Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Evolutionary history of Spalacidae inferred from fossil occurrences and molecular phylogeny

Ya HE[†] *Key Laboratory of Southwest China Wildlife Resources Conservation, Institute of Ecology, Institute of Rare Animals and Plants of School of Life Sciences, China West Normal University, Nanchong, Sichuan, 637009, China and Natural History Research Center, Shanghai Natural History Museum, Shanghai Science & Technology Museum, Shanghai, 200041, China. Email: hey@sstm.org.cn*
Shuzhan HU[†] *Key Laboratory of Southwest China Wildlife Resources Conservation, Institute of Ecology, Institute of Rare Animals and Plants of School of Life Sciences, China West Normal University, Nanchong, Sichuan, 637009, China. Email: hushuzhan1990@sina.com*
Deyan GE* *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, China. Email: gedy@ioz.ac.cn*
Qisen YANG *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, 100101, China. Email: yangqs@ioz.ac.cn*
Thomas CONNOR *Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, 48823, USA. Email: connort2@msu.edu*
Caiquan ZHOU* *Key Laboratory of Southwest China Wildlife Resources Conservation, Institute of Ecology, Institute of Rare Animals and Plants of School of Life Sciences, China West Normal University, Nanchong, Sichuan, 637009, China. Email: drcqzhou1@163.com*

Keywords
Africa, climate change, dispersal–vicariance analysis, Eurasia, evolution, fossil, Spalacidae

*Correspondence authors.
[†]These authors contributed equally.

Submitted: 25 October 2018
Returned for revision: 28 November 2018
Revision accepted: 19 July 2019
Editor: DR

doi: 10.1111/mam.12170

ABSTRACT

1. The Spalacidae is a family of strictly subterranean rodents with a long evolutionary history. It is unclear how ecological changes have influenced the evolutionary history of these mammals, and the phylogenetic relationship of the subfamilies within Spalacidae is controversial.
2. Through compiling fossil records, reconstructing molecular phylogeny from molecular data, determining the date of divergence, and analysing their geographical evolution based on molecular data and fossil taxa, we explore the origin and evolutionary process of Spalacidae in detail. Diversification within Spalacidae dates to the Late Oligocene, approximately 25 million years ago, based on molecular data.
3. This family originated in South and East Asia in the Late Oligocene, and then split into four clades. The first clade includes Rhizomyinae, which was highly diversified in South Asia in the Early-to-Middle Miocene. Then Rhizomyinae from Asia migrated to northern Africa in multiple waves through the Afro-Eurasian land bridge. Its range largely contracted in the Late Miocene, notably in Central Asia. The second clade includes the extinct Tachyoryctoidinae, which was confined to East and Central Asia, and survived from the Late Oligocene to the Late Miocene. The third clade includes Spalacinae, which have remained around the Mediterranean region since the Late Oligocene with slight trend of northward expansion. The fourth clade is Myospalacinae. Ancient genera of this subfamily in East Asia dispersed eastward during the Late Miocene and reached northern China and south-east Russia.
4. The general distribution pattern of Spalacidae has persisted since the Late Miocene. Extinction of Tachyoryctoidinae and clear range contraction of

Rhizomyinae in Central and East Asia are likely to have resulted from increased aridification, while the slight northward expansion of Myospalacinae and Spalacinae since the Quaternary was probably a response to a similar northward expansion of suitable vegetation for these animals.

INTRODUCTION

It is generally recognised that the current species diversity and distribution patterns of different organisms are mainly related to environmental changes from the Late Miocene to the Quaternary (Hewitt 2000, Hewitt et al. 2004, Outlaw & Voelker 2008). Climate change during these periods greatly influenced species in different regions (Sandel et al. 2011). The abundance of both fossils and extant species of mammals makes them ideal candidates to study the evolution of terrestrial animals and to interpret their response to environmental changes at a global scale. Previous studies have demonstrated clear trends of diversity increases and population expansions in ground-dwelling mammals, particularly in open grassland ecosystems (Bobe & Behrensmeyer 2004, Mihlbachler et al. 2011, Ge et al. 2014). This was probably a response to a significant increase in the proportion of C_4 grass species in the Late Miocene (Pagani et al. 1999, Bonnefille 2010, Strömberg 2011). In contrast, prominent extinction and range contraction were observed in arboreal taxa (Goswami et al. 2011, Ge et al. 2013, Lv et al. 2013), which were prevalent early in eutherian evolution (Trofimov & Szalay 1994, Ji et al. 2002, Luo et al. 2003). However, it is unclear how these ecological changes have influenced the evolutionary history and distribution of strictly subterranean mammals that require more stable habitat conditions.

Spalacidae is one of the oldest families of living rodents (excluding the Platacanthomyidae) in the superfamily Muroidea (Norris 2017). Extant members of Spalacidae, which consists of three subfamilies, Myospalacinae, Rhizomyinae, and Spalacinae (Norris 2017), are strictly subterranean mammals characterised by low migration capacity and strong dependence on suitable environmental factors (Nevo 1999). Tachyoryctoidinae, a group of mid-tertiary extinct endemic rodents of East and Central Asia, was recently assigned as a closely related subfamily of Spalacinae based on craniodental morphology (Wang & Qiu 2018). The distinct biological characteristics of Spalacidae make it a good candidate for studying the evolutionary history of subterranean mammals and their response to global ecological changes. Furthermore, the current diversity of Spalacidae (36 extant species) is eclipsed by the high diversity of Sciuridae (278 extant species), Cricetidae (681 extant species), and Muridae (730 extant species; Musser & Carleton 2005). Compared to the highly species-rich families in Rodentia that diverged in the same period, Spalacidae shows a low diversity and narrow distribution.

The geographical ranges of Spalacidae species show that each of the three extant subfamilies occupies its own geographical area: Rhizomyinae in South and South-East Asia and the eastern part of Africa; Spalacinae in south-eastern Europe, North Africa, the Middle East, and western Asia; and Myospalacinae in Central and East Asia (mainly in China and Mongolia). However, the extinct Tachyoryctoidinae, which includes a large number of species assigned to *Tachyoryctoides* and its closely related genera, was unearthed in South and Central Asia, clearly overlapping with the range of Rhizomyinae and Myospalacinae (Wang & Qiu 2018). *Prokanisamys kowalskii* (Lindsay 1996), the earliest fossil record of Rhizomyinae, was unearthed in Zinda Pir Dome, Pakistan (and lived ~23.3 million years ago, Mya; Wessels & De Bruijn 2001, Lindsay et al. 2005, Flynn et al. 2013). The earliest fossil of Spalacinae was *Vetusspalax progressus*, which was found in Bosnia and Herzegovina and dated to ~24 Ma (De Bruijn et al. 2013). Several species within Tachyoryctoidinae were unearthed in Central and East Asia, and dated to the Late Oligocene (Wang & Qiu 2012, 2018).

Previous work on fossils of Spalacidae has been focused mostly on the abundance and morphological diversification of different species, as well as the phylogenetic relationship among taxa using morphological characteristics (Hugueney & Mein 1993, Flynn 2009, Şen & Sarıca 2011, López-Antoñanzas et al. 2013, De Bruijn et al. 2015). However, it is unclear how the geographical distribution pattern of Spalacidae formed in their evolutionary history. A comprehensive review of the evolutionary history of this family including information on extant taxa and fossils is lacking.

Phylogenetic work on Spalacidae, conducted using molecular data from extant species and morphological features of fossils, has resulted in different hypotheses on their phylogenetic relationship (Fig. 1). According to the fossil records, Flynn (2009) demonstrated that within Spalacidae, the subfamily Myospalacinae shares more features with Rhizomyinae than with Spalacinae, supporting the theory that Myospalacinae and Rhizomyinae are the most closely related taxa (Fig. 1a). De Bruijn et al. (2015) reconstructed the evolutionary history of the Rhizomyinae and the

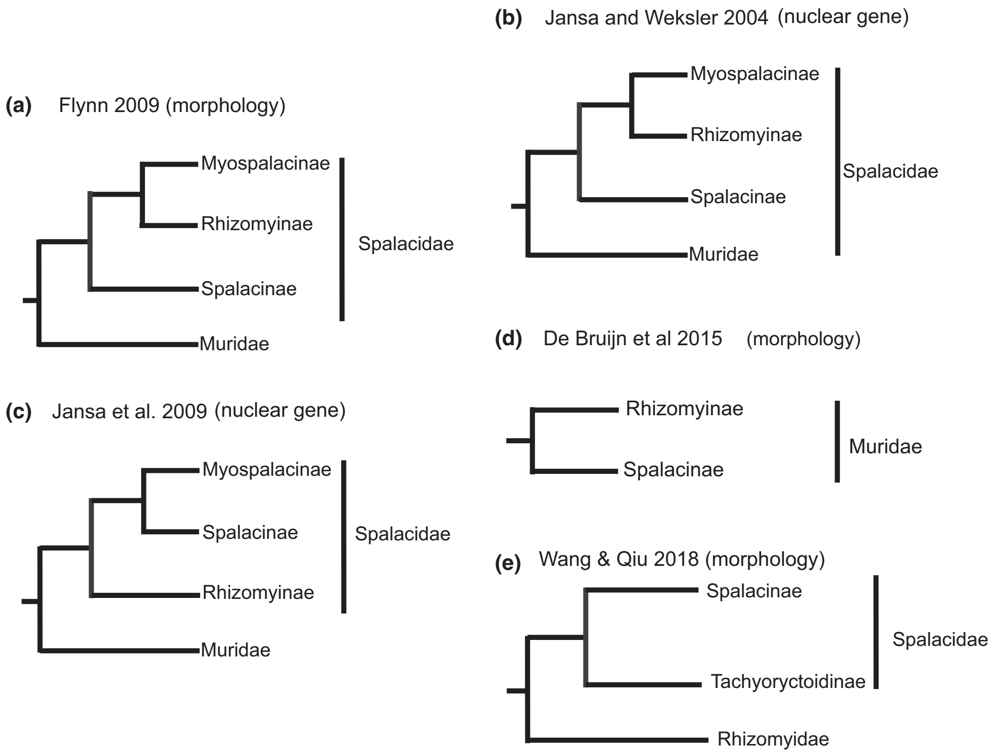

Fig. 1. Different hypotheses for the phylogeny of three subfamilies (Myospalacinae, Spalacinae, and Rhizomyinae) within the family Spalacidae, inferred from morphology (a, d, e), from molecular data with one nuclear gene (IRBP; b), and from molecular data with two nuclear genes (IRBP and GHR; c).

Spalacinae using fossil records and suggested that these two groups do not share the same murid ancestor and developed separately (Fig. 1d). After analysing the phylogenetic relationship of the three subfamilies using one nuclear gene (IRBP), Jansa and Weksler (2004) suggested that Myospalacinae and Rhizomyinae are the most closely related, while Spalacinae is a basal relative to these subfamilies. Lin et al. (2014) also concluded there was a sister group relationship between Rhizomyinae and Myospalacinae, which, they argued, together form the sister group of the more basal Spalacinae (Fig. 1b). By contrast, Jansa et al. (2009) obtained different results using two nuclear genes (IRBP and GHR); they recovered a sister clade consisting of Myospalacinae and Spalacinae, while finding that Rhizomyinae is a basal relative to these two subfamilies (Fig. 1c). Wang and Qiu (2018) assigned Tachyoryctoidinae and Spalacinae to the family Spalacidae and considered Rhizomyidae as a separate family (Fig. 1e) by using morphological data from craniodental morphology of fossils, but Myospalacinae was not included in their analyses. There have thus been many studies to investigate the phylogeny of Spalacidae using fossil morphology or molecular methods with differing results, but none has used a combination of fossil occurrences and molecular data in order to understand the evolutionary history of Spalacidae.

The extant species of Spalacidae are generally accepted as a monophyletic group. In previous studies using genetic data, the monophyletic status of Spalacidae was supported by examining a single nuclear gene of 90 species that was sampled from major lineages of muroid rodents (Jansa & Weksler 2004), two complete sequences of mitochondrial DNA obtained for about 30 species (Norris et al. 2004), a concatenated data set of five nuclear genes and one mitochondrial gene in a 900-species tree of Rodentia (Steppan & Schenk 2017), and a concatenated supermatrix of 11 genes that included 1265 taxa and aligned 15535 sites (Fabre et al. 2012). This point of view has also been accepted by major monographs of extant mammals, including '*Mammal Species of the World*' (Musser & Carleton 2005), and the '*Handbook of the Mammals of the World*' (Norris 2017), which are often considered the top authoritative references on the taxonomy of extant mammals. These references provide a basic framework to understand the higher-level phylogenetic relationships within Spalacidae.

In the present study, we aim to: 1) trace the evolutionary history of Spalacidae by integrating fossil occurrences with molecular data from GenBank; 2) recalibrate the diversification time of lineages within Spalacidae; and 3) infer the phylogenetic relationship and geographical evolutionary process of Spalacidae. To resolve these problems, 341 fossil records and a data set containing six DNA fragments were used in this research.

METHODS

Compiling fossil records

The fossil records of Spalacidae (including scientific name, geological age, and longitude and latitude of unearthed group) were mainly obtained from Fossilworks (the Paleobiology Database: http://fossilworks.org/bridge.pl?a=home) and the National Infrastructure of Mineral Rock and Fossil Resources for Science and Technology of China (http://www.nimrf.net.cn/pub/msbz.jsp). Additionally, to ensure the completeness of the fossil information, we consulted the Zoological Record (from 1864 to 2014) provided by the Thomson Reuters' Web of Knowledge (http://apps.webofknowledge.com/). Systematic studies that gave comprehensive reviews on the classification of Myospalacinae (Zheng 1994), Rhizomyinae (Flynn 1982, 2009, López-Antoñanzas et al. 2013, 2015, De Bruijn et al. 2015), Spalacinae (De Bruijn et al. 2015), and Tachyoryctoidinae (Wang & Qiu 2012, 2018) provided the basic framework for compiling fossil occurrences in different periods. Valid names of each genus and species were used as key words in our searches for original references in the Zoological Record.

Phylogenetic analysis

Twenty-eight species, representing all extant genera of Spalacidae, were selected for a phylogenetic analysis. Six mitochondrial gene sequences were used to reconstruct the family's phylogeny: Cytochrome b (Cytb), cytochrome oxidase subunit I (*cox1*), NADH dehydrogenase 4 (ND4), mitochondrial D-loop (D-loop), 12S ribosomal DNA (12S), and 16S ribosomal DNA (16S). Twenty-four species from Cricetidae, five species from Muridae, *Glis glis*, *Lepus townsendii,* and *Ochotona princeps* were used as outgroup taxa. All of these sequences were downloaded from GenBank and aligned using Muscle 3.8.31 (Edgar 2004). We used PartitionFinder 2 (Lanfear et al. 2017) to select the best scheme for setting up a MrBayes block for partition definitions. A total length of 6937 base pairs, including gaps, was generated from the alignment. We constructed the phylogenetic tree in the program MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). We set the main parameters as follows: two million chain generations, trees sampled every 1000 generations, and the first 800 trees discarded as burn-in. The phylogenetic tree was displayed in FigTree 1.4.4 (Rambaut 2018). Detailed information on the GenBank accessions of sequences included in the present study is given in Appendix S1.

Divergence time estimation

The divergence times among lineages were recalibrated by using BEAST version 1.8.2 (Drummond et al. 2012). One calibration point was used in calibrating the divergence time: the split of *Mus* and *Rattus* approximately 15.9 Mya. This age was the median age from the online tool 'TimeTree: The Timescale of Life' (http://www.timetree.org/, Hedges et al. 2015), which was derived from a large collection of previous studies (84 publications, searched on 10 May 2019). The General Time Reversible model was used as the substitution model, and the Yule process of speciation was selected for the tree prior and combined with a relaxed molecular clock model. The search chain was run for 20 million generations and was sampled every 1000 generations. The log files and tree files that were generated were analysed in LogCombiner v1.5.4 (Rambaut & Drummond 2010) and TreeAnnotator v1.5.4 (Rambaut & Drummond 2008) in the BEAST package, respectively; the first 25% of generations were discarded as burn-in. The final results were tested in Tracer version 1.4.1 (Rambaut & Drummond 2007) and illustrated in FigTree v1.4.4 (Rambaut 2018).

Ancestral distribution inference

Large numbers of species within Spalacidae were extinct; in particular, the geographical range in Central Asia could not be included in inferring the ancient distribution of Spalacidae if we just included extant species. According to the results of many previous studies, incorporating fossil information in phylogeny-based biogeographical analyses can improve the reconstruction of past events (Nauheimer et al. 2012, Meseguer et al. 2015). Therefore, we manually added the extinct genera to the phylogenetic tree from the BEAST analyses and kept one species for each extant genus to avoid the influence of imbalanced sampling in analyses. The distribution of each genus was used to infer the geographical evolution of Spalacidae. All outgroup taxa were removed in this analysis. The placement of extinct genera was based on the phylogeny produced by López-Antoñanzas et al. (2013, 2015) and Wang and Qiu (2018), and the time ranges were compiled from all available literature sources (Appendices S2 and S3).

Statistical dispersal–vicariance analysis (S-DIVA; Yu et al. 2010) and Bayesian Binary MCMC (BBM; Ronquist & Huelsenbeck 2003) implemented in RASP 4.1 (Yu et al. 2015) were used to infer the geographical distribution evolution of Spalacidae. These two methods do not require trees with branch lengths in analyses. We predefined four areas for these genera: 1) South and East Asia; 2) the Tibetan Plateau and inland arid regions of Central Asia; 3)

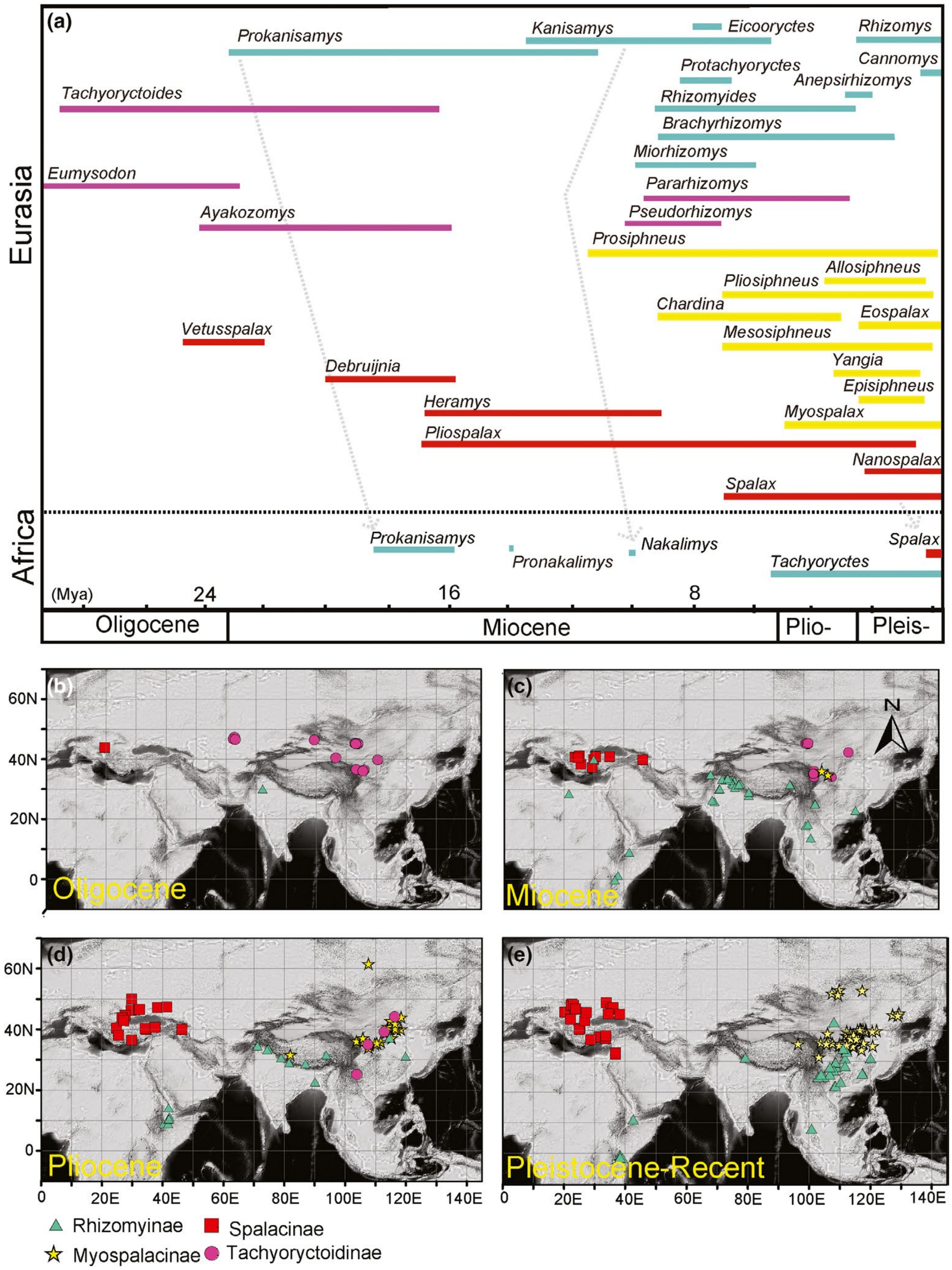

Fig. 2. The time span and worldwide distribution of Spalacidae since the Oligocene. The time span of fossil genera of Spalacidae on two continents; the dotted arrows linking the genera indicate the possible dispersal trends between continents (a). Fossil occurrences of Rhizomyinae, Tachyoryctoidinae, Spalacinae, and Myospalacinae during the Oligocene (b), the Miocene (c), the Pliocene (d), and from the Pleistocene to recent times (e).

south-eastern Europe, the eastern Mediterranean area, and northernmost Africa; and 4) Central and East Africa. Twenty thousand trees were introduced into the software RASP 4.1, and the first 5000 trees were discarded as burn-in. The number of unit areas allowed in ancestral distributions was set at four with the gamma (+G) site change ratio and other parameters set at the default values of RASP 4.1.

RESULTS

Fossil records and historical distribution of Spalacidae

We compiled 341 fossil records of Spalacidae for the present study, and their species names, occurrence times, and localities are given in Appendix S2. The time span of each genus and the transcontinental migration events that occurred in Eurasia and Africa are illustrated in Fig. 2a. Occurrences of these fossils are displayed in Fig 2b–e.

Prokanisamys (De Bruijn et al. 1981), the earliest genus of Rhizomyinae, occurred in Pakistan from the Late Oligocene to the Earliest Miocene (~24-23 Ma, Lindsay et al. 2005) before appearing in Africa (19-18 Ma, Wessels 2009) in the Early Miocene. In the Late Miocene, there were five genera of Rhizomyinae in Asia (*Kanisamys, Rhizomyides, Protachyoryctes, Eicooryctes,* and *Miorhizomys*) and three genera in Africa (*Pronakalimys, Nakalimys,* and *Tachyoryctes*), making this the most prosperous period for Rhizomyinae. In the Pliocene, there were four genera of Rhizomyinae in Asia (*Rhizomyides, Brachyrhizomys, Anepsirhizomys,* and *Cannomys*) and only one genus in Africa (*Tachyoryctes*). After the Pliocene, the diversity of Rhizomyinae continued to decrease, leaving two genera in Asia (*Rhizomys* and *Cannomys*) and one genus in Africa (*Tachyoryctes*). The overall geographical range of the Rhizomyinae contracted dramatically from the Miocene to the current period (Fig 2b–e).

The earliest species of Tachyoryctoidinae, *Eumysodon spurius*, was unearthed in Kazakhstan and dated to 28.4–23.03 Mya. Meanwhile, the genus *Tachyoryctoides* was highly diversified in East Asia, and a large number of fossil species were found in Mongolia and China of the Oligocene age. Currently, the five genera *Eumysodon*, *Ayakozomys*, *Tachyoryctoides*, *Pararhizomys,* and *Pseudorhizomys* (the

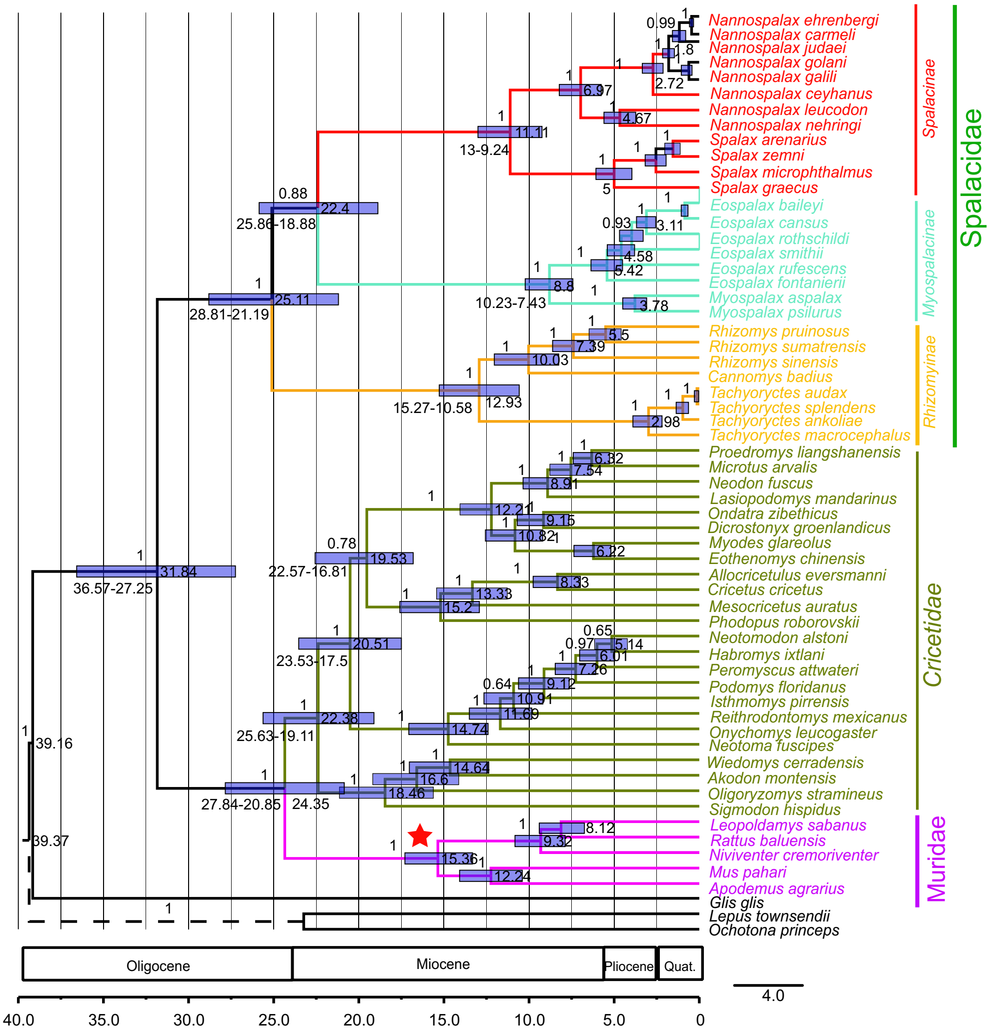

Fig. 3. Time-calibrated phylogeny of Spalacidae. The asterisks indicate the nodes for the split of *Rattus* and *Mus* as a calibration point. The horizontal bars show the 95% highest posterior density. The node labels give the ages; the branch labels give the posterior probabilities and 95% highest posterior density values of ages.

latter two in the Late Miocene) are included in this subfamily (Wang & Qiu 2018).

The earliest genus of Spalacinae, *Vetusspalax*, was dated to the Late Oligocene, approximately 24 Mya (De Bruijn et al. 2013, 2015). *Heramys* and *Debruijnia* were dated to the Early Miocene (Hugueney & Mein 1993). In the Late Miocene, there were two genera of Spalacinae in Eurasia (*Heramys* and *Pliospalax*). *Spalax* extended from Europe (Topachevskiy et al. 1998) to North Africa in the Late Pleistocene (McKenna & Bell 1997).

The earliest fossil of Myospalacinae was dated to the Late Miocene. In the Late Miocene, there was only *Prosiphneus*. The diversity of Myospalacinae increased rapidly after the Miocene, so that six genera were present in Eurasia in the Pliocene. The Pleistocene was also a prosperous period for Myospalacinae (five genera: *Allosiphneus, Yangia, Eospalax, Episiphneus,* and *Myospalax*). After the Pleistocene, only two genera survived (*Eospalax* and *Myospalax*).

Phylogenetic relationship, divergence time, and ancestral distribution

Phylogenetic reconstruction based on six DNA fragments revealed a sister group relationship between Spalacinae and Myospalacinae, which together form the sister group of the more basal Rhizomyinae (Fig. 3, Appendix S4). The divergence time of Spalacidae is also summarised in Fig. 3. The Spalacidae family split from other taxa of rodents approximately 31.84 Mya (36.57–27.25 Mya, 95% highest posterior density). The most recent common ancestor of this family was calculated to have occurred in the Late Oligocene, approximately 25.11 Mya (28.81–21.19 Mya, 95% highest posterior density). The divergence of living genera of Rhizomyinae between African and Asian localities was estimated to have occurred in the Late Miocene around 12.93 Mya (15.27–10.58 Mya, 95% highest posterior density). The origination of Spalacidae was deduced as area "1", which refers to South and East Asia, and had a support value of 74% in S-DIVA and 73% in BBM (Fig. 4a).

DISCUSSION

The evolutionary history of Spalacidae

The fossil occurrences and molecular phylogenetic reconstruction provided consistent estimates of the origin date of Spalacidae. This family probably split from other rodents during the Late Oligocene, approximately 32 Mya. Divergence time within this family was dated to approximately 25 Mya based on molecular data of extant species. The split of Rhizomyinae between Asia and Africa was dated to approximately 13 Mya. These dates are generally earlier than those of previous studies based on molecular data, which dated the split of Spalacinae and Rhizomyinae to 19.8 Mya (Steppan et al. 2004) and the split of taxa within Rhizomyinae to 8.9 Mya (Šumbera et al. 2018).

Geographical evolutionary history reconstruction revealed the origin centre of Spalacidae to be South and East Asia (Figs 2 and 4). The inconsistency between the known earliest fossil records and origin centre inferred in the present analyses is probably due to incomplete sampling of fossils in South and East Asia. Multiple intercontinental migration events between Eurasia and Africa (Fig. 4a, b) are likely to have occurred during the evolutionary history of Spalacidae (López-Antoñanzas et al. 2013).

Rhizomyinae represents the early branch of this family (Fig. 3). The earliest fossil record of Rhizomyinae to date, *Prokanisamys* (De Bruijn et al. 1981), was first found in Pakistan and dated to the Late Oligocene (~24 Mya). The genus was found in Africa and dated to the Early Miocene (19–18 Mya) and unearthed in Thailand and dated to the Middle Miocene (Fig. 2a). The postcranial skeleton of *Prokanisamys* indicates that this genus was not fossorial (Flynn 1982, 1985). This assumption was supported by its wide geographical range (South-East Asia to North Africa). Because fossils of *Prokanisamys* in Africa appeared later than the same genus in Asia, it can be inferred that Rhizomyinae probably migrated from Asia to Africa in the Early Miocene. Moreover, morphological studies of fossils have found that Rhizomyinae members developed burrowing adaptations after 10 Mya. As this early group of animals lacked some of the advanced fossorial traits found later in their lineage (Flynn 2009), their long-distance migration between Eurasia and Africa was more feasible. In the Early Miocene, the contraction of the Tethys Sea along with tectonic activity in East Africa established a land bridge between Africa and Eurasia which divided the Mediterranean Sea from the Indian Ocean (Rögl 1999). This allowed for the exchanging of plants and animals between Africa and Eurasia, which is evidenced by the presence of *Pronakalimys* in Africa during the Middle Miocene (López-Antoñanzas et al. 2005, López-Antoñanzas & Knoll 2010). The divergence time between African and Asian Rhizomyinae was dated around 13 Mya based on molecular data (Fig. 3). López-Antoñanzas et al. (2013) argued that from a morphological viewpoint, the extant African Rhizomyines (*Tachyoryctes*) share more synapomorphies with Asian species than with the ancient African taxa. *Protachyoryctes* and *Eicooryctes* are the closest Asian counterparts of this genus. Therefore, it is likely that Rhizomyinae migrated from Asia to Africa in three separate waves (Fig. 2a).

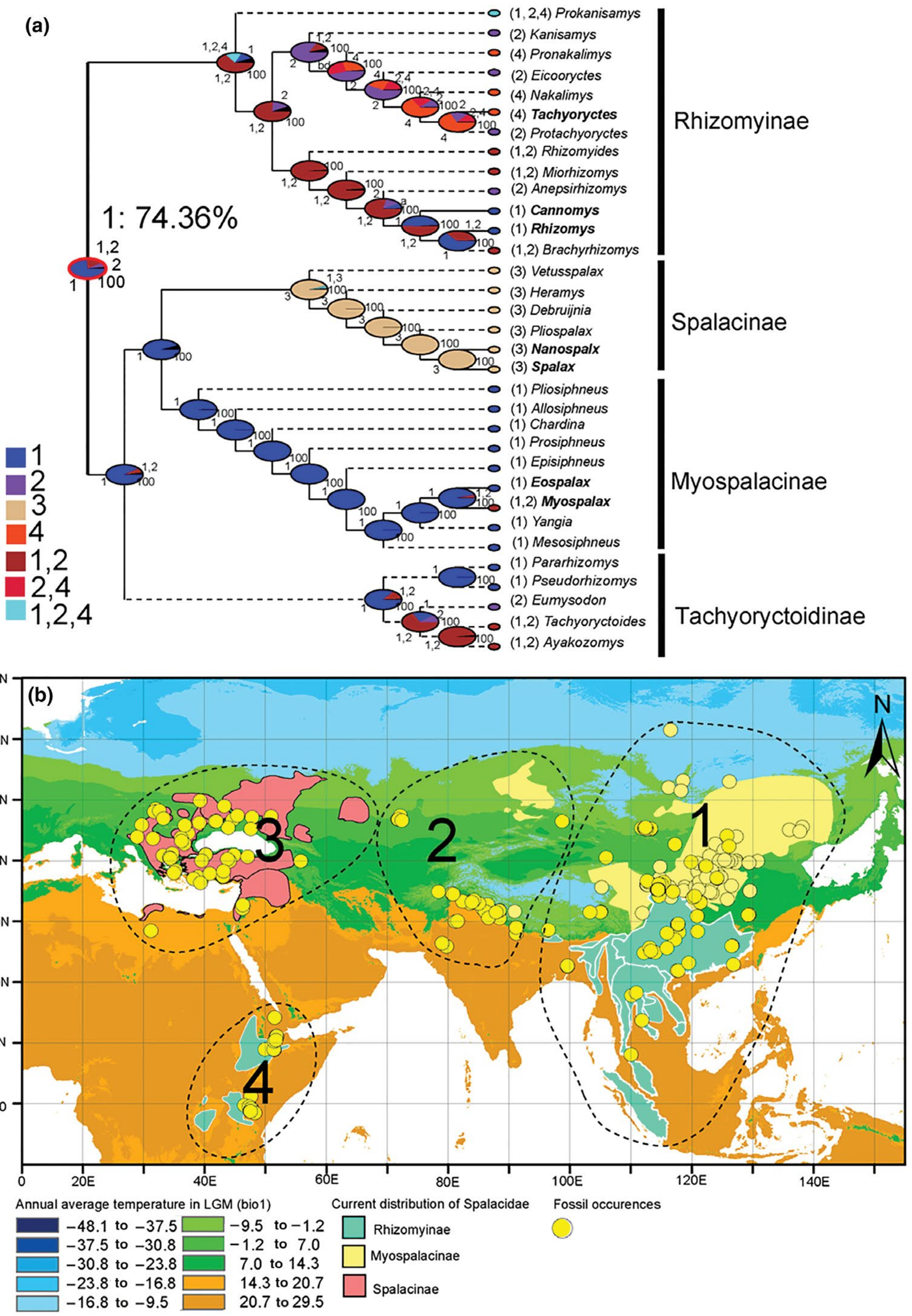

Fig. 4. The phylogeny reconstruction and origination site inference of Spalacidae based on S-DIVA. (a) The reconstructed phylogenetic tree and the inference results. The legend specifies the predefined areas used in the analyses. Solid lines show the branch of extant genera (in bold), and dotted branches show the placement of fossil genera with uncertainty. (b) The predefined areas used to infer the origination of Spalacidae, which was mapped on the annual average temperature (Bio 1) in the last glacial maximum (original layer downloaded from WorldClim, http://www.worldclim.org/past), and the current distribution of Spalacidae (downloaded from the IUCN, http://oldredlist.iucnredlist.org/). Four predefined areas including (1): South and East Asia; (2) the Tibetan Plateau and inland arid regions of Central Asia; (3) south-eastern Europe, the eastern Mediterranean area, and northernmost Africa; and (4) Central and East Africa. Dots show the distribution of fossils. The current geographical range of each of the three families of Spalacidae is indicated.

The phylogenetic position of Tachyoryctoides and its closely related genera, the subfamily Tachyoryctoidinae, was controversial for decades. It has been included in the families Rhizomyidae (Chaline et al. 1977), Spalacidae (Flynn et al. 1985), Cricetidae (Kordikova & De Bruijn 2001), and Muridae (De Bruijn et al. 2015). Recently, Wang and Qiu (2018) assigned it to Spalacidae by using 53 craniodental characteristics, 12 of which supported its close relatedness to *Spalax*. Depending on the discovery of more materials, there is a possibility for correctly placing Tachyoryctoides at a more basal position (Wang & Qiu 2018). The genus *Pararhizomys* was found in several Late Miocene sites in northern China and Mongolia (Fig. 2; Li 2010). Zhang et al. (2005) assigned *Pararhizomys* to *incertae sedis*, but they pointed out that it is morphologically similar to spalacines in some aspects. Flynn (2009) thought *Pararhizomys* from the Late Neogene was implicated in the origin of Myospalacinae. By following the study of Wang and Qiu (2018), we placed *Tachyoryctoides*, *Ayakozomys*, *Eumysodon*, *Pararhizomys*, and *Pseudorhizomys* in Tachyoryctoidinae. S-DIVA and BBM analyses showed South and East Asia as the most probable centre of origin of these subfamilies.

Given the distribution of fossils (Fig. 2b–d), it is likely that ancestors of Myospalacinae spread eastward in Asia in the Late Miocene and reached northern China. *Prosiphneus* (Teilhard de Chardin 1926), the earliest known genus of Myospalacinae (Zhou 1988), was found in northern China (Zheng et al., 2004). After the origination of Myospalacinae in northern China, this subfamily was confined mainly to a limited region in East Asia, with slight range expansion since the Pleistocene. Based on the morphology of fossils, Flynn (2009) concluded that zokors evolved forelimbs adapted to burrowing around the beginning of the Late Miocene. The narrow distribution of these taxa can likely be attributed to their specialised lifestyle in which they have evolved to live underground. In addition, Myospalacinae habitat is characterised by moist soils and degraded grassland dominated by forbs (Shi 1998, Ma et al. 1998), which limits their dispersal capability.

The fourth branch of Spalacidae is the Spalacinae, which originated in south-eastern Europe in the Oligocene and has shown limited large-scale migration other than to northern Africa since that time (Fig. 2). Living animals are truly blind. The earliest unearthed Spalacines were believed to be fossorial rodents because the morphology of these species suggested limited dispersal ability (Flynn 1982, Savic & Nevo 1990, Kryštufek & Griffiths 2002, De Bruijn et al. 2015). However, according to their fossil records and current distribution, this subfamily showed a slight range expansion in south-eastern Europe and extending to Africa (Fig. 2b-e). The earliest fossil record of Spalacinae is *Vetusspalax progressus* (De Bruijn et al. 2013), unearthed in the eastern Mediterranean area and dated to the Late Oligocene (about 24 Mya). Marine barriers that formed between Anatolia and the Balkans were believed to facilitate the separation of *Spalax* from *Nannospalax* (Hadid et al. 2012).

Fossil sites in South-East Asia are clearly exceeded in number by those in Europe and northern China (Fig. 1). The warm, wet environment in South and East Asia prohibits fossils preservation. Moreover, the incomplete sampling of fossil taxa is a common problem in palaeontological studies (Mannion et al. 2013). Fossil taxa from South and East Asia, for example, remain less explored and studied compared to taxa in Europe and Central Asia that are often subject to more comprehensive studies. Comprehensive sampling of fossil taxa, as well as integrative studies using ancient DNA and extant taxa, is needed for a more robust conclusion on the phylogenetic relationships within Spalacidae.

Influences of the global environment on the evolution of Spalacidae

Spalacidae represents the earliest split in the muroid superfamily (excluding perhaps the Platacanthomyinae; Steppan et al. 2004). Compared to other families (including Muridae, Sciuridae, and Cricetidae) that diverged in the same period, Spalacidae has not featured high species diversity throughout its evolutionary history. The ancient split but low diversity of Spalacidae can probably be attributed to its unique lifestyle: species in the family are highly specialised for subterranean habitats, which provide protection from predation and environmental fluctuation above the ground (Burda et al. 2007). However, subterranean niches are highly challenging, due to the absence of most sensory cues, low food supply, high energetic costs of digging, and stressful microenvironmental conditions (Nevo 1979). Specialised morphological construction for digging is likely to have limited the dispersal of Spalacidae. The past and current distribution of Spalacidae overlaps regions where climate change was not extreme in Asia, south-eastern Europe, and Africa (Sandel et al. 2011). For example, considering the annual temperature in the last glacial maximum, the distribution of Spalacidae largely overlaps with regions of temperate climate (see Fig. 4b). Together with the relatively stable underground environmental conditions, a temperate climate is likely to have been a driver of slow differentiation and dispersal in Spalacidae. This is largely different from the patterns seen in lagomorphs and squirrels of large-scale range expansion or contraction in the Late Quaternary (Ge et al. 2013, Lv et al. 2013, Ge et al. 2014).

Rhizomyinae represents the basal branches of Spalacidae, and the diversity of Rhizomyinae reached a maximum of nine genera distributed in Eurasia and Africa in the Late Miocene (Fig. 2). It also showed the largest geographical range when compared with the other two subfamilies. Deciduous forests and bush woods, abundant in the temperate zone of Eurasia (López-Antoñanzas et al. 2015), appear to have provided habitats for the diversification of Rhizomyinae in this region. After the Middle Miocene, the diversity of genera reached a maximum. Fossil Rhizomyinae in northern China indicate a range expansion in this period. Continuous cooling and drying in Eurasia caused the extinction of several genera in Rhizomyinae and also led to the origination of new taxa adapted to new environments. Most species in Rhizomyinae showed preferences for bamboo forests (Xu 1984), which were mainly confined to tropical and subtropical regions as a result of climate change. The diversity and distribution of Rhizomyinae decreased sharply after the Late Miocene, prominently in Central Asia (Figs 2 and 3). This is likely to have resulted from dramatic changes in the landscape and accelerated aridification in this region. In the Quaternary, the complex terrain to the south-east of the Tibetan Plateau and the Hengduan Mountains is widely regarded as an important Ice Age refugium for animals and plants (Chen et al. 2010, Zhang et al. 2010). During that period, forests in the south-eastern part of the Tibetan Plateau are likely to have sheltered Rhizomyinae.

Species within Tachyoryctoidinae display strong specialisations for digging, particularly in the *Pararhizomys* and *Pseudorhizomys* genera (Wang & Qiu 2018). Diversification among species within this group suggests environmental heterogeneity in the regions where they were found. The uplift of the Tibetan Plateau and strengthening of Asian monsoons accelerated the expansion of arid or semi-arid grassland in central and northern China, inducing speciation within Tachyoryctoidinae.

Myospalacinae exhibit fossorial traits in their earliest fossil records (Zheng et al. 2004). Myospalacinae featured rapid differentiation and a large increase in the number of genera after the Late Miocene (Fig. 2a). The Tibetan Plateau uplift greatly affected the evolution of plateau species (Chen et al. 2010, Liu et al. 2012, Zhou et al. 2012), and habitat heterogeneity in this region was also probably a direct cause of the accelerated formation of new species (Zhou et al. 2012). Many studies have shown that the influence of the Tibetan Plateau uplift on climate and environmental changes was key to species differentiation (Liu et al. 2006, 2012, Zhou et al. 2012). Myospalacinae was no exception, and these changes caused rapid differentiation of this subfamily. The Quaternary Period was colder than the Pliocene and was characterised by frequent glacial and interglacial periods (Shi 1998). Many species of Myospalacinae in the central and north-eastern parts of the Loess Plateau went extinct, and only a few taxa survived after the Pleistocene. However, slight northward expansion of Myospalacinae occurred since the Pleistocene (Fig. 2e). Maximum entropy niche-based modelling suggests that suitable habitat for plateau zokor will have increased by 6% in 2050 (Su et al. 2015). This is likely to be due to northward expansion of their favourite food plants that are dominated by alpine and subalpine forbs, such as *Potentilla anserina, Potentilla nivea*, *Saussurea likiangensis*, *Saussurea superba*, *Bistorta vivipara*, and *Thalictrum alpinum* (Wang et al. 2000, Cui et al. 2014). Several of these plant taxa showed rapid species radiation and range expansion after the Pliocene (Wang et al. 2009, Paule 2010, Kendrick et al. 2013).

According to fossil records and their current distribution, Spalacinae has not shown high diversity and expansion in their evolutionary history. Only a slight northward expansion of Spalacinae is evidenced by fossil occurrences and their current distribution (Fig 2c–e). Moreover, the climate has been relatively stable in south-eastern Europe and the eastern Mediterranean area, where Spalacinae has been distributed since their origination. According to data on plant assemblages from south-eastern Europe, it was warm and humid in the Early Miocene, and major vegetation changes occurred after 14 Ma, with slight cooling and some records of drying (Ivanov et al. 2011). These slight climate changes are unlikely to have greatly influenced the evolutionary dynamics of this subfamily. Only one or two genera have been present in each epoch since origination. However, climate oscillations probably did affect the speciation and genetic diversity of *Spalax* and *Nannospalax*, two extant genera of Spalacinae (Hadid et al. 2012).

CONCLUSION

It can be inferred from the fossil record and the reconstructed phylogeny based on molecular data that Spalacidae originated in South and East Asia in the Late Oligocene. Rhizomyinae spread to Africa via the land bridge between Eurasia and Afro-Arabia over multiple waves of expansion, which eventually led to independent evolution in Eurasia and Africa. It suffered large-scale range contraction in the Late Miocene. Tachyoryctoidinae was prosperous from the Late Oligocene in Central and East Asia, before suffering extinction in the Late Miocene. Spalacinae originally lived in south-eastern Europe and the eastern Mediterranean area, and did not spread to East Africa until the Pleistocene. Myospalacinae originated in China and showed slight northward expansion since the Pleistocene. The relatively moderate geographical changes in the evolutionary history of Spalacidae are likely to be a function of the family's strictly subterranean lifestyle, which slowed and limited their long-distance migration.

ACKNOWLEDGEMENTS

We deeply appreciate the contributors to the Paleobiology Database and GenBank for making scientific data publicly available. We thank Prof. Lawrence Flynn for sending important references and Prof. Zhaoqun Zhang for his comments on this manuscript. We appreciate two anonymous reviewers and Drs Danilo Russo and Nancy Jennings for providing their valuable comments to improve this manuscript. Deyan Ge is sponsored by the Newton Advanced Fellowship of the Royal Society of the United Kingdom (NA150142). Our research was sponsored by the Natural Science Foundation of China (Nos. 30770256, 31572293, and 31872958) and via a grant (Y229YX5105) from the Key Laboratory of Zoological Systematics and Evolution of the Chinese Academy of Sciences.

REFERENCES

Bobe R, Behrensmeyer AK (2004) The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeography Palaeoclimatology Palaeoecology* 207: 399–420.

Bonnefille R (2010) Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change* 72: 390–411.

Burda H, Sumbera R, Begall S (2007) Microclimate in burrows of subterranean rodents - revisited. In: Begall S, Burda H, Schleich CE (eds) *Subterranean Rodents,* 21–33. Springer, Berlin, Heidelberg, Germany.

Chaline J, Mein P, Petter F (1977) Les grandes lignes d'une classification evolutive des Muroidea. *Mammalia* 41: 245–252.

Chen WC, Liu SY, Liu Y, Hao H, Zeng B (2010) Phylogeography of the large white-bellied rat *Niviventer excelsior* suggests the influence of Pleistocene glaciations in the Hengduan Mountains. *Zoological Science* 27: 487–493.

Cui XF, Xie JX, Zhang SD, Lin GH, Zhang TZ, Su JP (2014) Relationship between overwintering preference and nutritional content of the foods of plateau zokor (*Eospalax baileyi*). *Acta Theriologica Sinica* 34: 340–347.

De Bruijn H, Hussain ST, Leinders JJM (1981) Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. *Proceeding of the Koninklijke Nederlandse Akademie Wetenschappen Series B* 84: 71–79.

De Bruijn H, Marković Z, Wessels W (2013) Late Oligocene rodents from Banovići (Bosnia and Herzegovina). *Palaeodiversity* 6: 63–105.

De Bruijn H, Bosma AA, Wessels W (2015) Are the Rhizomyinae and the Spalacinae closely related? Contradistinctive conclusions between genetics and palaeontology. *Palaeobiodiversity and Palaeoenvironments* 95: 257–269.

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology Evolution* 29: 1969–1973.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.

Fabre PH, Hautier L, Dimitrov D, Douzery EJ (2012) A glimpse on the pattern of rodent diversification: a phylogenetic approach. *BMC Evolutionary Biology* 12: 88.

Flynn LJ (1982) A revision of fossil rhizomyid rodents from northern India and their correlation to a rhizomyid biochronology of Pakistan. *Geobios* 15: 583–588.

Flynn LJ (1985) Evolutionary patterns and rates in Siwalik Rhizomyidae (Rodentia). *Acta Zoologica Fennica* 170: 141–144.

Flynn LJ (2009) The antiquity of Rhizomys and independent acquisition of fossorial traits in subterranean muroids. *Bulletin of American Museum of Natural History* 331: 128–156.

Flynn LJ, Jacobs LL, Lindsay EH (1985) Problems in muroid phylogeny: relationship to other rodents and origin of major groups. In: Luckett PEA (ed.) *Evolutionary Relationships Among Rodents. A Multidisciplinary Analysis*, 589–616. NATO ASI Serie A: Life Sciences. Springer Science and Business Media, New York, USA.

Flynn LJ, Lindsay EH, Pilbeam D, Raza SM, Morgan ME, Barry JC, et al. (2013) The Siwaliks and Neogene evolutionary biology in South Asia. In: Wang XM, Flynn LJ, Fortelius M (eds) *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*, 353–372. Columbia University Press, New York, USA.

Ge DY, Wen ZX, Xia L, Zhang ZQ, Erbajeva M, Huang CM, Yang QS (2013) Evolutionary history of lagomorphs in response to global environmental change. *PLoS ONE* 8: e59668.

Ge DY, Liu X, Lv XF, Zhang ZQ, Xia L, Yang QS (2014) Historical biogeography and body form evolution of ground squirrels (Sciuridae: Xerinae). *Evolutionary Biology* 41: 99–114.

Goswami A, Prasad GV, Upchurch P, Boyer DM, Seiffert ER, Verma O, Gheerbrant E, Flynn JJ (2011) A radiation of arboreal basal eutherian mammals beginning in the late Cretaceous of India. *Proceedings of the National Academy of Sciences of the United States of America* 108: 16333–16338.

Hadid Y, Nemeth A, Snir S, Pavlicek T, Csorba G, Kazmer M, et al. (2012) Is evolution of blind mole rats determined by climate oscillations? *PLoS ONE* 7: e30043.

Hedges SB, Marin J, Suleski M, Paymer M, Kumar S (2015) Tree of life reveals clock-like speciation and diversification. *Molecular Biology and Evolution* 32: 835–845.

Hewitt G (2000) The genetic legacy of the Quaternary ice ages. *Nature* 405: 907–913.

Hewitt CL, Willing J, Bauckham A, Cassidy AM, Cox CM (2004) New Zealand marine biosecurity: delivering outcomes in a fluid environment. *New Zealand Journal of Marine and Freshwater Research* 38: 429–438.

Huelsenbeck JP, Ronquist F (2001) Mrbayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.

Hugueney M, Mein P (1993) A comment on the earliest Spalacinae (Rodentia, Muroidea). *Journal of Mammalian Evolution* 1: 215–223.

Ivanov D, Utescher T, Mosbrugger V, Syabryaj S, Djordjevic-Milutinovic D, Molchanoff S (2011) Miocene vegetation and climate dynamics in eastern and central Paratethys (Southeastern Europe). *Palaeogeography Palaeoclimatology Palaeoecology* 304: 262–275.

Jansa SA, Weksler M (2004) Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP gene sequences. *Molecular Phylogenetics Evolution* 31: 256–276.

Jansa SA, Giarla TC, Lim BK (2009) The phylogenetic position of the rodent genus *Typhlomys* and the geographic origin of Muroidea. *Journal of Mammalogy* 90: 1083–1094.

Ji Q, Luo ZX, Yuan CX, Wible JR, Zhang JP, Georgi JA (2002) The earliest known eutherian mammal. *Nature* 416: 816–822.

Kendrick LM, Geraldine AA, Richard H, Laurie M (2013) Phylogeographical patterns in the widespread arctic—alpine plant *Bistorta vivipara* (Polygonaceae) with emphasis on western North America. *Journal of Biogeography* 40: 845–856.

Kordikova EG, De Bruijn H (2001) Early Miocene rodents from the Aktau Mountains (South-Eastern Kazakhstan). *Senkenbergiana Lethaea* 81: 391–405.

Kryštufek B, Griffiths HI (2002) Species richness and rarity in European rodents. *Ecography* 25: 120–128.

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34: 772–773.

Li Q (2010) Pararhizomys (Rodentia, Mammalia) from the Late Miocene of Baogeda Ula, central Nei Mongol. *Vertebrata Palasiatica* 48: 48–62.

Lin GH, Wang K, Deng XG, Nevo E, Zhao F, Su JP, Guo SC, Zhang TZ, Zhao H (2014) Transcriptome sequencing and phylogenomic resolution within Spalacidae (Rodentia). *BMC Genomics* 15: 32.

Lindsay EH (1996) A new eumyarionine cricetid from Pakistan. *Acta Zoologica Cracoviensia* 39: 279–288.

Lindsay EH, Flynn LJ, Cheema IU, Barry JC, Downing K, Rajpar AR, Raza SM (2005) Will Downs and the Zinda Pir Dome. *Palaeontologia Electronica* 8: 1–19.

Liu JQ, Wang YJ, Wang AL, Hideaki O, Abbott RJ (2006) Radiation and diversification within the Ligularia-Cremanthodium-Parasenecio complex (Asteraceae) triggered by uplift of the Qinghai-Tibetan Plateau. *Molecular Phylogenetics Evolution* 38: 31–49.

Liu M, Qu JP, Yang M, Wang ZL, Wang YL, Zhang YM, Zhang ZB (2012) Effects of quinestrol and levonorgestrel on populations of plateau pikas, *Ochotona curzoniae*, in the Qinghai-Tibetan Plateau. *Pest Management Science* 68: 592–601.

López-Antoñanzas R, Knoll F (2010) The oldest known Massoutiera (Rodentia: Ctenodactylinae). *Mammalia* 74: 461–464.

López-Antoñanzas R, Sen S, Koufos GD (2005) A ctenodactylid rodent (Mammalia: Rodentia) from the Middle Miocene of Chios Island (Greece). *Geobios* 38: 113–126.

López-Antoñanzas R, Flynn LJ, Knoll F (2013) A comprehensive phylogeny of extinct and extant Rhizomyinae (Rodentia): evidence for multiple intercontinental dispersals. *Cladistics* 29: 247–273.

López-Antoñanzas R, Knoll F, Wan S, Flynn LJ (2015) Causal evidence between monsoon and evolution of rhizomyine rodents. *Scientific Reports* 5: 9008.

Luo ZX, Ji Q, Wible JR, Yuan CX (2003) An early cretaceous tribosphenic mammal and metatherian evolution. *Science* 302: 1934–1940.

Lv XF, Ge DY, Xia L, Zhang ZQ, Li S, Yang QS (2013) The evolution and paleobiogeography of flying squirrels (Sciuridae, Pteromyini) in response to global environmental change. *Evolutionary Biology* 40: 117–132.

Ma YZ, Li JJ, Fang XM (1998) Pollen assemblage in 30.6-5.0 Ma redbeds of Linxia region and climate evolution. *Chinese Science Bulletin* 43: 301–304.

Mannion PD, Benson RBJ, Butler RJ (2013) Vertebrate palaeobiodiversity patterns and the impact of sampling bias. *Palaeogeography Palaeoclimatology Palaeoecology* 372: 1–4.

McKenna MC, Bell SK (1997) *Classification of Mammals Above the Species Level*. Columbia University Press, New York, USA.

Meseguer AS, Lobo JM, Ree R, Beerling DJ, Sanmartín I (2015) Integrating fossils, phylogenies, and niche models into biogeography to reveal ancient evolutionary history: the case of *Hypericum* (Hypericaceae). *Systematic Biology* 64: 215–232.

Mihlbachler MC, Rivals F, Solounias N, Semprebon GM (2011) Dietary change and evolution of horses in North America. *Science* 331: 1178–1181.

Musser GG, Carleton MD (2005) Superfamily Muroidea. In: Wilson DE, Reeder M (eds) *Mammal Species of the World, a Taxonomic and Geographic Reference*, 894–1531. Johns Hopkins University Press, Baltimore, Maryland, USA.

Nauheimer L, Metzler D, Renner SS (2012) Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* 195: 938–950.

Nevo E (1979) Adaptive convergence and divergence of subterranean mammals. *Annual Review of Ecology and Systematics* 10: 269–308.

Nevo E (1999) *Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Global Convergence*. Oxford University Press, Oxford, UK.

Norris RW (2017) Family Spalacidae. In: Wilson DE, Lacher TE, Mittermeier RA (eds) *Handbook of the Mammals of the World, Vol 7, Rodents II*, 108–142. Lynx Edicions, Barcelona, Spain.

Norris RW, Zhou K, Zhou C, Yang G, Kilpatrick CW, Honeycutt RL (2004) The phylogenetic position of the zokors (Myospalacinae) and comments on the families of muroids (Rodentia). *Molecular Phylogenetics and Evolution* 31: 972–978.

Outlaw DC, Voelker G (2008) Pliocene climatic change in insular Southeast Asia as an engine of diversification in *Ficedula* flycatchers. *Journal of Biogeography* 35: 739–752.

Pagani M, Freeman KH, Arthur MA (1999) Late Miocene atmospheric CO_2 concentrations and the expansion of C_4 grasses. *Science* 285: 876–879.

Paule J (2010) *Evolutionary patterns and processes in the genus* Potentilla *L. (Rosaceae)*. PhD thesis, Ruperto-Carola University of Heidelberg, Germany.

Rambaut A (2018) *FigTree v1.4.4*. http://tree.bio.ed.ac.uk/software/figtree/.

Rambaut A, Drummond AJ (2007) *Tracer version 1.4.1*. http://beast.bio.edsac.uk/Tracer.

Rambaut A, Drummond AJ (2008) *TreeAnnotator 1.5.4*. http://beast.bio.ed.ac.uk.

Rambaut A, Drummond AJ (2010) *LogCombiner v1. 5.4 MCMC Output Combiner*. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, UK.

Rögl F (1999) Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography. *Geologica Carpathica* 50: 339–349.

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.

Sandel B, Arge L, Dalsgaard B, Davies RG, Gaston KJ, Sutherland WJ, Svenning JC (2011) The influence of late Quaternary climate-change velocity on species endemism. *Science* 334: 660–664.

Savic I, Nevo E (1990) The Spalacidae: evolutionary history, speciation and population biology. *Progress in Clinical and Biological Research* 335: 129–153.

Şen S, Sarıca N (2011) Middle-Late Miocene Spalacidae (Mammalia) from western Anatolia, and the phylogeny of the family. *Yerbilimleri* 32: 21–50.

Shi YF (1998) *Uplift and Environmental Changes of Qinghai-Xizang (Tibetan) Plateau in the Late Cenozoic*. Guangdong Science & Technology Press, Guangzhou, China.

Steppan SJ, Schenk JJ (2017) Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. *PLoS ONE* 12: e0183070.

Steppan SJ, Adkins RM, Anderson J (2004) Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. *Systematic Biology* 53: 533–553.

Strömberg CAE (2011) Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences* 39: 517–544.

Su JH, Aryal A, Nan Z (2015) Climate change-induced range expansion of a subterranean rodent: implications for rangeland management in Qinghai-Tibetan Plateau. *PLoS ONE* 10: e0138969.

Šumbera R, Krásová J, Lavrenchenko LA, Mengistu S, Bekele A, Mikula O, Bryja J (2018) Ethiopian highlands as a cradle of the African fossorial root-rats (genus *Tachyoryctes*), the genetic evidence. *Molecular Phylogenetics and Evolution* 126: 105–115.

Teilhard de Chardin P (1926) Descriptions des Mammifères tertiaires de Chine et de Mongolie. *Annales de Paléontologie* 15: 1–52.

Topachevskiy V, Nesin V, Topachevskiy I (1998) Biozonal microtheriological scheme (stratigraphic distribution of small mammals–Insectivora, Lagomorpha, Rodentia) of Neogene of the northern part of Eastern Paratethys. *Vestnik Zoologii* 32: 76–87.

Trofimov BA, Szalay FS (1994) New cretaceous marsupial from Mongolia and the early radiation of Metatheria. *Proceedings of the National Academy of Sciences of the United States of America* 91: 12569–12573.

Wang BY, Qiu ZX (2012) *Tachyoryctoides* (Muroidea, Rodentia) fossils from early Miocene of Lanzhou Basin, Gansu Province, China. *Swiss Journal of Palaeontology* 131: 107–126.

Wang BY, Qiu ZX (2018) *Late Miocene Pararhizomyines from Linxia Basin of Gansu, China*. Palaeontologia Sinica 31, Chinese Science Press, Beijing, China.

Wang QY, Zhang YM, Wei WH, Bian JH (2000) Food habit of the Plateau zokor. *Acta Theriologica Sinica* 20: 193–199.

Wang YJ, Susanna A, Von Raab-Straube E, Milne R, Liu JQ (2009) Island-like radiation of Saussurea (Asteraceae: Cardueae) triggered by uplifts of the Qinghai-Tibetan Plateau. *Biological Journal of the Linnean Society* 97: 893–903.

Wessels W (2009) Miocene rodent evolution and migration: Muroidea from Pakistan, Turkey, and northern Africa. *Geologica Ultraiectina* 307: 1–290.

Wessels W, De Bruijn H (2001) Rhizomyidae from the Lower Manchar Formation (Miocene, Pakistan). *Annals of Carnegie Museum* 70: 143–168.

Xu LH (1984) Studies on the biology of the hoary bamboo rat (*Rhizomys pruinosus* Blyth). *Acta Theriologica Sinica* 4: 99–105.

Yu Y, Harris AJ, He XJ (2010) S-DIVA (statistical dispersal–vicariance analysis): a tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution* 56: 848–850.

Yu Y, Harris AJ, Blair C, He XJ (2015) RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. *Molecular Phylogenetics and Evolution* 87: 46–49.

Zhang ZQ, Flynn LJ, Qiu ZD (2005) New materials of *Pararhizomys* from northern China. *Palaeontologia Electronica* 8: 1–9.

Zhang JX, Yan XD, Shi JF, Gong QY, Weng XC, Liu YJ (2010) Structural modifications of the brain in acclimatization to high-altitude. *PLoS ONE* 5: e11449.

Zheng SH (1994) Classification and evolution of the Siphneidae. *National Science Museum Monographs* 8: 57–76.

Zheng SH, Zhang ZQ, Cui N (2004) On some species of *Prosiphneus* (Siphneidae, Rodentia) and the origin of Siphneidae. *Vertebrata Palasiatica* 42: 297–315.

Zhou XY (1988) The Pliocene micromammalian fauna from Jingle, Shanxi, a discussion of the age of Jingle Red Clay. *Vertebrata Palasiatica* 26: 181–197.

Zhou WW, Wen Y, Fu JZ, Xu YB, Jin JQ, Ding L, Min MS, Che J, Zhang YP (2012) Speciation in the *Rana chensinensis* species complex and its relationship to the uplift of the Qinghai-Tibetan Plateau. *Molecular Ecology* 21: 960–973.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Summary of the DNA data sets used in the analyses.

Appendix S2. Fossil occurrences of Spalacidae compiled from data bases and original references.

Appendix S3. Detailed information on scientific literature used for the fossils of Spalacidae listed in Appendix S2.

Appendix S4. Phylogeny of Spalacidae inferred from the concatenated data sets of six mitochondrial DNA fragments in Bayesian inferences.