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Subterranean Rodents

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Subterranean Rodents

News from Underground

With 52 Figures, 2 in Color

 Springer

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We dedicate this book to our friend
and colleague Mathias Kawalika
(*17.07.1962; †19.03.2006)



Main speakers and some participants of the symposium “Light from underground: challenges and insights in the third decade of research on subterranean rodents”, held at the International Mammalogical Congress IX in Sapporo, Japan (August 2005)

Last row (from left to right): Cristian Schleich, Ana Paula Cutrera, Simone Lange, Marie-Therese Bappert, Philip Dammann

Middle row: Ema Knotková, Regina Moritz, Sabine Begall, Yanming Zhang, Mathias Kawalika, Hynek Burda, František Sedláček

First row: Sanae Nanbu, Chizuko Suzuki, Shizuka Tokin, Paul Van Daele, Eileen Lacey, Mikhail Moshkin

Front: Eviatar Nevo

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Introduction

1 Subterranean Rodents: News from Underground

Sabine Begall, Hynek Burda, Cristian E. Schleich

Across the globe, in all continents but Australia and Antarctica, at least 250 extant rodent species (38 genera, 6 families – according to the classification applied) spend most of their lives in self-constructed burrows (Table 1.1, Fig. 1.1). Their subterranean ecotope is dark, microclimatically stable, hypoxic and hypercapnic, and deprived of most sensory cues available aboveground. The burrows offer shelter from predators and climatic extremes, but digging is energetically costly, and the yield of foraging is relatively low, because the productivity of the subterranean ecotope is rather low and the food resources (roots and underground plant storage organs like bulbs and tubers) are mostly unpredictably and unevenly scattered. These so-called subterranean rodents are specialized in multiple aspects for their unique way of life in which most events like foraging, mating, and breeding take place underground. Animals that inhabit underground self-made tunnels, but also forage (predominantly) above ground, are called fossorial. Needless to say, a continuum exists between fossorial and subterranean rodents, and in the present volume a categorical differentiation is mostly ignored on purpose. Another mammalian group sharing the same ecotope, but feeding on invertebrates, are subterranean non-rodent mammals like marsupial moles, certain armadillos, as well as “insectivore” moles (e.g. Talpidae) and golden moles (Chrysochloridae). Although the title of the book emphasizes that the focus is on subterranean rodents, we also encouraged the authors to glance at recent findings from studies on other subterranean mammals, and we hope that the reader will profit from this.

Most subterranean rodent taxa have already been scientifically described in the golden ages of alpha taxonomy 100–200 years ago (and, e.g. the blind mole-rat *Spalax* and the mole-vole *Ellobius talpinus* in 1770), and many subterranean dwellers have been familiar to local people for ages (*Spalax*

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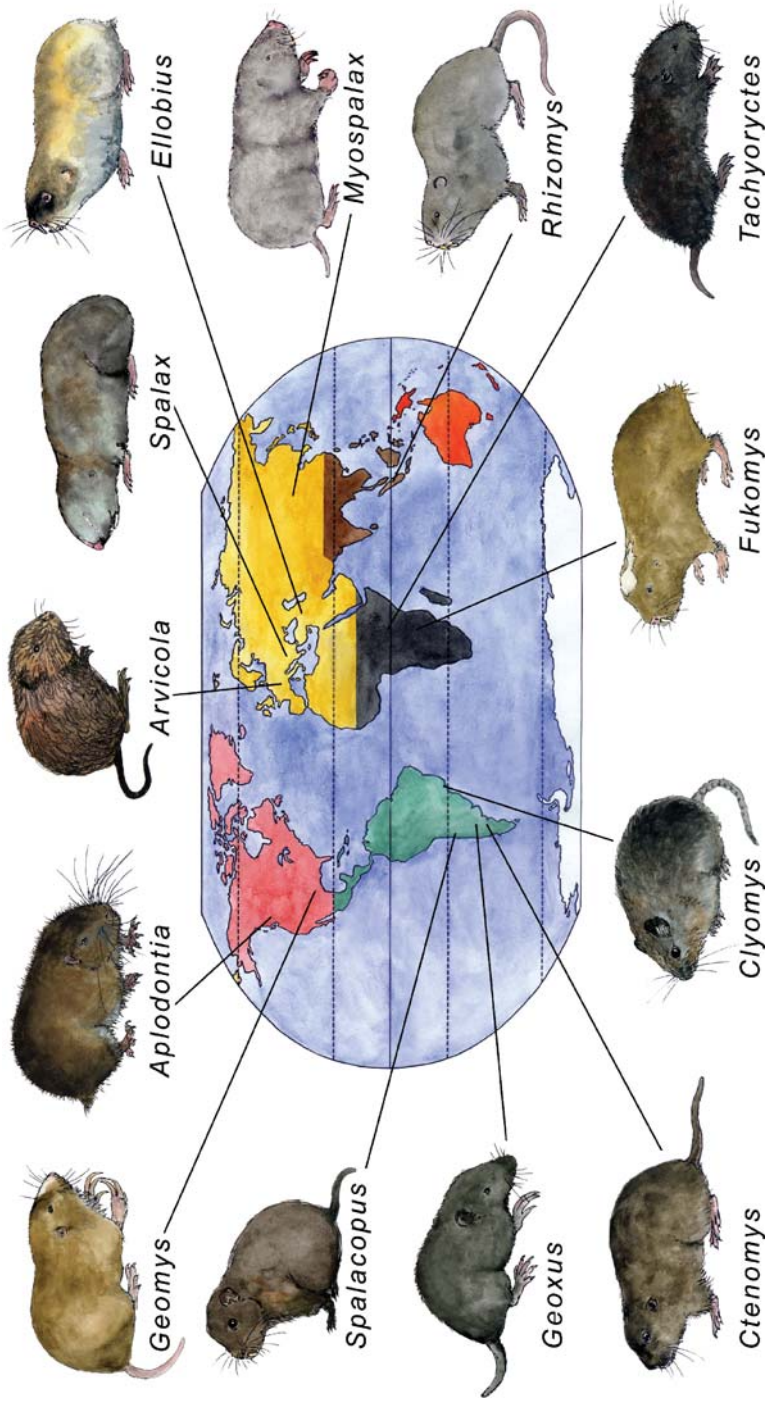


Fig. 1.1. Distribution of subterranean rodents across the planet. Different map colours mark the different zoogeographical regions. Only selected genera representing diverse families and subfamilies of subterranean rodents are depicted: *Geomys* (Geomyidae), *Aplodontia* (Aplodontidae), *Arvicola* (Muridae – Arvicolinae), *Spalax* (Muridae – Spalacinae), *Ellobius* (Muridae – Arvicolinae), *Myospalax* (Muridae – Myospalacinae), *Rhizomys* and *Tachyoryctes* (Muridae – Rhizomyinae), *Fukomys* (Bathyergidae), *Clyomys* (Echimyidae), *Ctenomys* (Octodontidae), *Geoxus* (Muridae – Sigmodontinae), *Spalacopus* (Octodontidae). The actual differences in body sizes were not considered. Classification adapted from McKenna and Bell (1997) (Table 1.1). Drawings by Marie-Therese Bappert



having been mentioned in the Bible and by Aristotle). Nevertheless, scientists mostly knew the different species only from museum specimens, and the biology of subterranean mammals has long remained unstudied, which can be partly assigned to their cryptic life-style and technical problems with capturing, keeping, breeding and monitoring underground dwellers. Furthermore, scientists have always been more attracted by animals coping with complicated environments and solving seemingly difficult and complex problems compared to those encountered underground (sensitive vision vs blindness, echolocation in a high frequency range vs hearing in a human auditory range, navigating across hundreds or thousands of kilometers vs maze orientation across tens of meters, thermoregulation in cold environments vs life in a thermally buffered burrow, etc.). However, since the seminal review article by Eviatar Nevo in 1979 (Nevo 1979) and the report of eusociality in the naked mole-rat by Jennifer U.M. Jarvis in 1981 (Jarvis 1981), interest in subterranean mammals in general and in subterranean rodents in particular has been awakened. Admittedly, at the beginning of the 1980s the knowledge was strongly biased, because the majority of papers dealt with Eurasian blind mole-rats (mainly *Spalax ehrenbergi*) and with American pocket gophers (Geomyidae).

In 1989, an international symposium on the evolution of subterranean mammals at the organismal and molecular levels was organized within the International Theriological Congress in Rome by Eviatar Nevo and late Osvaldo A. Reig, and an influential book (actually proceedings of the symposium) edited by both conveners was published in 1990 (Nevo and Reig 1990). Although this book covered such diverse topics as the ecophysiology, sensory biology, comparative morphology, ecology, taxonomy and phylogeny of diverse subterranean and fossorial mammals, it was the naked mole-rat which has become the most popular subterranean mammal, with its popularity also reaching beyond the scientific community. The intensive research resulted in the publication of a highly cited book (Sherman et al. 1991) and about 150 further scientific papers dealing with this species. We dare to say, however, that the impact of the naked mole-rat upon the

Table 1.1. Fossorial and subterranean genera of rodents. Classification adapted from McKenna and Bell (1997)

Suborder	Family Subfamily	Genus		
Hystricognatha	Bathyergidae			
	Bathyerginae	<i>Bathyergus</i> <i>Cryptomys</i> <i>Fukomys</i> <i>Georchus</i> <i>Heliophobius</i> <i>Heterocephalus</i>		
	Heterocephalinae			
	Octodontidae			
	Octodontinae	<i>Ctenomys</i> <i>Pithanotomys</i> <i>Spalacopus</i>		
	Echimyidae			
	Heteropsomyinae	<i>Carterodon</i> <i>Clyomys</i> <i>Euryzygomatomys</i>		
	Myomorpha	Muridae		
		Arvicolinae	<i>Arvicola</i> <i>Ellobius</i> <i>Hyperacrius</i> <i>Microtus</i> <i>Prometheomys</i>	
		Sigmodontinae	<i>Aepeomys</i> <i>Akodon</i> <i>Blarinomys</i> <i>Chelemys</i> <i>Euneomys</i> <i>Geoxus</i> <i>Kunsia</i> <i>Notiomys</i>	
Myospalacinae			<i>Eospalax</i> <i>Myospalax</i>	
Spalacinae			<i>Nannospalax</i> <i>Spalax</i>	
Rhizomyinae			<i>Cannomys</i> <i>Rhizomys</i> <i>Tachyoryctes</i>	
			Geomyidae	
Geomyinae			<i>Geomys</i> <i>Orthogeomys</i> <i>Pappogeomys</i> <i>Thomomys</i> <i>Zygogeomys</i>	
Sciuromorpha			Aplodontidae	<i>Aplodontia</i>

research of subterranean mammals in general was not as high as expected. On the contrary, most general biologists (including text-book authors) and biology students, let alone the interested non-scientific community, still regard the naked mole-rat as a typical, if not exclusive, subterranean rodent. Even many students of the naked mole-rat tend to explain its unique traits as exclusive adaptations to life underground, ignoring the plethora of other rodent taxa which also successfully occupy the underground niche, and display both convergent traits as well as different but not less effective and not less interesting solutions to problems of the underground existence.

Eight years later, in 1997, an international symposium dedicated to subterranean rodents took place within the framework of the International Theriological Congress in Acapulco (note that the topical scope was already narrower and more specific than that in Rome). A book based on the symposium edited by its conveners, Eileen A. Lacey, James L. Patton, and Guy N. Cameron, appeared in 2000 (Lacey et al. 2000). The end of the millennium was generally productive as far as books on subterranean mammals are concerned. In 1999, Nevo published his review of the research on evolution of subterranean mammals (Nevo 1999). In his book he showed how adaptive evolution of subterranean mammals involves structural and functional changes which are both regressive (degenerative) and progressive (compensatory) in nature. The mosaic convergent global evolution of subterranean mammals due to similar constraints and stresses is an example par excellence for an evidence for evolution through natural selection obtained through comparative methods. Subterranean mammals teach us a lot about the nature of adaptive radiation, species diversity in space and time, how phenotypes and genotypes regress, progress, and converge through molecular and organismal tinkering by natural selection. In another book published at that time, Bennett and Faulkes (2000) summarized their research and ideas on mainly South African mole-rats, pointing out that the naked mole-rats have hairy cousins which are not less interesting. In 2001 Nevo and colleagues published their book reviewing the achievements in research of blind mole-rats (Nevo et al. 2001). Finally, a booklet by Yevdokimov published in the same year (written in Russian and therefore, unfortunately, not easily accessible to most scientists) reviewed many studies on the mole-vole, *Ellobius talpinus*, by Russian authors, and particularly, long-term studies on behavioural and population ecology of this species carried out by the author himself (Yevdokimov 2001).

Given the exponential increase in the number of publications dealing with subterranean rodents, growth of the scientific community involved in the research of these subjects, introduction of new taxa, new research aspects, methods, and ideas in the field, we felt that time was more than

ripe, after 16 years from the symposium in Rome and 8 years from the symposium in Acapulco, to bring the interested scientists together again. The opportunity was given with the International Mammalogical Congress in Sapporo in 2005. Like the preceding symposia, the symposium in Sapporo was also very successful and we hope that the present book will become a milestone in the research of subterranean dwellers in the same way as its predecessors are. Most chapters of this volume are based on contributions presented at the Sapporo symposium on subterranean rodents. In our symposium the established scholars (“old stagers”) working with subterranean rodents for the past decades united with scientists just recently attracted by the subject. Accordingly, very different people and schools contributed to this volume. We were lucky to bring together not only researchers of different generations working in different fields, but also representing different geographical regions – not only by subjects of their interest, but also by their origin and affiliation. All in all, 40 authors from 12 different countries contributed to this volume.

To understand the biology of an organism it is important to look at its adaptations and, of course, scientists are bound to study them. Previous books gave much attention to this topic and are a good basis for students to start; hence, our aim was to expand the knowledge rather than to reproduce the established facts. The present book, which deals with a diverse array of modern topics, is divided into five sections: ecophysiology, sensory ecology, life histories, ecological and economical impacts, and molecular ecology and evolution. Short introductory chapters to each of the five parts give an overview of the respective field, and comment on the chapters. These introductions are followed by reviews on subjects currently studied in the respective field, but naturally, the reviews cannot cover the complete spectrum.

It may appear that a disproportionately large part of the book is dedicated to sensory biology and ecology. However, this fact also reflects the recent and current boom of studies and publications in this field. Thus, along with revisiting classical sensory topics like audition or vision, where recent years marked also significant new findings and ideas changing our view of sensory adaptations in underground dwellers, more exotic or thus far much less studied senses like magnetoreception or somatosensation have also been attracting attention of more and more research.

Besides trying to carry out a complete and current revision of the different areas of investigation on the biology of underground mammals, this book seeks to generate new visions and ideas (through the development of novel research aspects and methods) that constitute the basal stone of future symposia on subterranean mammals. Judging from earlier developments in the field, we expect that the eight-year periodic cycle between symposia and books on subterranean dwellers will shorten. It is our hope

that the impact of this book will reach beyond the ever growing community of researchers in the field. We hope that the case of subterranean rodents will finally attract the attention of authors of text-books in evolutionary biology, animal, sensory and behavioural ecology, biology of behaviour, and general zoology, and that the book will provide ideas and reading texts for seminars in organismal and molecular evolution and ecology.

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References

- Bennett NC, Faulkes CG (2000) African mole-rats: ecology and eusociality. Cambridge Univ Press, Cambridge
- Jarvis JUM (1981) Eusociality in a mammal: cooperative breeding in naked mole-rat colonies. *Science* 212:571–573
- Lacey EA, Patton JL, Cameron GN (2000) Life underground: the biology of subterranean rodents. Univ Chicago Press, Chicago
- McKenna MC, Bell S (1997) Classification of mammals above the species level. Columbia Univ Press, NY
- Nevo E (1979) Adaptive convergence and divergence of subterranean mammals. *Ann Rev Ecol Syst* 10:269–308
- Nevo E (1999) Mosaic evolution of subterranean mammals: regression, progression and global convergence. Oxford Univ Press, Oxford
- Nevo E, Reig OA (1990) Evolution of subterranean mammals at the organismal and molecular levels. Wiley-Liss, New York
- Nevo E, Ivanitskaya E, Beiles A (2001) Adaptive radiation of blind subterranean mole rats: naming and revisiting the four sibling species of the *Spalax ehrenbergi* superspecies in Israel: *Spalax galili* (2n=52), *S. golani* (2n=54), *S. carmeli* (2n=58), *S. judaei* (2n= 60). Backhuys Publishers b.v., Leiden, The Netherlands
- Sherman PW, Jarvis JUM, Alexander RD (1991) The biology of the naked mole-rat. Princeton Univ Press, Princeton, NJ
- Yevdokimov NG (2001) Population ecology of the common mole-vole (in Russian). Russ Acad Sci (Ural Sect) Press, Yekaterinburg

Part I
Ecophysiology

2 Adaptive Physiological Mechanisms in the Underground Dwellers

František Sedláček

The underground ecotope is unique and stressful in many aspects (for review see, e.g., Nevo 1999; Burda et al., this volume), and physiological adaptations – although less conspicuous than morphological adaptations – represent the core of underground life. It is assumed that physiology has been molded by convergent evolution to the same extent as morphology has been. However, although physiological adaptations attracted the interest of researchers since a few decades, only certain processes and aspects have been studied in a few species thus far. The problem has been pointed out already in the last comprehensive review of ecophysiology of subterranean mammals by Buffenstein (2000), and this bias has continued in recent years. The diverse subjects can be assigned to two main fields of research: 2.1) Energy and Material Fluxes cover the topics foraging, digestion, metabolic rate, thermal flux, body temperature, thermoneutral zone, blood transport, cardiac responses, ventilatory responses, acid-base balance, water flux, and mineral homeostasis; 2.2) Neuronal and Hormonal Regulation deal with circadian rhythms, sensory ecophysiology, reproductive physiology and endocrinology.

Before we look further into the subjects, we should address data on environmental parameters which are the starting point for ecophysiological studies and might help to create logical insights into adaptations. In the first chapter of this section (Chap. 3), Burda et al. review new data on microclimatic conditions in subterranean burrows. Although the parameters, e.g. temperature, humidity, oxygen concentration etc. are measured in standard ways, the right placement of devices into burrows, and particularly into (occupied) nests is, from a methodological point of view, a demanding operation.

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2.1 Energy and Material Fluxes

Research in this field highlights the potentials as well as the limits of survival and successful existence in the subterranean ecotope. Since foraging is energetically demanding, and the subterranean environment offers generally low plant food supply, digestion of cellulose is expected to be very effective. Following this reasoning, Dyer (1998) suggested that the controlled consumption of symbionts in feces by naked mole-rats (*Heterocephalus glaber*) might have helped to establish and maintain eusociality in these subterranean rodents. Regarding the gastrointestinal system, the animals' age might be an interesting factor (O'Connor et al. 2002; Yang et al. 2002), especially since naked mole-rats as well as Ansell's mole-rats (*Fukomys anselli*) are extraordinary long-lived mammals (Buffenstein 2005; Dammann and Burda 2006). Studies on metabolic rates could help to identify proximate factors of aging. In Chap. 4, Sedláček addresses the energetics of subterranean and fossorial rodents. Recent studies in this field are presented and the author tries to explain how the new data have complemented or changed our understanding of physiology of metabolism in subterranean rodents, or even how they determine new ways and open new horizons for future research in the field.

In the following chapter, Moshkin et al. present a complex study of energy balance and fluxes in the mole-vole (*Ellobius talpinus*) as a model species. Exploring species other than bathyergids or spalacids (the best studied subterranean rodents so far) prove to be very fruitful. Furthermore, the mole-vole originating from moderate zones with changing seasons represents a natural thermal experiment of great importance.

Thermal flux, i.e. heat exchange via conduction or convection, is of particular importance in the underground environment. During periods of high activity, this mechanism represents an effective way to dissipate metabolic heat. Daly and Buffenstein (1998) discussed the skin morphology in *H. glaber* with respect to the poor thermoinsulatory abilities while simultaneously facilitating heat transfer from the environment to the animal by thigmothermy. We may speculate also about another flux that equalizes individually different amounts of energy gained (food digested) by the colony members via inter-individual thermal exchange. Recently, also in some other mole-rats the role of body insulation was evaluated (Cortes et al. 2000, Cutrera and Antinuchi 2004, Zelová et al., in press – see Chap. 4). Naturally, thermal flux is closely bound to body temperature. The extent to which body temperature is regulated varies among subterranean rodents. The reactions to the ambient temperature fluctuations range from strict homeothermy (*Spalax ehrenbergi*) to heterothermy (*F. anselli*) and

poikilothermy (*H. glaber*). Further research in this field should focus on questions like: What is the thermoregulatory meaning of the body size in subterranean mole-rats and does Bergmann's rule apply in the subterranean ecotope, or why does the silvery mole-rat have long fur? The third important thermal parameter is the *thermoneutral zone*. In African mole-rats it ranges between 25 and 37°C reflecting probably relatively high and stable burrow temperatures and thermal properties of mole-rats' bodies. However, burrow temperatures measured in the field are often lower (see Chap. 3). The broad thermoneutral zone may be characteristic even within a single species - thus the silvery mole-rat exhibits a very broad thermoneutral zone ranging from 25 to 33°C (Zelová et al., in press). The evolutionary and ecological reasons for these intraspecific differences remain to be determined. It would be also of interest to study thermoregulation in holarctic subterranean voles - particularly those from mountainous regions (see Chap. 5).

In the subterranean environment, where air composition generally differs from above ground conditions, *blood transport* plays an important compensatory role. In subterranean rodents increased oxygen carrying capacity has been observed. This adaptation could be facilitated by elevated hemoglobin concentrations, increased red blood cell counts, and high intrinsic affinity for oxygen. The best studied subterranean rodent in this respect is the blind mole-rat *S. ehrenbergi* living, at least temporarily, under pronounced hypoxic and hypercapnic conditions (Shams et al. 2005a). In this species a series of studies revealed different parts of oxygen supply system on the molecular level (Yang et al. 1998; Avivi et al. 1999, 2005; Shams et al. 2004a, b, 2005b). Attenuated *ventilatory response* to the subterranean atmosphere is considered highly adaptive because it reduces the energetic respiratory costs associated with the deeper and more frequent breathing in a hypercapnic environment. Maina et al. (2001) observed in the naked mole-rat that lungs can functionally adapt to changing environmental conditions without exhibiting any apparent morphological changes. Therefore, studies of respiratory physiology in captive naked mole-rats (and perhaps also in other subterranean rodents) should be regarded cautiously. A similar problem of functional plasticity may apply also to studies of other parameters. Most physiological measurements are made under artificial laboratory conditions, which actually correspond, to surface environment and not to the real conditions faced by the animals underground.

2.2 Neural and Hormonal Regulation

Research in this field follows the course of information from (highly modified) sensory organs through neural and hormonal systems to the effectors. Sensory (and partly also neuronal) adaptations are the topic of a separate section in this volume (Part II: Sensory Ecology) and will therefore not be addressed here. The topics *reproductive physiology* and *endocrinology* are analyzed in detail by Bennett et al. (Chap. 6). Bennett and colleagues show how the reproductive strategies in solitary living as well as in social South African mole-rats are reflected in regulation networks which are, however, sensitive to environmental conditions. Synchronization of breeding with environmental changes and the dilemma between induced versus spontaneous ovulation are discussed. These aspects of reproduction are very important also for successful laboratory breeding of solitary mole-rats, which could be a bottle-neck for further studies.

Another interesting and important aspect of biology of subterranean dwellers, pertinent to their dark monotonous environment, is that of photoperiodicity and *circadian rhythms*. Also, this aspect is briefly reviewed in the sensory ecology section of this volume (chapter by Némec et al.). Circadian (and circannual) rhythmicity involves not only sensory but also more general physiological aspects. Despite the highly pronounced regression of visual organs and pathways, subterranean rodents of several species were shown to perceive changes in photoperiod and to display circadian rhythms of activity. The retina and the infraorbital Harderian glands are likely sources of light detection and activation of the associated neuroendocrine pathways (see Buffenstein 2000). The number of studies on circadian rhythms in subterranean mole-rats has increased drastically within the past years. Riccio and Goldman (2000) have observed in the naked mole-rat (*H. glaber*) an increase in the body temperature and metabolic rate at the end of the light phase in the circadian cycle, probably to prepare the body for following locomotory activity. The ability to entrain to 24-h light-dark cycles is expressed in *H. glaber*, *Georychus capensis*, *Fukomys damarensis*, *Cryptomys hottentotus*, *Fukomys darlingi* (Riccio and Goldman 2000; Oosthuizen et al. 2003; Richter et al. 2003; Gutjahr et al. 2004; Hart et al. 2004; Vasicek et al. 2005a) while in *C. hottentotus*, Negroni et al. (2003) could not demonstrate neither light synchronization nor circadian activity pattern. Large inter- and intraindividual variations in the rate and extent of entrainment, time of activity preference, and activity patterns complicate the studies (Oosthuizen et al. 2003; Vasicek et al. 2005b). Begall et al. (2002) showed that individually housed *Spalacopus cyanus* displayed a clear nocturnal endogenous activity pattern under laboratory conditions. In contrast, Urrejola et al. (2005) demonstrated that free-living *S. cyanus*

are diurnal. Physical and social environments in which captive animals are housed may contribute to the observed differences in activity between field and laboratory populations (Urrejola et al. 2005). Obviously, the underground ecotope has not a consistent effect on the temporal patterning of activity. In *S. ehrenbergi* a plausible synchronization mechanism was presented (Tobler et al. 1998, Tobler and Deboer 2001). Further studies have shifted their focus to mechanisms on molecular level (Avivi et al. 2001, 2002, 2004; Oster et al. 2002). Hannibal et al. (2002) revealed that *Spalax* expresses melanopsin in ganglion cells projecting to the circadian clock, thus supporting the role of melanopsin as a circadian photopigment. According to Hough et al. (2002) the expression of a heat shock protein bound to the lens has also undergone adaptive changes corresponding to the subterranean evolution of the blind mole-rat. Surely, more studies in this field will follow in the next few years.

References

- Avivi A, Resnick MB, Nevo E, Joel A, Levy AP (1999) Adaptive hypoxic tolerance in the subterranean mole rat *Spalax ehrenbergi*: the role of vascular endothelial growth factor. *FEBS Lett* 452:133–140
- Avivi A, Albrecht U, Oster H, Joel A, Beiles A, Nevo E (2001) Biological clock in total darkness: the Clock/MOP3 circadian system of the blind subterranean mole rat. *Proc Natl Acad Sci USA* 98:13751–13756
- Avivi A, Oster H, Joel A, Beiles A, Albrecht U, Nevo E (2002) Circadian genes in a blind subterranean mammal II: conservation and uniqueness of the three period homologs in the blind subterranean mole rat, *Spalax ehrenbergi* superspecies. *Proc Natl Acad Sci USA* 99:11718–11723
- Avivi A, Oster H, Joel A, Beiles A, Albrecht U, Nevo E (2004) Circadian genes in a blind subterranean mammal III: molecular cloning and circadian regulation of cryptochrome genes in the blind subterranean mole rat, *Spalax ehrenbergi* superspecies. *J Biol Rhythms* 19:22–34
- Avivi A, Shams I, Joel A, Lache O, Levy AP, Nevo E (2005) Increased blood vessel density provides the mole rat physiological tolerance to its hypoxic subterranean habitat. *Faseb J* 19:1314–1316
- Begall S, Daan S, Burda H, Overkamp GJF (2002) Activity patterns in a subterranean social rodent, *Spalacopus cyanus* (Octodontidae). *J Mammal* 83:153–158
- Buffenstein R (2000) Ecophysiological responses of subterranean rodents to underground habitats. In: Lacey EA, Patton JL, Cameron GN (eds) *Life underground: the biology of subterranean rodents*. Univ of Chicago Press, Chicago, pp 62–110
- Buffenstein R (2005) The naked mole-rat: a new long-living model for human aging research. *J Gerontol A* 60:1369–1377
- Cortes A, Miranda E, Rosenmann M, Rau JR (2000) Thermal biology of the fossorial rodent *Ctenomys fulvus* from the Atacama desert, northern Chile. *J Therm Biol* 25:425–430
- Cutrerera AP, Antinuchi CD (2004) Fur changes in the subterranean rodent *Ctenomys talarum*: possible thermal compensatory mechanism. *Rev Chil Hist Nat* 77:235–242
- Daly TJM, Buffenstein R (1998) Skin morphology and its role in thermoregulation in mole-rats, *Heterocephalus glaber* and *Cryptomys hottentotus*. *J Anat* 193:495–502

- Dammann P, Burda H (2006) Sexual activity and reproduction delay ageing in a mammal. *Curr Biol* 16:R117–R118
- Dyer BD (1998) A hypothesis about the significance of symbionts as a source of protein in the evolution of eusociality in naked mole rats. *Symbiosis* 24:369–383
- Gutjahr GH, Rensburg LJ, Malpaux B, Richter TA, Bennett NC (2004) The endogenous rhythm of plasma melatonin and its regulation by light in the highveld mole-rat (*Cryptomys hottentotus pretoriae*): a microphthalmic, seasonally breeding rodent. *J Pineal Res* 37:185–192
- Hannibal J, Hindersson P, Nevo E, Fahrenkrug J (2002) The circadian photopigment melanopsin is expressed in the blind subterranean mole rat, *Spalax*. *Neuroreport* 13:1411–1414
- Hart L, Bennett NC, Malpaux B, Chimimba CT, Oosthuizen MK (2004) The chronobiology of the Natal mole-rat, *Cryptomys hottentotus natalensis*. *Physiol Behav* 82:563–569
- Hough RB, Avivi A, Davis J, Joel A, Nevo E, Piatigorsky J (2002) Adaptive evolution of small heat shock protein/alpha B-crystallin promoter activity of the blind subterranean mole rat, *Spalax ehrenbergi*. *Proc Natl Acad Sci USA* 99:8145–8150
- Maina JN, Gebreegziabher Y, Woodley R, Buffenstein R (2001) Effects of change in environmental temperature and natural shifts in carbon dioxide and oxygen concentrations on the lungs of captive naked mole-rats (*Heterocephalus glaber*): a morphological and morphometric study. *J Zool Lond* 253:371–382
- Negróni J, Bennett NC, Cooper HA (2003) Organization of the circadian system in the subterranean mole rat, *Cryptomys hottentotus* (Bathyergidae). *Brain Res* 967:48–62
- Nevo E (1999) Mosaic evolution of subterranean mammals: regression, progression and global convergence. Oxford Univ Press, Oxford
- O'Connor TP, Lee A, Jarvis JUM, Buffenstein R (2002) Prolonged longevity in naked mole-rats: age-related changes in metabolism, body composition and gastrointestinal function. *Comp Biochem Physiol A* 133:835–842
- Oosthuizen MK, Cooper HM, Bennett NC (2003) Circadian rhythms of locomotor activity in solitary and social species of African mole-rats (Family: Bathyergidae). *J Biol Rhythms* 18:481–490
- Oster H, Avivi A, Joel A, Albrecht U, Nevo E (2002) A switch from diurnal to nocturnal activity in *S. ehrenbergi* is accompanied by an uncoupling of light input and the circadian clock. *Curr Biol* 12:1919–1922
- Riccio AP, Goldman BD (2000) Circadian rhythms of locomotor activity in naked mole-rats (*Heterocephalus glaber*). *Physiol Behav* 71:1–13
- Richter TA, Malpaux B, Fleming PA, Molteno AJ, Bennett NC (2003) Melatonin secretion in a strictly subterranean mammal, the Damaraland mole-rat (*Cryptomys damarensis*). *J Zool Lond* 261:313–319
- Shams I, Avivi A, Nevo E (2004a) Hypoxic stress tolerance of the blind subterranean mole rat: Expression of erythropoietin and hypoxia-inducible factor 1 alpha. *Proc Natl Acad Sci USA* 101:9698–9703
- Shams I, Nevo E, Avivi A (2004b) Ontogenetic expression of erythropoietin and hypoxia-inducible factor-1 alpha genes in subterranean blind mole rats. *Faseb J* 18
- Shams I, Avivi A, Nevo E (2005a) Oxygen and carbon dioxide fluctuations in burrows of subterranean blind mole rats indicate tolerance to hypoxic-hypercapnic stresses. *Comp Biochem Physiol A* 142:376–382
- Shams I, Nevo E, Avivi A (2005b) Erythropoietin receptor spliced forms differentially expressed in blind subterranean mole rats. *Faseb J* 19
- Tobler I, Deboer T (2001) Sleep in the blind mole rat *Spalax ehrenbergi*. *Sleep* 24:147–154