotterand, 1975). This chromosomal change comprises several unique innovations in mammals: a high diversity of X-autosome centric fusions and the existence of sex-reversed (XY) females (Veyrunes *et al.*, 2004, 2010a, b). The morphological, ecological, chromosomal, and genetic diversity of this genus provides a valuable comparative tool for testing hypotheses on rates and patterns of evolutionary change (Britton-Davidian *et al.*, 2012).

Whereas many species of the Asian and African subgenera are often absent from comparative approaches (but see Macholán, 2006), the subgenus *Mus* has represented an ideal taxonomic framework with which to investigate biological and molecular processes of evolution, and in doing so has provided important milestones for biomedical research (Peters *et al.*, 2007). The subgenus *Mus* harbours two highly prolific models for evolutionary studies on speciation modes at different

Cambridge University Press
978-0-521-76066-9 - Evolution of the House Mouse
Edited by Miloš Macholán, Stuart J. E. Baird, Pavel Munclinger and Jaroslav Piálek
Excerpt
More information

timescales: the *M. musculus* lineage and *M. spretus*. The availability of both natural hybrid zones and laboratory resources (inbred and wild strains, backcross and recombinant panels) coupled with the house mouse genome sequence assembly opens enriching research avenues in a variety of fields: genetics of speciation (Oka *et al.*, 2007; Payseur and Place, 2007; Macholán *et al.*, 2007a, 2008a, 2011; Geraldes *et al.*, 2008; Piálek *et al.*, 2008; Dean and Nachman, 2009; see also in this volume Laukaitis and Karn, Chapter 7; Baird and Macholán, Chapter 14; Ganem, Chapter 15; Oka and Shiroishi, Chapter 17; Forejt *et al.*, Chapter 19; Goüy de Bellocq *et al.*, Chapter 18), tempo and modes of molecular evolution, chromosomal evolution (Hauffe *et al.*, Chapter 16), mating systems and social behaviour (Frynta *et al.*, 2005; see also König and Lindholm, Chapter 5; Ganem, Chapter 15), genetics of complex traits (Salcedo *et al.*, 2007; Laurie *et al.*, 2007; Takada *et al.*, 2008; see also Hermann and Bauer, Chapter 12), determinism of morphological variation (Kawakami and Yamamura, 2008; Burgio *et al.*, 2009; see also Klingenberg and Navarro, Chapter 6), chemical and acoustic communication (Stopka *et al.*, Chapter 8; Penn and Musolf, Chapter 9; Musolf and Penn, Chapter 10), reproductive traits (Fennessy, 1997; Elliott *et al.*, 2001; L'Hote *et al.*, 2007; Dean and Nachman, 2009; Laissue *et al.*, 2009; see also Forejt *et al.*, Chapter 19), adaptation (Ilmonen *et al.*, 2007; Kurzweil *et al.*, 2009; see also Teschke *et al.*, Chapter 13). In addition, the discovery of aberrant sex chromosome determinism systems (XY females, XO/XO males and females) within the African pygmy mouse suggests that the subgenus *Nannomys* has the potential to become a reference model for the identification of genes involved in the mammalian male-determining gene pathway (Jotterand-Bellomo, 1988; Veyrunes *et al.*, 2010a).

## Taxonomic diversity in the subgenus *Mus*

### The *M. musculus* species group

#### *M. musculus* Linnaeus, 1758, including subspecies *musculus*, *domesticus*, *castaneus*, *gentilulus*, *molossinus*

**Type locality**
Uppsala County, Uppsala, Sweden.

**Taxonomic issues**
From the 1970s to the end of the 1990s, controversy prevailed as to the taxonomic status that should be given to the subunits of commensal mice. From their very early studies characterizing allozyme variation among *musculus*, *domesticus*, and *castaneus*, the group of L. Thaler in Montpellier kept the subspecific denomination of these units. As stated in Auffray *et al.* (1990a), their conception of

*M. musculus* as a polytypic species composed of several subspecies able to exchange genes was in accordance with the recommendation of taxonomists (Corbet, 1990). Subspecific status was also used by the group of K. Moriwaki in their early studies on *M. m. molossinus* (Moriwaki *et al.*, 1981). The alternative approach was to give species status to the major genetic lineages of commensal mice (Sage *et al.*, 1993). In doing so, the subspecific denomination was available for populations differing by their coat colour and geographic range, such as the well-known *poschiavinus* or *praetextus*, which are now, however, listed among the synonyms of *domesticus* (Musser and Carleton, 2005). Another rationale for maintaining the species status of the commensal mice was its use by the companies providing the mouse strains, such as the Jackson Laboratory (JAX®; see table 2 in Sage *et al.*, 1993). Here, again, these companies have now adopted the subspecific nomenclature (Eppig, 2010). Among evolutionary biologists, the concept of the house mouse as a species complex is being abandoned with time. In the 1990 special issue of the *Biological Journal of the Linnean Society* on the house mouse, one-third of the papers considered *Mus musculus* as a species complex, while there were only 13% in the second special issue in 2005. In the present volume, none of the chapters dealing with the polytypic aspect of the house mouse consider it as a species complex.

## Distribution

Five subspecies are currently recognized on the basis of distinct molecular-based lineages (Tucker, 2007; see also Suzuki and Aplin, Chapter 2; Yonekawa *et al.*, Chapter 4; Bonhomme and Searle, Chapter 11). *M. m. musculus* is found from central and northern Europe to northeast Asia. *M. m. domesticus* occurs in western Europe (including Norway; Jones *et al.*, 2010), Africa (coastal areas and Maghreb), and the Middle East to southwest Iran; it subsequently expanded its range to the Americas and Oceanian islands through passive transport with humans. The distribution area of *M. m. castaneus* extends from central to Southeast Asia. The two other subspecies have a much more restricted range: the recently rehabilitated *M. m. gentilulus* (Harrison, 1970; Duplantier *et al.*, 2002) occurs along the south-eastern coast of Arabia to Oman, as well as Madagascar, and *M. m. molossinus*, which is a hybrid subspecies between *M. m. musculus and M. m. castaneus*, is found in Japan (Yonekawa *et al.*, Chapter 4). Numerous studies indicate that these subspecies are not completely reproductively isolated, and in regions of secondary contact there is evidence of genetic exchanges ranging from limited introgression (i.e. *M. m. domesticus* and *M. m. musculus* in Europe; see also Cucchi *et al.*, Chapter 3; Bonhomme and Searle, Chapter 11; Baird and Macholán, Chapter 14) to broad overlap (i.e. *M. m. musculus* and *M. m. castaneus* in China; Guénet and

Bonhomme, 2003), and complete admixture (i.e. *M. m. molossinus*; see Yonekawa *et al.*, Chapter 4).

### Phylogenetic relationships between subspecies

Progress has been made in unravelling the history of the radiation of *M. musculus* from its palaeontological Indo-Pakistani cradle. Two alternative hypotheses have been put forward (see Tucker, 2007: figure 2.2). The first considers that the three most widespread subspecies diverged following expansion from this cradle (Boursot *et al.*, 1996; Din *et al.*, 1996), whereas the second proposes a more western area of origin located within the current range of *M. m. domesticus*, with a subsequent expansion giving rise to the subspecies (Prager *et al.*, 1998). The answer may well lie in between these two areas (Duvaux *et al.*, 2011). Only the analysis of additional specimens from west-central Asia may provide the key to the geographic origin of the radiation as well as to its mode and tempo.

## *M. spretus* Lataste, 1883

### Type locality

Oued Magra, north of Hodna, Algeria.

### Distribution

Endemic to the western Mediterranean climatic zone of western Europe (southern France, Spain, Portugal, Balearic Islands) and north Africa (Morocco, Algeria, Tunisia, Libya) (1.1a).

### Description and diagnosis

*M. spretus* is a short-tailed wild mouse (head and body length / tail length (HB / T): *ca.* 1.51; Cucchi *et al.*, 2006). Morphometric, allozymic, and molecular criteria provide species-specific reliable diagnostic characters (Britton-Davidian and Thaler, 1978; Darviche and Orsini, 1982; Boursot *et al.*, 1985; Macholán, 1996a, b; Khammes and Aulagnier, 2006; but see below). This mouse possesses the standard G-banded karyotype with two distinctive features: a small Y chromosome and a set of subtelomeric rDNA clusters, which is a unique trait in the genus (Brannan *et al.*, 2001; Cazaux *et al.*, 2011). In addition, small differences in chromosomal architecture compared to the house mouse genome have been documented (Palmer *et al.*, 1995; Perry and Ashworth, 1999).

### Phylogenetic relationships

Molecular markers place *M. spretus* within the Palaearctic European *M. musculus* SG along with *M. musculus*, *M. spicilegus*, *M. macedonicus*, and *M. cypriacus*

Cambridge University Press
978-0-521-76066-9 - Evolution of the House Mouse
Edited by Miloš Macholán, Stuart J. E. Baird, Pavel Munclinger and Jaroslav Piálek
Excerpt
More information

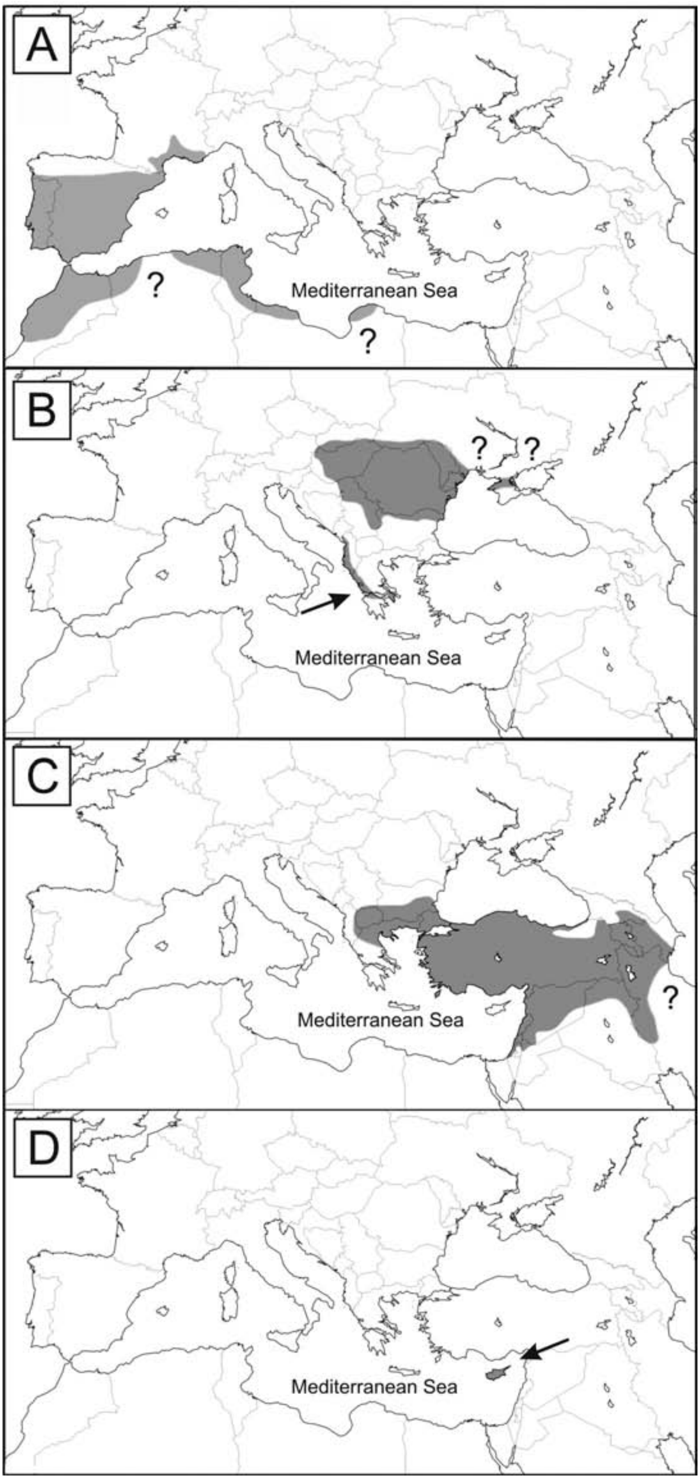

**Figure 1.1** Distribution of the species of the *Mus musculus* subgroup. (a) *Mus spretus* from Amori *et al*. (2008). (b) *Mus spicilegus* from Coroiu *et al*. (2008) and Mitsainas *et al*. (2009). (c) *Mus macedonicus* from Kryštufek and Vohralík (2008). (d) *Mus cypriacus* from Amori and Hadjisterkotis (2008).

(Suzuki *et al.*, 2004; see also the '*M. musculus*' SG in Suzuki and Aplin, Chapter 2). Sister-species relationships within this group are, however, less clear, as nuclear and mtDNA sequences often lead to conflicting tree topologies (Tucker *et al.*, 2005; Tucker, 2007). *M. spretus* evolved in north Africa, where the oldest fossil was discovered at a date which is in agreement with molecular-based estimates (1.5 Mya in Dejager *et al.*, 2009). Phylogeographical analyses have highlighted a genetic diversity gradient from highly variable populations in north Africa to almost monomorphic ones in southern France, with intermediate values in the Iberian Peninsula (Boursot *et al.*, 1985). This diversity pattern supports the north African origin of this species, with a colonization of Europe via Spain involving two founder and/or bottleneck events through Gibraltar and the Pyrenees.

### Ecology/behaviour

This species is commonly found in grasslands, dry shrublands, and agricultural fields. In southern France, its eastern distribution limit coincides with that of the Mediterranean oak (*Quercus coccifera*) (Orsini *et al.*, 1982). Over its whole distribution area, this species is sympatric with *M. m. domesticus*, but rarely syntopic, as *M. spretus* has limited water requirements and typically inhabits drier areas than the house mouse (Sicard *et al.*, 1985; Pouliquen-Young, 1994). Traces of horizontal transfer through introgression have been documented between *M. spretus* and *M. m. domesticus*, indicating that the two species do meet on rare occasions in the wild and are capable of producing offspring (Greene-Till *et al.*, 2000; Hardies *et al.*, 2000; Orth *et al.*, 2002b). The population and social structure of this species have been extensively studied by Hurst and co-workers, providing information on micro-habitat use and dispersion (Gray *et al.*, 1998; Gray and Hurst, 1997), social and territorial organization (Hurst *et al.*, 1994, 1996, 1997), as well as an original hygienic behaviour (Hurst and Smith, 1995). As is the case for *M. spicilegus*, studies on the reproductive system of *M. spretus* have revealed a suite of behavioural traits all of which, except for testis size (Frynta *et al.*, 2009), are indicative of a monogamous mating system (Cassaing and Isaac, 2007; Cassaing *et al.*, 2010).

### Points of interest

The discovery that crossbreeding *M. spretus* and laboratory mouse strains produced viable and fertile progeny (Bonhomme *et al.*, 1978), provided an invaluable tool for the construction of high-density mouse genetic maps (Dejager *et al.*, 2009). This unique contribution stemmed from the high degree of genetic divergence between *M. spretus* and the laboratory strains. Various backcross panels were established and made accessible to the scientific

Cambridge University Press
978-0-521-76066-9 - Evolution of the House Mouse
Edited by Miloš Macholán, Stuart J. E. Baird, Pavel Munclinger and Jaroslav Piálek
Excerpt
More information

community through the European Collaborative Interspecific Backcross network. Since then, the production of interspecific recombinant congenic strains and the ongoing genome sequencing project of an *M. spretus* strain now constitute a set of genetic resources that are fundamental for studying the genetics of complex traits (see Dejager *et al.*, 2009). As *M. spretus* and *M. musculus* are nevertheless valid species, the ability to produce interspecific progeny has paved the way for the analysis of genomic interactions during speciation (Hale *et al.*, 1993; Biddle *et al.*, 1994; Pilder *et al.*, 1997; Hemberger *et al.*, 2001; Zechner *et al.*, 2002; Shi *et al.*, 2004).

#### Unresolved issues

What is the short-tailed mouse reported in the Cyrenaic, Libya (Orsini *et al.*, 1982)? The sister-species relationships within the European SG need to be clarified.

### *M. spicilegus* Petényi, 1882, including subspecies *spicilegus*, *adriaticus*

#### Type locality

Rakos Plains, Budapest, Hungary.

#### Distribution

Southeast Austria, south Slovakia, Hungary, Romania, Bulgaria, Moldavia, Serbia, Montenegro, and south Ukraine (Fig. 1.1b). Recent studies show an extension into Albania, northwest, west, southwest, and southeast Greece (Macholán and Vohralík, 1997; Macholán *et al.*, 2007b; Bauer *et al.*, 1998; Mitsainas *et al.*, 2009). It occurs sympatrically with *M. musculus* over its whole range.

#### Description and diagnosis

*M. spicilegus* is a short-tailed field mouse (HB / T: 1.35–1.39; Orsini *et al.*, 1983) characterized by a unique behaviour: mound-building (Holz *et al.*, 2009; see below for details). Morphometric and morphological characters discriminate this wild mouse from its European congeners (Orsini *et al.*, 1983; Macholán, 1996a, b; Cserkesz *et al.*, 2008). Chromosomal studies document the presence of the standard karyotype with 2n = 40 acrocentric chromosomes, the only exception being a minute Y chromosome as in the other wild-living European species (Bulatova and Kotenkova, 1990).

#### Phylogenetic relationships/subspecies

*M. spicilegus* clearly belongs to the Palaearctic *M. musculus* SG within the subgenus *Mus*, where it shares a sister-taxon relationship with *M. macedonicus*

Cambridge University Press
978-0-521-76066-9 - Evolution of the House Mouse
Edited by Miloš Macholán, Stuart J. E. Baird, Pavel Munclinger and Jaroslav Piálek
Excerpt
More information

(Suzuki *et al.*, 2004; but see Tucker *et al.*, 2005). *M. spicilegus* is sympatric with both *M. m. musculus* and *M. m. domesticus* in the northern and southern part of its range, respectively. Recent analyses have supported the existence of a distinct subspecies in Montenegro, based on morphological and molecular evidence: *M. s. adriaticus* (Kryštufek and Macholán, 1998). In addition, the study of new samples throughout Greece has uncovered a highly distinct mtDNA lineage in Sterea Ellada (southeast Greece; Mitsainas *et al.*, 2009).

### Ecology/behaviour

This species is the only one in the genus to display mound-building activity. During autumn, individuals cooperate in collecting various seeds and plant stems that are then covered with earth, forming a tumulus (up to almost 2 m in diameter and 40 cm high; Holz *et al.*, 2009). This communal nesting in tumuli occurs as an over-wintering strategy to limit food shortage, predation, and thermoregulatory losses (Holz *et al.*, 2009). Microsatellite analyses have identified occupants as male and female parents and their juvenile progeny, ranging between 1 and 21 mice (Garza *et al.*, 1997; Patris and Baudoin, 2000; Dobson and Baudoin, 2002). *M. spicilegus* was the first mouse species to be described with a monogamous mating system. Indeed, although polygyny may occur, social monogamy is supported by several associated behavioural traits: paternal care of pups, social and pair bonding, agonistic interactions, socio-spatial associations (Gouat and Feron, 2005; Feron and Gouat, 2007; Poteaux *et al.*, 2008).

### Points of interest

The unique behavioural particularities of *M. spicilegus* (mound-building, monogamy) undoubtedly represent the main attractions of this species. Given the available phylogenetic context, comparative studies between closely related species using various modern approaches will enlighten the evolutionary processes involved in their emergence.

### Unresolved issues

The geographical distribution and taxonomic status of the newly identified lineages within *M. spicilegus* warrant further investigation.

## *M. macedonicus* Petrov and Ruzič, 1983, including subspecies *macedonicus* and *spretoides*

### Type locality

Macedonia.