

# Are the Rhizomyinae and the Spalacinae closely related? Contradistinctive conclusions between genetics and palaeontology

Hans de Bruijn<sup>1</sup> · Anneke A. Bosma<sup>1</sup> · Wilma Wessels<sup>1</sup>

Received: 18 November 2014 / Revised: 12 February 2015 / Accepted: 15 April 2015 / Published online: 5 July 2015

© Senckenberg Gesellschaft für Naturforschung and Springer-Verlag Berlin Heidelberg 2015. This article is published with open access at Springerlink.com

**Abstract** The reconstruction of the evolutionary history of the Rhizomyinae and the Spalacinae based on the fossil record strongly suggests that these do not share the same murid ancestor and developed separately since the early Oligocene. This conclusion is supported by the difference in evolutionary dynamics between these groups during the Miocene and Pliocene. Molecular genetic studies of extant representatives of the Rhizomyinae, Spalacinae and Myospalacinae, however, suggest that these subfamilies share similarities that distinguish them from all other Muridae. As a result, geneticists unite these subfamilies into the family Spalacidae and consider the Spalacidae and the Muridae to be sister lineages. Until the conflict between the two disciplines is resolved we prefer to maintain the Rhizomyinae and the Spalacinae as two subfamilies within the family Muridae (superfamily Muroidea).

**Keywords** Oligocene · Miocene · Rodentia · Spalacinae · Rhizomyinae · Phylogeny

## Introduction

The aim of this review is to compare the results presented by palaeontologists and geneticists who investigated the phylogenetic relationship of the Rhizomyinae and the Spalacinae. In

---

This article is a contribution to the special issue “Old worlds, new ideas. A tribute to Albert van der Meulen”.

---

✉ Wilma Wessels  
w.wessels@uu.nl

<sup>1</sup> Department of Earth Sciences, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands

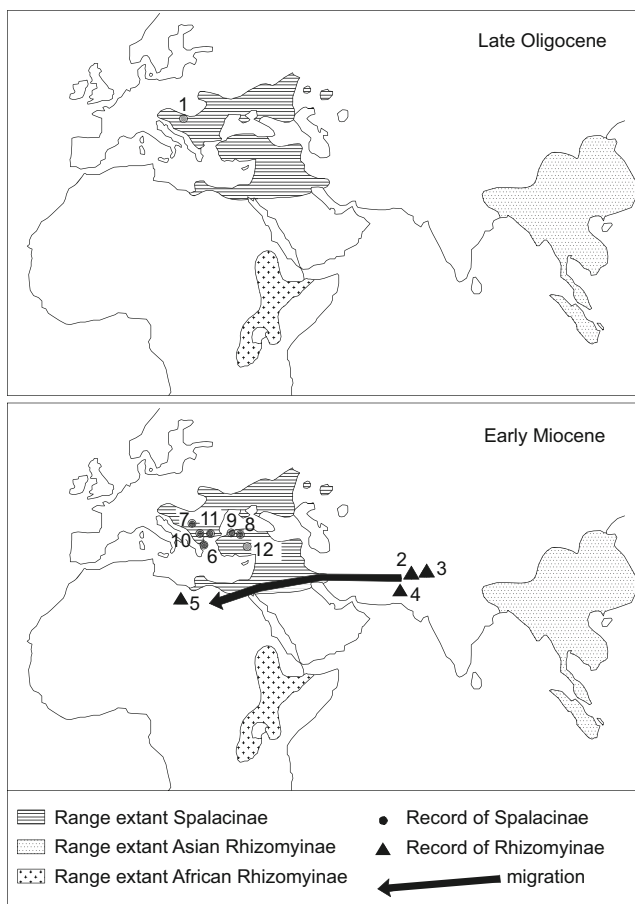
spite of the progress made in both disciplines during the last decade, conclusions remain conflicting.

In the classification of extant mammals by Wilson and Reeder (2005), the fossorial rodents Myospalacinae, Rhizomyinae (including the Tachyoryctinae) and Spalacinae are united into the family Spalacidae, separate from all other Muridae, thus returning to the classical arrangement of Thomas (1896). This view is supported by recent genetic studies which unanimously suggest that the Rhizomyinae and Spalacinae represent the same early branch of the Muridae (in the Muroidea).

The fossil record, however, suggests that the muroid ancestor of each of these subfamilies was different and that their ancestors adapted to a fossorial mode of life during a different period and in a different geographical area. Most palaeontologists therefore interpret the adaptations to a fossorial mode of life shared by these subfamilies to have developed independently (e.g. Flynn et al. 1984; Sen and Sarica 2011). The classification of McKenna and Bell (1997), which includes fossil genera, follows this view and considers the Myospalacinae, Rhizomyinae and Spalacinae to be separate subfamilies of the family Muridae. Other subfamilies of the Muridae containing fossorial species are the extant Arvicolinae and Sigmodontinae and the extinct Anomalomyinae and Tachyoryctoidinae (McKenna and Bell 1997).

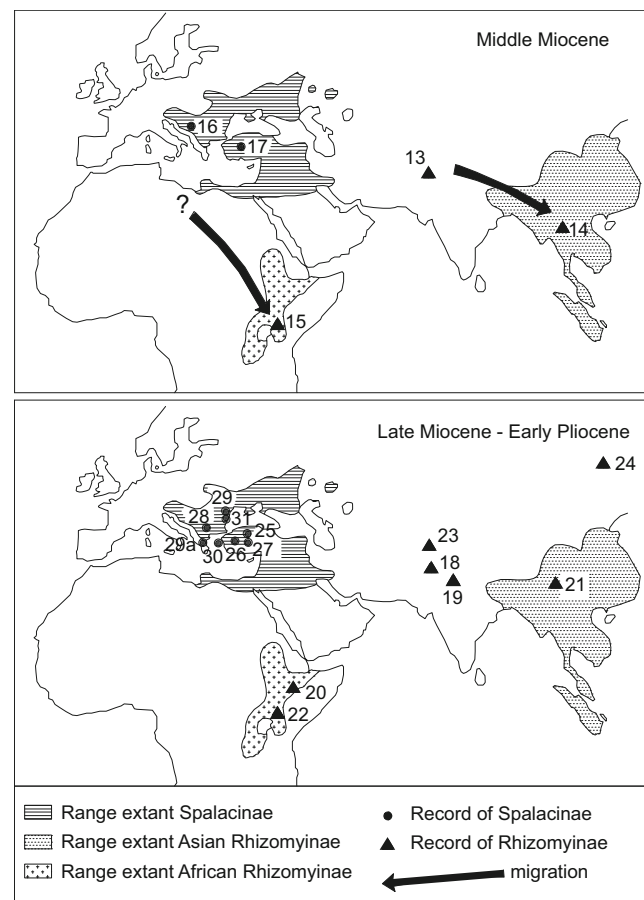
The geographic distribution of the extant Myospalacinae, Rhizomyinae and Spalacinae shows that each of the three subfamilies occupies its own geographical area, the Myospalacinae in eastern Asia (mainly China and Mongolia), the Rhizomyinae in south and southeastern Asia (*Rhizomys* and *Cannomys*) and in the eastern part of Africa (*Tachyoryctes*) and the Spalacinae in southeastern Europe and Anatolia (Figs. 1 and 2).

Here, we restrict the discussion to the Rhizomyinae and Spalacinae because these two subfamilies are represented by



**Fig. 1** Sketch maps of present day Eurasia and North Africa showing the major occurrences of the genera and species of the Rhizomyinae and Spalacinae during the late Oligocene and early Miocene. 1 *Vetuspalax progressus*, Banovići, Bosnia and Herzegovina (De Bruijn et al. 2013), 2 *Prokanisamys kowalskii*, Zinda Pir Dome, Pakistan (Lindsay 1996), 3 *Prokanisamys arifi*, Banda daud Shah, Pakistan (De Bruijn et al. 1981), 4 *Prokanisamys arifi* and *P. major*, Gaj River, Pakistan (Wessels and De Bruijn 2001), 5 *Prokanisamys* sp., Jebel Zelten, Libya (Wessels et al. 2003), 6 *Heramys eviensis*, Aliveri, Greece (Klein Hofmeijer and De Bruijn 1985), 7 *Heramys* sp., Sibnica, Serbia (Marković 2003), 8 *Debruijnina arpati*, Keseköy, northeast Anatolia (Ünay 1996), 9 *Debruijnina* sp., Söke, Dededag, western Anatolia (Sen and Sarica 2011), 10 *Pliospalax* sp., Karydia, northeastern Greece (Theocharopoulos 2000); 11 *Pliospalax* sp., Antonios, northeastern Greece (Vasileiadou and Koufos 2005), 12 *Pliospalax* sp., Çatalarkaç, central Anatolia (not published)

many living species, and both have an exceptionally good fossil record. An overview of the genera and species included in each of these subfamilies is given in Table 1. Author names are provided for in this table, but are omitted in the text. The taxonomic levels applied are family, subfamily, genus and species, following McKenna and Bell (1997) for the Muridae. We neither use tribe, subgenus nor subspecies. Therefore, the Rhizomyinae, as used here, includes the Asian as well as the African genera. Furthermore, we include *Sinapospalax* into *Pliospalax* because the differences in dental pattern of the cheek teeth of the species in these genera are very subtle (Figs. 3, 4, 5



**Fig. 2** Sketch maps of present day Eurasia and northern Africa showing the major occurrences of the genera and species of the Rhizomyinae and Spalacinae during the middle Miocene and late Miocene–early Pliocene. 13 *Kanisamys indicus* and *K. potwarensis*, Potwar plateau, Pakistan (Wood 1937; Flynn 1982), 14 *Prokanisamys benjavuni*, Li Basin, Thailand (Mein and Ginsburg 1985), 15 *Pronakalimys andrewsi*, Fort Ternan, Kenya (Tong and Jaeger 1992), 16 *Pliospalax* sp., Vraccvići, Serbia (Marković 2003), 17 *Pliospalax*, div. species, diverse localities, Anatolia (Ünay et al. 2003, Sen and Sarica 2011), 18 *Eicooryctes*, *Kanisamys*, *Miorhizomys*, *Protachyoryctes*, *Rhizomyiodes*, Potwar Plateau, Pakistan (Flynn 1982; López-Antoñanzas et al. 2012), 19 *Kanisamys*, *Miorhizomys*, *Protachyoryctes*, *Rhizomyiodes*, Haritalyangar and Bilaspur, India (Flynn 1982), 20 *Tachyoryctes makooka*, Digiba Dora, Ethiopia (Wesselman et al. 2009), 21 *Miorhizomys nagrii*, *M. tetrachorax*, Lufeng, China (Flynn and Qi 1982; Flynn 2009), 22 *Nakalimys lavocati*, Nakali, Kenya (Flynn and Sabatier 1984), 23 *Rhizomyiodes carbonelli*, Pul-e Charki, Afghanistan (Brandy 1979), *Rhizomyiodes mirzadi*, Bamian Basin, Afghanistan (Lang and Lavocat 1968), 24 *Brachyrhizomys shajius*, Yushe Basin, China (Flynn 1993), *Brachyrhizomys shansius*, Yushe Basin, China (Teilhard de Chardin 1942), 25 *Heramys anatolicus*, Sinap, Anatolia; *Pliospalax incliniformis*, Sinap, Anatolia, *Pliospalax sinapensis*, Sinap, Anatolia (Sarica and Sen 2003), 26 *Pliospalax complicatus*, Amasya, Anatolia (Sen and Sarica 2011), 27 *Pliospalax*, div. sp., div. localities Anatolia (Ünay 1996; Sen and Sarica 2011), 28 *Pliospalax macovei*, Beresti, Malusteni, Romania (Kormos 1932), 29 *Spalax odessanus*, Odessa, Ukraine (Topachevski 1969), 29a *Spalax odessanus*, Kara Burun, Greece (De Bruijn 1984), 30 *Pliospalax sotirisi*, Rhodes, Greece (De Bruijn et al. 1970), 31 *Pliospalax compositodontus*, Andriivka, Ukraine (Topachevski 1969)

and 6). *Eumyarion kowalskii*, a species which plays an important role in our discussion, has been transferred by

**Table 1** The genera and species of the Rhizomyinae and Spalacinae

Subfamily and genus	Species	Occurrences	Distribution
Spalacinae Gray, 1821			
<i>Spalax</i> Gldenstaedt, 1770 (including <i>Namospalax</i> Palmer, 1903)	<sup>a</sup> <i>Spalax microphthalmus</i> Gldenstaedt, 1770 At least 16 extant species	extant extant	Russia, Ukraine Balkan, Caucasus, Turkey, coastal area SE Mediterranean
<i>Spalax odessanus</i> Topachevski, 1969		Early Pliocene	Ukraine, Anatolia
<i>Pliospalax</i> Kormos, 1932 (Including <i>Sinospalax</i> Sarica and Sen, 2003)	<sup>a</sup> <i>Pliospalax macovei</i> (Simionescu, 1930) <i>Pliospalax compositodontus</i> Topachevski, 1969 <i>Pliospalax sotirisi</i> De Bruijn et al. 1970 <i>Pliospalax tourkobouniensis</i> De Bruijn and Van der Meulen, 1975 <i>Pliospalax canakkalensis</i> nay, 1978 <i>Pliospalax primitivus</i> nay, 1978 <i>Pliospalax marmarensis</i> nay, 1990 <i>Pliospalax incliniformis</i> (Sarica and Sen, 2003) <i>Pliospalax sinapensis</i> (Sarica and Sen, 2003) <i>Pliospalax berdikensis</i> (Sen and Sarica, 2011) <i>Pliospalax complicatus</i> Sen and Sarica, 2011	Pliocene Early Pliocene Late Miocene / Early Pliocene Early Pliocene Middle Miocene Middle Miocene Middle Miocene Late Miocene Late Miocene Middle Miocene Late Miocene / Early Pliocene	Rumania, Anatolia Ukraine Greece Greece Anatolia Anatolia Anatolia Anatolia Anatolia Anatolia Anatolia
<i>Heramys</i> Klein Hofmeijer and De Bruijn, 1985	<sup>a</sup> <i>Heramys eviensis</i> Klein Hofmeijer and De Bruijn, 1985 <i>Heramys anatolicus</i> Sarica and Sen, 2003 <sup>a</sup> <i>Debruijnia arpati</i> nay, 1996	Early Miocene Late Miocene Early Miocene	Greece Anatolia Anatolia
<i>Vetusspalax</i> De Bruijn, Markovi and Wessels, 2013	<sup>a</sup> <i>Vetusspalax progressus</i> De Bruijn, Markovi and Wessels, 2013	Late Oligocene	Bosnia and Herzegovina
Rhizomyinae Winge, 1887			
<i>Rhizomys</i> Gray, 1831	<sup>a</sup> <i>Rhizomys sinensis</i> Gray, 1831 3 extant species	extant extant	China China
<i>Tachyoryctes</i> Rppell, 1835	<sup>a</sup> <i>Tachyoryctes splendens</i> Rppell, 1835 13 extant species <i>Tachyoryctes pliocenicus</i> Sabatier, 1978 <i>Tachyoryctes konjiti</i> Sabatier, 1982 <i>Tachyoryctes makooka</i> Wesselman, Black and Asnake, 2009	extant extant Pliocene Pleistocene Late Miocene	Northeast Africa Northeast Africa Ethiopia Ethiopia Ethiopia
<i>Cannomys</i> Thomas, 1915	<sup>a</sup> <i>Cannomys badius</i> (Hodgson, 1841)	extant	SE Asia
<i>Protachyoryctes</i> Hinton, 1933	<sup>a</sup> <i>Protachyoryctes tatroti</i> Hinton, 1933	Late Miocene	India
<i>Kanisamys</i> Wood, 1937	<sup>a</sup> <i>Kanisamys indicus</i> Wood, 1937 <i>Kanisamys sivalensis</i> Wood, 1937 <i>Kanisamys nagrii</i> Prasad, 1968 <i>Kanisamys potwarensis</i> Flynn, 1982	Middle and Late Miocene Middle and Late Miocene Late Miocene Middle and Late Miocene	Pakistan, India India, Pakistan India, Pakistan India, Pakistan

**Table 1** (continued)

Subfamily and genus	Species	Occurrences	Distribution
<i>Brachyrhizomys</i> Teilhard de Chardin, 1942	<sup>a</sup> <i>Brachyrhizomys shansius</i> (Teilhard de Chardin, 1942)	Late Miocene / Early Pliocene	China
	<i>Brachyrhizomys shajius</i> Flynn, 1993	Late Miocene / Early Pliocene	China
	<i>Brachyrhizomys hehoensis</i> Zheng, 1980	Late Miocene / Early Pliocene	Tibet
	<i>Brachyrhizomys naquensis</i> Zheng, 1980	Late Miocene / Early Pliocene	Tibet
<i>Rhizomyides</i> Bohlin, 1946	<sup>a</sup> <i>Rhizomyides punjabiensis</i> (Colbert, 1933)	Late Miocene	India, Pakistan
	<i>Rhizomyides sivalensis</i> (Lydekker, 1884)	Late Miocene	India, Pakistan
	<i>Rhizomyides mirzadi</i> Lang and Lavocat, 1968	Late Miocene	Afghanistan
	<i>Rhizomyides saktiensis</i> Gupta, Verma and Tewari, 1978	Late Miocene	India
	<i>Rhizomyides carbonelli</i> Brandy, 1979	Late Miocene	Afghanistan
	<i>Rhizomyides platytomeus</i> Flynn, Heintz, Sen and Brunet, 1983	Late Miocene	Afghanistan
	<i>Rhizomyides pinjoricus</i> (Hinton, 1933)	Late Pliocene	India
<i>Prokanisamys</i> De Bruijn, Hussain and Leinders, 1981	<sup>a</sup> <i>Prokanisamys arifi</i> De Bruijn, Hussain and Leinders, 1981	Early and Middle Miocene	India, Pakistan
	<i>Prokanisamys benjavuni</i> (Mein and Ginsburg, 1985)	Early and Middle Miocene	Thailand, Pakistan
	<i>Prokanisamys kowalskii</i> (Lindsay, 1996)	Early Miocene	Pakistan
	<i>Prokanisamys major</i> Wessels and De Bruijn, 2001	Early and Middle Miocene	Pakistan
<i>Anepsirhizomys</i> Flynn, 1982	<sup>a</sup> <i>Anepsirhizomys opdykei</i> Flynn 1982	Pliocene	Pakistan
<i>Eicooryctes</i> Flynn, 1982	<sup>a</sup> <i>Eicooryctes kaulialensis</i> Flynn, 1982	Late Miocene	Pakistan
<i>Nakalimys</i> Flynn and Sabatier, 1984	<sup>a</sup> <i>Nakalimys lavocati</i> Flynn and Sabatier, 1984	Late Miocene	Kenya
<i>Pronakalimys</i> Tong and Jaeger, 1992	<sup>a</sup> <i>Pronakalimys andrewsi</i> Tong and Jaeger, 1992	Middle Miocene	Kenya
<i>Miorhizomys</i> Flynn, 2009	<sup>a</sup> <i>Miorhizomys nagrii</i> (Hinton, 1933)	Late Miocene / Early Pliocene	China, India, Pakistan
	<i>Miorhizomys pilgrimi</i> (Hinton, 1933)	Late Miocene / Early Pliocene	China, India, Pakistan
	<i>Miorhizomys blacki</i> (Flynn, 1982)	Late Miocene / Early Pliocene	China
	<i>Miorhizomys choristos</i> (Flynn, 1982)	Late Miocene	India, Pakistan
	<i>Miorhizomys micrus</i> (Flynn, 1982)	Late Miocene	India
	<i>Miorhizomys tetracharax</i> (Flynn, 1982)	Late Miocene	China, India, Pakistan
	<i>Miorhizomys harii</i> (Prasad, 1968)	Late Miocene / Early Pliocene	India

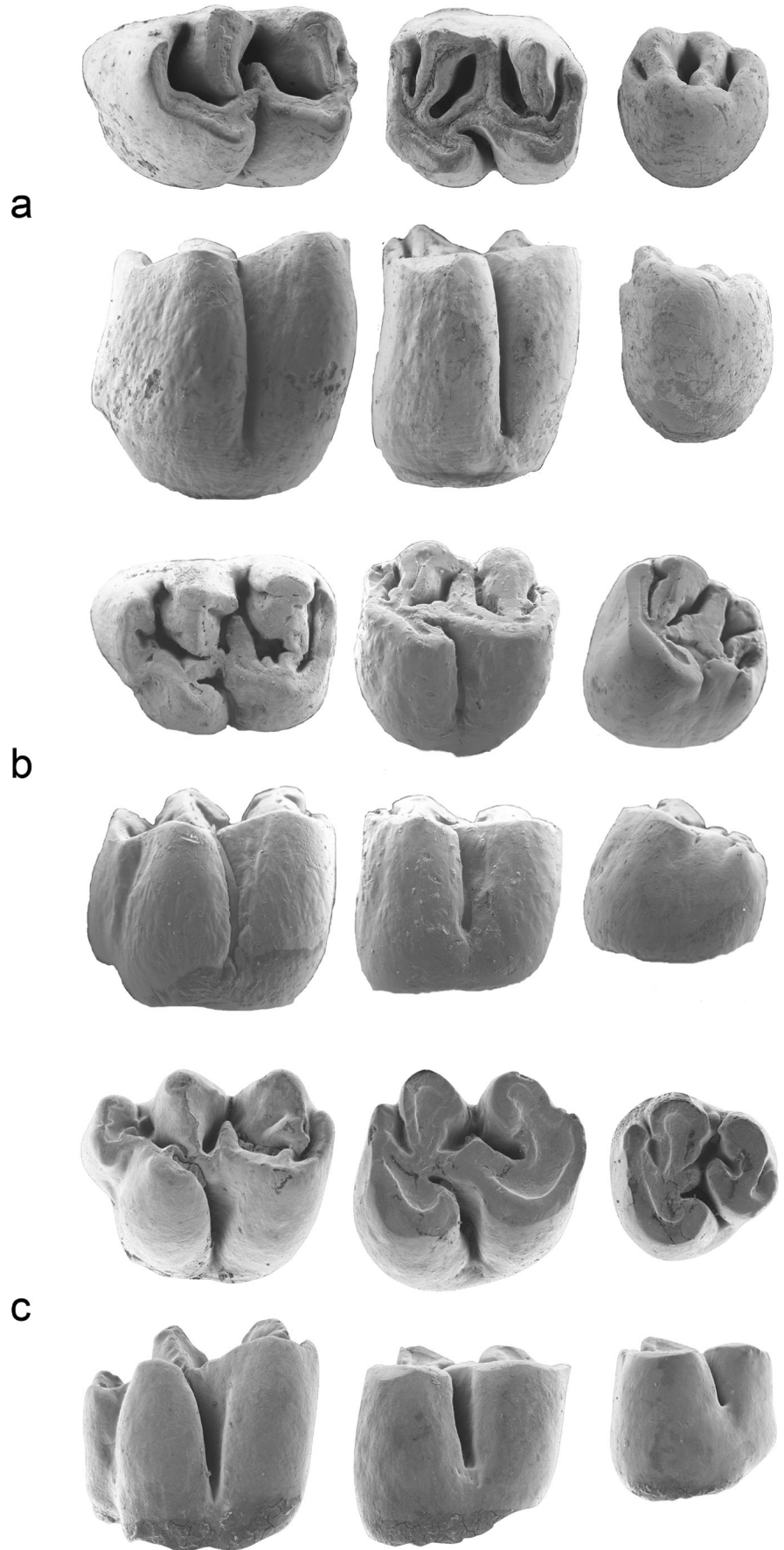
<sup>a</sup> Type species

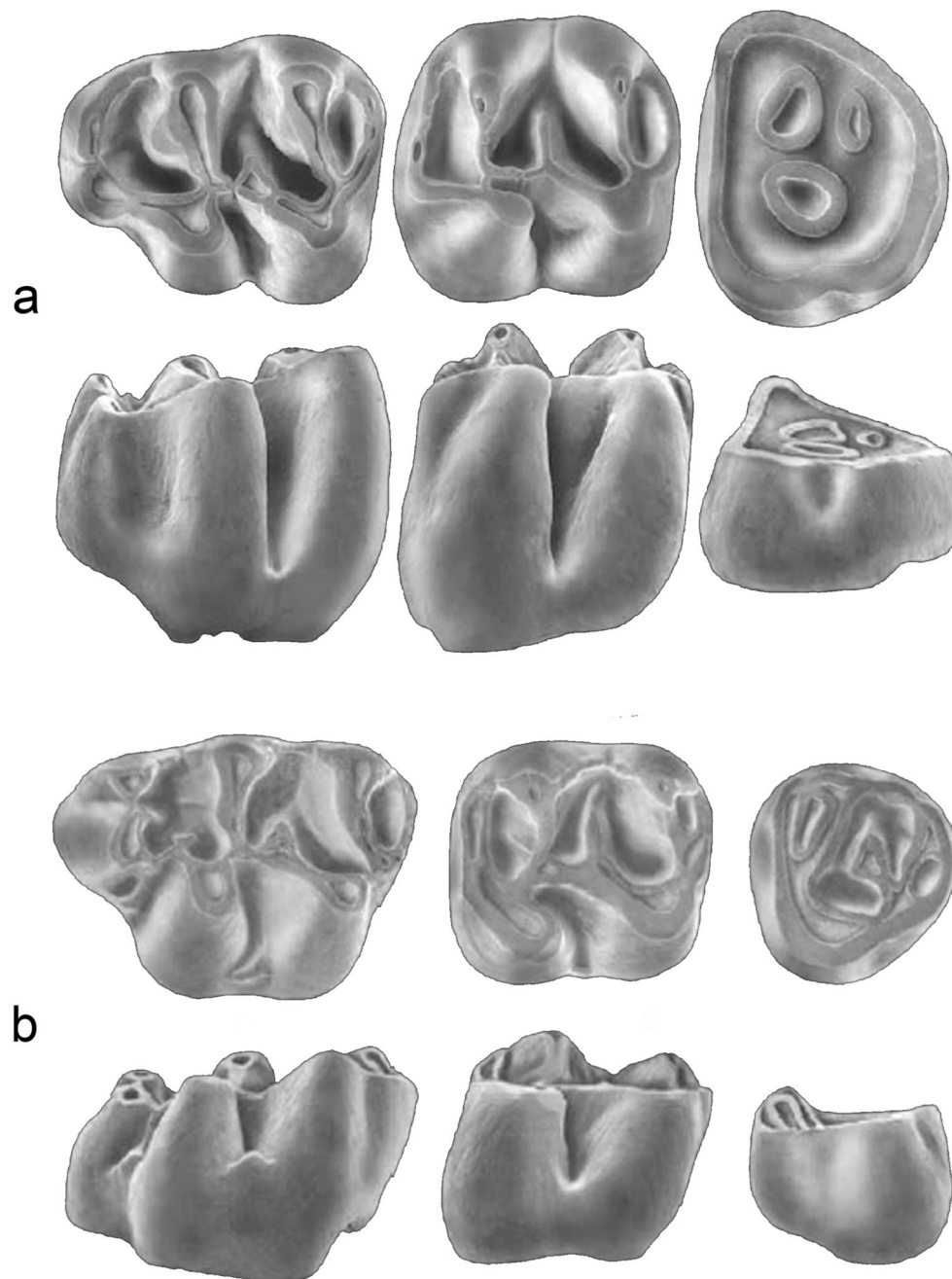
Wessels and De Bruijn (2001) to *Prokanisamys* because its cheek teeth lack the, for *Eumyarion* characteristic, strong anterior arm of the protocone in the M1 as well as the posterior arm of the hypoconid in the m1 (Figs. 4 and 6). Since this transfer has been ignored by some authors (e.g. Flynn et al. 2013) we explicitly state that we adhere to our earlier generic allocation. For the sake of comparison, the tooth rows are depicted as if they are of the same size (Figs. 3, 4, 5 and 6).

### Concise review of the molecular genetic studies

A number of molecular phylogenetic studies have been performed with the aim, among (many) other aims, of testing the hypothesis that the Rhizomyinae and the Spalacinae belong to the same early branch of the Muroidea. These studies are listed in Table 2. The results in general strongly indicate that the Rhizomyinae and the Spalacinae, together with the

**Fig. 3** Upper molars (M1, M2, M3), occlusal and lingual view. **a** *Heramys eviensis*, Aliveri, Greece (Klein Hofmeijer and De Bruijn 1985), **b** *Debruijnina arpati*, Keseköy, Anatolia (Ünay 1996), **c** *Vetusspalax progressus*, Banovići, Bosnia and Herzegovina (De Bruijn et al. 2013). The specimens are not to scale





**Fig. 4** Upper molars (M1, M2, M3), occlusal and lingual view. **a** *Kanisamys indicus*, Gaj River, Pakistan (Wessels and De Bruijn 2001), **b** *Prokanisamys arifi*, Gaj River, Pakistan (Wessels and De Bruijn 2001). The specimens are not to scale

Myospalacinae, form a separate clade within the Muroidea (Jansa and Weksler 2004; Norris et al. 2004; Blanga-Kanfi et al. 2009; Jansa et al. 2009; Gogolevskaya et al. 2010). Michaux et al. (2001), Norris et al. (2004) and Steppan et al. (2004), on the basis of their data, proposed placing the Rhizomyinae and the Spalacinae in a separate family, Spalacidae, leaving the family name Muridae to all other members of the superfamily Muroidea. The close relationship between the Myospalacinae and Rhizomyinae and the Spalacinae has been confirmed in a study by Lin et al. (2014)

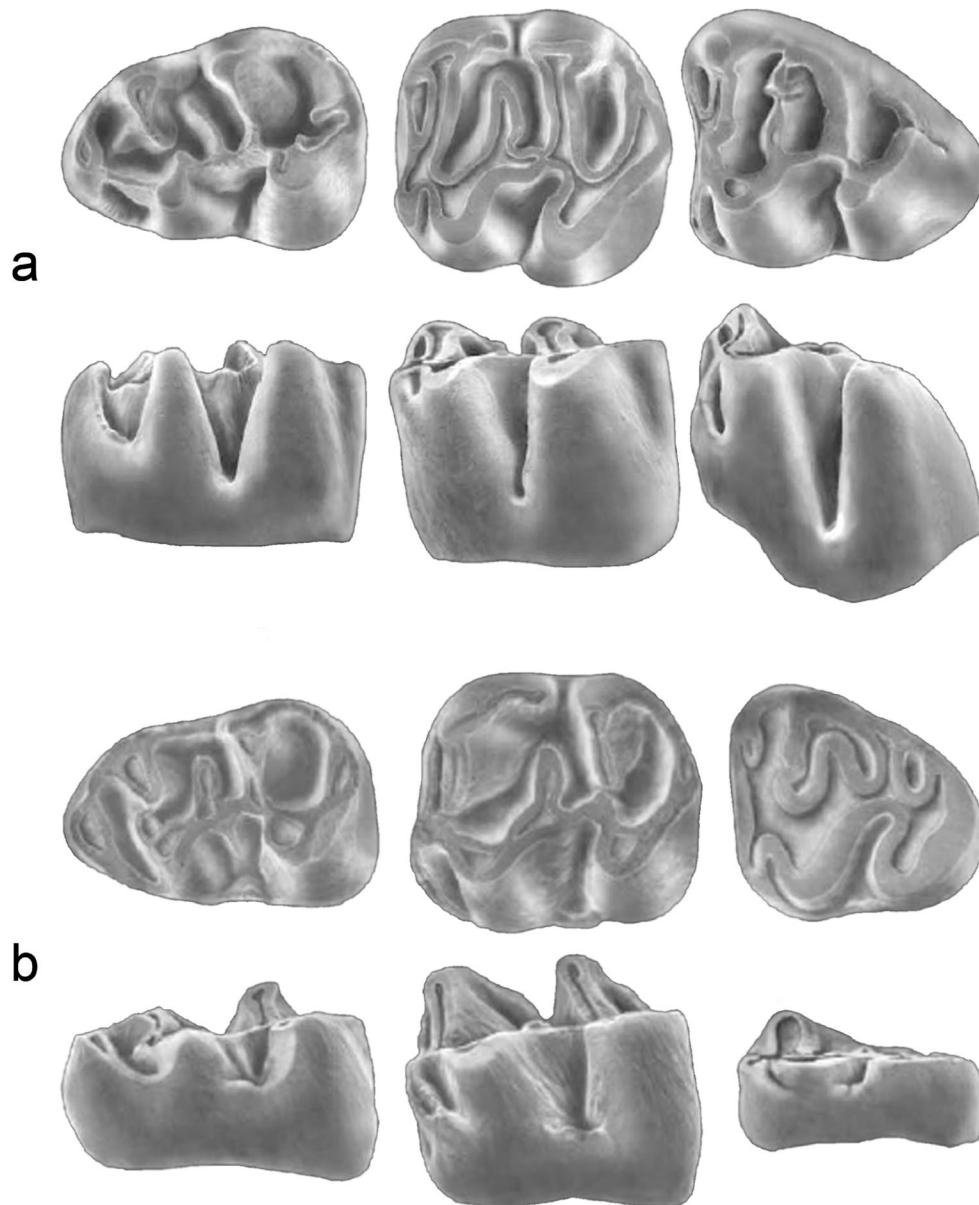
based on the results of transcriptome sequencing. Cytogenetic studies comparing chromosomes of species of the Rhizomyinae and the Spalacinae (e.g. by comparative painting) have not been performed.

#### Concise review of the fossil data

Most of the early fossil representatives of the Rhizomyinae and Spalacinae are known by dental remains only, so their life-style

**Fig. 5** Lower molars (m1, m2, m3), occlusal and labial view. **a** *Heramys eviensis*, Aliveri, Greece (Klein Hofmeijer and De Bruijn 1985), **b** *Debruijnia arpati*, Keseköy, Anatolia (Ünay 1996), **c** *Vetusspalax progressus*, Banovići, Bosnia and Herzegovina (De Bruijn et al. 2013). The specimens are not to scale





**Fig. 6** Lower molars (m1, m2, m3, occlusal and labial view. **a** *Kanisamys indicus* Gaj River, Pakistan (Wessels and De Bruijn 2001), **b** *Prokanisamys arifi* Gaj River, Pakistan (Wessels and De Bruijn 2001). The specimens are not to scale

has to be inferred from the teeth, which introduces uncertainty. The development of dental similarity in these subfamilies as an adaptation to a fossorial life-style makes it difficult to distinguish grades from clades: the occurrence of the same morphologies in taxa does not necessarily mean that they are closely related as these morphologies can be derived independently (Wood 1965).

#### The Spalacinae Gray, 1821

The origin, taxonomy and phylogeny of the Spalacinae have been discussed by many authors (e.g. Petter 1961; De Bruijn et al. 1970; Fejfar 1972; De Bruijn 1984; Klein Hofmeijer and De Bruijn 1985; De Bruijn and Saraç 1991; Huguency and Mein 1993; Ünay 1996; Sen and Sarica 2011). The genera

*Rhizospalax* (now in the Castoridae) and *Prospalax* (now in the Anomalomyinae) have in the past been considered to be Spalacinae. Fejfar (1972) suggested that the origin of the Anomalomyinae and Spalacinae was in the Tachyoryctoidinae, while others defended the view that the Anomalomyinae, the Tachyoryctoidinae and the Spalacinae are not closely related (Klein Hofmeijer and De Bruijn 1985; De Bruijn and Saraç 1991).

The first fossil true spalacine was recognised by Kormos in 1932—*Pliospalax macovei* from the Pliocene of Romania. A number of *Pliospalax* species of middle Miocene to late Pliocene age (Europe, Turkey and Ukraine) have been described since, with the first record of the subfamily pushed back in time by such new finds as *Heramys eviensis* (early



**Table 2** Molecular genetic studies analyzing phylogenetic relationships among Muroidea including Rhizomyinae and Spalacinae

Genetic marker(s) <sup>a</sup>	Species considered <sup>b</sup>	Reference
LCAT	<i>Rhizomys pruinosus</i> (R) <i>Nannospalax ehrenbergi</i> (S) <i>Nannospalax leucodon</i> (S)	Robinson et al. (1997)
LCAT	<i>Rhizomys pruinosus</i> (R) <i>Nannospalax ehrenbergi</i> (S) <i>Nannospalax leucodon</i> (S)	Michaux and Catzeflis (2000)
IRBP	<i>Rhizomys pruinosus</i> (R) <i>Spalax zemni</i> (S)	DeBry and Sagel (2001)
LCAT; vWF	<i>Rhizomys pruinosus</i> (R) <i>Tachyoryctes</i> sp. (R) <i>Nannospalax ehrenbergi</i> (S)	Michaux et al. (2001)
IRBP	<i>Rhizomys pruinosus</i> (R) <i>Tachyoryctes splendens</i> (R) <i>Spalax zemni</i> (S)	Jansa and Weksler (2004)
12S rRNA; cytochrome b	<i>Rhizomys pruinosus</i> (R) <i>Rhizomys sinensis</i> (R) <i>Nannospalax ehrenbergi</i> (S)	Norris et al. (2004)
GHR; BRCA1; RAG1 c-myc	<i>Rhizomys pruinosus</i> (R) <i>Tachyoryctes splendens</i> (R) <i>Spalax ehrenbergi</i> (S)	Steppan et al. (2004)
ADRA2B; CB1; GHR IRBP; RAG2; vWF	<i>Rhizomys pruinosus</i> (R) <i>Tachyoryctes</i> sp. (R) <i>Spalax ehrenbergi</i> (S) <i>Spalax zemni</i> (S)	Blanga-Kanfi et al. (2009)
IRBP; GHR	<i>Rhizomys pruinosus</i> (R) <i>Tachyoryctes splendens</i> (R) <i>Spalax zemni</i> (S) <i>Spalax ehrenbergi</i> (S)	Jansa et al. (2009)
B1 SINE; 4.5S <sub>1</sub> RNA	<i>Tachyoryctes splendens</i> (R); <i>Spalax microphthalmus</i> (S)	Gogolevskaya et al. (2010)

(R), Rhizomyinae; (S), Spalacinae

<sup>a</sup> Nuclear genes: ADRA2B, BRCA1, CB1, c-myc, GHR, IRBP, LCAT, RAG1/2 and vWF. Mitochondrial genes: 12S rRNA and cytochrome b. Other markers: 4.5S<sub>1</sub> RNA and B1 SINE. ADRA2B, Alpha 2B adrenergic receptor; BRCA1, breast cancer gene 1; CB1, cannabinoid receptor 1; GHR, growth hormone receptor; IRBP, interphotoreceptor retinoid binding protein; LCAT, lecithin cholesterol acyl transferase; RAG1, recombination activating gene 1; RAG2, recombination activating gene 2; rRNA, ribosomal RNA; SINE, short interspersed element; vWF, von Willebrand factor

<sup>b</sup> In all studies one individual per species was examined. These individuals are (probably) the same in Robinson et al. (1997), Michaux and Catzeflis (2000) and Michaux et al. (2001), and the same in Jansa and Weksler (2004), Steppan et al. (2004) and Jansa et al. (2009)

Miocene, MN4, Greece; Klein Hofmeijer and De Bruijn 1985), *Debruijnina arpati* (early Miocene, MN3, Anatolia; Ünay 1996) and *Vetuspalax progressus* (late Oligocene, MP30, Bosnia and Herzegovina; De Bruijn et al. 2013). The dentitions of these species share unmistakably spalacine characteristics, namely, (1) anterior wall of the protocone of the M1 being almost at right angles to the base of the crown; (2) fusion of the anterocone of the M1 into the anteroloph; (3) forward position of the metaconid of the m1 at the expense of

the anteroconid. *Heramys*, *Debruijnina* and *Vetuspalax* do not represent one evolutionary lineage because the older *Vetuspalax* shows more derived characteristics than the younger *Debruijnina* (Figs. 3, 4, and 5). This points to an early radiation of the Spalacinae in southeastern Europe and the eastern Mediterranean area during the Oligocene. The fossil and extant geographical ranges of the Spalacinae roughly overlap (Figs. 1, 2), suggesting that the earliest spalacines recognised were already fossorial rodents because these are

known to be limited in their dispersal abilities (Flynn 1982, 1990; Savič and Nevo 1990; Kryštufek and Griffiths 2002). The fossil record thus provides strong evidence that the Spalacinae developed a fossorial life-style much earlier than, and independently from, the Rhizomyinae.

#### The Rhizomyinae Winge, 1887

Hypothetically the earliest rhizomyine is supposed to have been a non-fossorial cricetine from the late Oligocene of southeast Asia (Wessels et al. 2003, 2008). *Prokanisamys kowalskii* from the earliest Miocene of Pakistan is the oldest record of the Rhizomyinae recognised. *Prokanisamys* has a wide geographical range in southeast Asia and reached North Africa during the early Miocene (Fig. 1; Wessels et al. 2003; Wessels 2009). Although the postcranial skeleton of *Prokanisamys* is not known, it is assumed that the species of that genus were not fossorial (Flynn 1982, 1985), an assumption supported by its wide geographical range. The adaptation to a fossorial life-style in the rhizomyines of southeast Asia seems to have taken place during the early late Miocene, and in the tachyoryctines of northeast Africa during the late Miocene and the Pliocene (Flynn 1982, 1990; Flynn and Sabatier 1984; Tong and Jaeger 1992; Wesselman et al. 2009). The rather poor fossil record of the African rhizomyines—there is no record of the group between the early Miocene *Prokanisamys* sp. from Libya and the late middle Miocene *Pronakalimys* from Kenya—does not confirm hypothesised explanations for the multiple migrations of Rhizomyinae from Asia to Africa as interpreted in López-Antoñanzas et al. (2012). From a biological point of view, a long-distance migration of fossorial, territorial rodents is unlikely (Kryštufek and Griffiths 2002), so our working hypothesis is that the non-fossorial *Prokanisamys* migrated from Asia to Africa where it developed a fully fossorial mode of life independent of its Asian counterparts.

#### The lower incisors of the Spalacinae and Rhizomyinae

The lower incisors of many species of Spalacinae and Rhizomyinae show two longitudinal ribs in combination with the derived type ten or eleven microstructure of the enamel (Kalthoff 2000). This need not necessarily mean that these two groups are closely related, because the same traits of the lower incisors occur in a number of other subfamilies of the Muridae, such as in the late Oligocene and Miocene Eumyarioninae and Cricetodontinae. Apparently, this combination of characteristics of lower incisors developed a number of times in different subfamilies.

#### The evolutionary dynamics of the Rhizomyinae and Spalacinae

Table 3 summarises the numbers of genera and species of the Rhizomyinae and the Spalacinae in the four time slices defined in Figs. 1 and 2. The Spalacinae show a generic decline during the middle Miocene which is almost certainly an artefact due to the paucity of studies on the collections from the middle Miocene of Anatolia. Their representation in terms of numbers of genera and species (Table 3) during the late Miocene/early Pliocene probably reflects reality. The Rhizomyinae play a modest role until the late Miocene, when they became very diverse, in particular in the northern part of the Indian subcontinent. This radiation may well correlate with the development of a fossorial life-style, which may have enhanced a mosaic type of evolution.

#### Conclusions

The discrepancy between the opinions of geneticists and palaeontologists on the relationship of the Rhizomyinae and Spalacinae is intriguing and not understood. Explanations may perhaps be sought in the restrictions inevitably connected with the methods used in the genetic studies of Table 2 and in the incompleteness inherent to the fossil record. New insights may be obtained through the application of advanced molecular genetic techniques (genome and transcriptome sequencing) such as those which have already been used for rhizomyine and spalacine species by Zhao et al. (2013), Fang et al. (2014) and Lin et al. (2014).

Although the fossil record of the Rhizomyinae and Spalacinae is relatively good, it is clear that much of the earliest history of these subfamilies is not documented. The oldest spalacine known, *Vetusspalax* from the late Oligocene of southeast Europe, has a much too derived dentition to be ancestral to all later ones. The radiation of the Spalacinae must thus have occurred earlier in the Oligocene. The oldest rhizomyine known, the non-fossorial *Prokanisamys* from the

**Table 3** The number of genera and species of the Rhizomyinae and Spalacinae<sup>a</sup>

Time slice	Rhizomyinae		Spalacinae	
	Genera	Species	Genera	Species
Late Miocene/Pliocene	9	26	3	8
Midde Miocene	3	7	1	4
Early Miocene	1	4	2	2
Late Oligocene	0	0	1	1

<sup>a</sup> Only published species, as mentioned in Table 1

earliest Miocene of the Indian subcontinent, can not yet be traced to a specific muroid ancestor.

Until the differences in opinion between geneticists and palaeontologists are resolved, we propose to classify the Rhizomyinae and the Spalacinae as separate subfamilies within the Muridae.

**Acknowledgements** This paper is to honour Albert van der Meulen, friend and colleague. The paper benefitted from the constructive comments of the reviewers Dr. M. Huguency and Dr. L.J. Flynn. Figures 1 and 2 were made by the late Tom van Hinte, and Tilly Bouten assisted with the Scanning Electron Microscopy.

**Open Access** This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

## References

- Blanga-Kanfi, S., Miranda, H., Penn, O., Pupko, T., DeBry, R. W., & Huchon, D. (2009). Rodent phylogeny revised, analysis of six nuclear genes from all major rodent clades. *BMC Evolutionary Biology*. doi:10.1186/1471-2148-9-71.
- Bohlin, B. (1946). The fossil mammals from the Tertiary deposit of Taben-buluk, Part II: simplicitentata, carnivora, artiodactyla, perissodactyla, and primates. Sino-Swedish Expedition Publication. *Palaeontologica Sinica n.s. C 8B(28)*, 1–259.
- Brandy, L. D. (1979). Rongeurs nouveaux du Néogène d' Afghanistan. *Comptes Rendus de l'Academie des Sciences de Paris D*, 289, 81–83.
- Brujin, H. de (1984). Remains of the mole-rat *Microspalax odessanus* Topachevski, from Karaburun (Greece, Macedonia) and the family Spalacidae. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B*, 87(4), 417–425.
- Brujin, H. de, & Saraç, G. (1991). Early Miocene faunas from the eastern Mediterranean area. Part 1, The genus *Eumyarion*. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B*, 94(1), 1–36.
- Brujin, H. de, Dawson, M. R., & Mein, P. (1970). Upper Pliocene Rodentia, Lagomorpha and Insectivora (Mammalia) from the Isle of Rhodes (Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B*, 73(5), 535–584.
- Brujin, H. de, & Meulen, A. J. van der (1975). The early Pleistocene rodents from Tourkobounia-1 (Athens, Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B*, 78(4), 314–338.
- Brujin, H. de, Hussain, S. T., & Leinders, J. M. (1981). Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B*, 84(1), 71–99.
- Brujin, H. de, Marković, Z., & Wessels, W. (2013). Late Oligocene rodents from Banovići (Bosnia and Herzegovina). *Palaeodiversity*, 6, 63–105.
- Colbert, E. H. (1933). Two new rodents from the lower Siwalik beds of India. *American Museum Novitates*, 633, 1–6.
- DeBry, R. W., & Sagel, R. M. (2001). Phylogeny of Rodentia (Mammalia) inferred from the nuclear-encoded gene IRBP. *Molecular Phylogenetics and Evolution*, 19(2), 290–301.
- Fang, X., Nevo, E., Han, L., Levanon, E. Y., Zhao, J., Avivi, A., et al. (2014). Genome-wide adaptive complexes to underground stresses in blind mole rats *Spalax*. *Nature Communications*, 5, 3966. doi:10.1038/ncomms4966.
- Fejfar, O. (1972). Ein neuer Vertreter der Gattung *Anomalomys* Gaillard, 1900 (Rodentia, Mammalia) aus dem europäischen Miozän (Karpat). *Neues Jahrbuch für Paläontologie, Abhandlungen*, 141(2), 168–193.
- Flynn, L. J. (1982). A revision of fossil rhizomyid rodents from northern India and their correlation to a rhizomyid biochronology of Pakistan. *Geobios*, 15(4), 583–588.
- Flynn, L. J. (1985). Evolutionary patterns and rates in Siwalik Rhizomyidae (Rodentia). *Acta Zoologica Fennica*, 170, 141–144.
- Flynn, L. J. (1990). The natural history of rhizomyid rodents. In E. Nevo & O. Reig (Eds.), *Evolution of subterranean mammals at the organismal and molecular levels* (pp. 155–183). New York: A.R. Liss.
- Flynn, L. J. (1993). A new bamboo rat from the Late Miocene of the Yushe Basin. *Vertebrata Palasiatica*, 311, 95–101.
- Flynn, L. J. (2009). The antiquity of *Rhizomys* and independent acquisition of fossorial traits in subterranean Muroids. *Bulletin of the American Museum of Natural History*, 331, 128–156.
- Flynn, L. J., & Qi, G. (1982). The age of the Lufeng, China, hominoid locality. *Nature*, 298(5876), 746–747.
- Flynn, L. J., & Sabatier, M. (1984). A muroid rodent of Asian affinity from the Miocene of Kenya. *Journal of Vertebrate Paleontology*, 3(3), 160–165.
- Flynn, L. J., Heintz, E., Sen, S., & Brunet, M. (1983). A new Pliocene tachyoryctine (Rhizomyidae, Rodentia) from Lataband, Sarobi Basin, Afghanistan. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B*, 86, 61–68.
- Flynn, L. J., Jacobs, L. L., & Lindsay, E. H. (1984). Problems of muroid phylogeny, relationship to other rodents and origin of major groups. In W. P. Luckett & J. L. Hartenberger (Eds.), *Evolutionary relationships among rodents, a multidisciplinary analysis* (Nato ASI series A, pp. 589–616). New York: Plenum Press.
- Flynn, L. J., Lindsay, E. H., Pilbeam, D., Raza, M. S., Morgan, M. E., Barry, J. C., Badgley, C. E., Behrensmeyer, A. K., Cheema, I. U., Rajnar, R. A., & Opdyke, N. D. (2013). The Siwaliks and Neogene evolutionary biology in South Asia. In X. Wang, L. J. Flynn, & M. Fortelius (Eds.), *Fossil mammals of Asia* (Neogene Biostratigraphy and Chronology, pp. 353–372). New York: Columbia University Press.
- Gogolevskaya, I. K., Veniaminova, N. A., & Kramerov, D. A. (2010). Nucleotide sequences of B1 SINE and 4.5S(I) RNA support a close relationship of zokors to blind mole rats (Spalacinae) and bamboo rats (Rhizomyinae). *Gene*, 460(1–2), 30–38. doi:10.1016/j.gene.2010.04.002.
- Gray, J. E. (1821). On the natural arrangement of vertebrate animals. *London Medical Repository*, 15, 296–310.
- Gray, J. E. (1831). Characters of three new genera (*Helictis*, *Paguma* and *Rhizomys*), including two new species of Mammalia from China. Proceedings of the Committee of Science and Correspondence of the Zoological Society of London, part 1, 94–96.
- Güldenstaedt, A. I. (1770). *Peregusna nova mustelae* species. *Novi Commentari Academiae Scientiarum Imperialis Petropolitanae*, 14, 441–455.
- Gupta, S. S., Verma, B. C., & Tewari, A. P. (1978). New fossil hominoid material from the Siwaliks of Kangra District, Himachal Pradesh. *Journal of the Paleontological Society of India*, 27, 111–115.
- Hinton, M. A. C. (1933). Diagnoses of new genera and species of rodents from the Indian Tertiary deposits. *Annals and Magazine of Natural History*, 10, 620–622.
- Hodgson, B. H. (1841). New species of *Rhizomys* discovered in Nepal (*R. badius*, Bay Bamboo Rat). *Calcutta Journal of Natural History*, 2, 60–61, 410–411.

- Hugueney, M., & Mein, P. (1993). A comment on the earliest Spalacinae (Rodentia, Muroidea). *Journal of Mammalian Evolution*, 1(3), 215–223.
- Jansa, S. A., & Weksler, M. (2004). Phylogeny of muroid rodents, relationships within and among major lineages as determined by IRBP gene sequences. *Molecular Phylogenetics and Evolution*, 31(1), 256–276. doi:10.1016/j.ympev.2003.07.002.
- Jansa, S. A., Giarla, T. C., & Lim, B. K. (2009). The phylogenetic position of the rodent genus *Typhlomys* and the geographic origin of Muroidea. *Journal of Mammalogy*, 90(5), 1083–1094.
- Kalthoff, D. C. (2000). Die Schmelzmicrostruktur in den Incisiven der hamsterartigen Nagetiere und anderer Myomorpha (Rodentia, Mammalia). *Palaeontographica A*, 269, 1–193.
- Klein Hofmeijer, G., & Bruijn, H. de (1985). The mammals from the lower Miocene of Aliveri (island of Evia, Greece). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen B*, 88(2), 185–198.
- Kormos, T. (1932). Neue Pliozäne Nagetiere aus der Moldau. *Paläontologische Zeitschrift*, 14(3), 193–200.
- Kryštufek, B., & Griffiths, H. I. (2002). Species richness and rarity in European rodents. *Ecography*, 25, 120–128.
- Lang, J., & Lavocat, R. (1968). Première découverte d'une faune de vertébrés dans le Tertiaire d'Afghanistan et datation de la série de Bamian. *Comptes Rendus de l'Académie des Sciences de Paris D*, 266, 79–82.
- Lin, G. H., Wang, K., Deng, X. G., Nevo, E., Zhao, F., Su, J. P., Guo, S. C., Zhang, T. Z., & Zhao, H. (2014). Transcriptome sequencing and phylogenomic resolution within Spalacidae (Rodentia). *BMC Genomics* 15, 32. doi:10.1186/1471-2164-15-32.
- Lindsay, E. H. (1996). A new eumyarionine cricetid from Pakistan. *Acta Zoologica Cracoviensia*, 39(1), 279–288.
- López-Antoñanzas, R., Flynn, L. J., & Knoll, F. (2012). A comprehensive phylogeny of extinct and extant Rhizomyinae (Rodentia), evidence for multiple intercontinental dispersals. *Cladistics*, 29(3), 247–273. doi:10.1111/j.1096-0031.2012.00426.x.
- Lydekker, R. L. (1884). Rodents and new ruminants from the Siwaliks and synopsis of Mammalia. *Paleontographica Indica*, 10, 134–185.
- Marković, Z. (2003). The Miocene small mammals of Serbia, a review. In J. W. F. Reumer, & W. Wessels (Eds.), *Distribution and migration of Tertiary mammals in Eurasia*. *Deinsea*, 10, 393–398.
- McKenna, M. C., & Bell, S. K. (1997). *Classification of mammals above the species level*. New York: Columbia University Press.
- Mein, P., & Ginsburg, L. (1985). Les rongeurs Miocènes de Li (Thaïlande). *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences* 2, 301(19), 1369–1374.
- Michaux, J., & Catzeflis, F. (2000). The bushlike radiation of muroid rodents is exemplified by the molecular phylogeny of the LCAT nuclear gene. *Molecular Phylogenetics and Evolution*, 17(2), 280–293.
- Michaux, J., Reyes, A., & Catzeflis, F. (2001). Evolutionary history of the most speciose mammals, molecular phylogeny of muroid rodents. *Molecular Biology and Evolution*, 18(11), 2017–2031.
- Norris, R. W., Zhou, K., Zhou, C., Yang, G., Kilpatrick, W. C., & Honeycutt, R. L. (2004). The phylogenetic position of the zokors (Myospalacinae) and comments on the families of muroids (Rodentia). *Molecular Phylogenetics and Evolution*, 31(3), 972–978. doi:10.1016/j.ympev.2003.10.020.
- Palmer, T. S. (1903). Some new generic names of mammals. *Science New Series*, 17, 873.
- Petter, F. (1961). Affinités des genres *Spalax* et *Brachyuromys* (Rongeurs, Cricetidae). *Mammalia*, 25, 485–497.
- Prasad, K. N. (1968). The vertebrate fauna from the Siwalik beds of Haritalyangar, Himachal Pradesh, India. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, 39, 1–56.
- Robinson, M., Catzeflis, F., Briolay, J., & Mouchiroud, D. (1997). Molecular phylogeny of rodents, with special emphasis on murids, evidence from nuclear gene LCAT. *Molecular Phylogenetics and Evolution*, 8(3), 423–434. doi:10.1006/mpev.1997.0424.
- Rüppell, E. (1835). Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. *Säugethiere*, 1, 36.
- Sabatier, M. (1978). Un nouveau *Tachyoryctes* (Mammalia, Rodentia) du bassin Pliocène de Hadar (Ethiopie). *Geobios*, 11, 95–99.
- Sabatier, M. (1982). Les Rongeurs du site Pliocène à Homonidés de Hadar (Ethiopie). *Paleovertebrata*, 12(1), 1–56.
- Sarica, N., & Sen, S. (2003). Spalacidae (Rodentia). In M. Fortelius, J. Kappelman, S. Sen, & R. L. Bernor (Eds.), *Geology and paleontology of the Miocene Sinap formation, Turkey* (pp. 141–162). Columbia University Press: New York.
- Savič, I. R., & Nevo, E. (1990). The Spalacidae, evolutionary history, speciation and population biology. In E. Nevo & O. A. Reig (Eds.), *Evolution of subterranean mammals at the organismal and molecular levels* (pp. 129–154). New York: Wiley-Liss.
- Sen, S., & Sarica, N. (2011). Middle-Late Miocene Spalacidae (Mammalia) from western Anatolia, and the phylogeny of the family. *Bulletin of the Earth Sciences Application Centre of the Hacettepe University*, 32(1), 21–50.
- Simionescu, I. (1930). Vertebratele Pliocene de la Malușteni (Covurlui). *Publications du Fondation Vasile Adamachi, Akademia Romana*, 9(49), 83–151.
- Steppan, S. J., Adkin, R. M., & Anderson, J. (2004). Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. *Systematic Biology*, 53(4), 533–553. doi:10.1080/10635150490468701.
- Teilhard de Chardin, P. (1942). New rodents of the Pliocene and lower Pleistocene of north China. *Publications of the Institute of Geology*, 9, 1–101.
- Theocharopoulos, K. D. (2000). Late Oligocene-middle Miocene *Democricetodon*, *Spanocricetodon* and *Karydomys* n. gen. from the eastern mediterranean area. *Gaia*, 8, 1–116.
- Thomas, O. (1896). On the genera of rodents, An attempt to bring up to date the current arrangement of the order. *Proceedings of the Zoological Society of London*, 64, 1012–1028.
- Thomas, O. (1915). Notes on the Asiatic bamboo-rats (*Rhizomys* etc.). *Annals and Magazine of Natural History*, 8(16), 56–61.
- Tong, H., & Jaeger, J. J. (1992). Muroid rodents from the Middle Miocene Fort Ternan locality (Kenya) and their contribution to the phylogeny of muroids. *Palaeontographica Abteilung A, Paleozoologie-Stratigraphie*, 229(1–3), 51–73.
- Topachevski, V. A. (1969). Fauna of the USSR, mammals, mole rats, Spalacidae. In Academy of Sciences of the USSR, (Ed.), *Fauna of the USSR, Mammals* (Zoological Institute, new series, Vol. 99, pp. 1–150). New Delhi: Amerind Publishing Co Pvt. Ltd.
- Ünay, E. (1978). *Pliospalax primitivus* and *Anomalomys gaudryi* Gaillard from the *Anchitherium* fauna of Sarıçay. *Bulletin of the Geological Society of Turkey*, 21, 121–128.
- Ünay, E. (1990). A new species of *Pliospalax* (Rodentia, Mammalia) from the Middle Miocene of Paşalar, Turkey. *Journal of Human Evolution*, 19, 445–453.
- Ünay, E. (1996). On fossil Spalacidae (Rodentia). In R. L. Bernor (Ed.), *The evolution of western Eurasian Neogene Mammal Faunas* (pp. 246–252). New York: Columbia University Press.
- Ünay, E., Bruijn, H. de, & Saraç, G. (2003). A preliminary zonation of the continental Neogene of Anatolia based on rodents. In J. W. F. Reumer, & W. Wessels (Eds.), *Distribution and migration of Tertiary mammals in Eurasia*. *Deinsea* 10, 539–548.
- Vasileiadou, K., & Koufos, G. D. (2005). The micromammals from the Early/Middle Miocene locality of Antonios, Chalkidiki, Greece. *Annales de Paleontologie*, 91, 197–225.
- Wesselman, H. B., Black, M. T., & Asnake, M. (2009). Small mammals. In Y. Haile-Selassi & G. WoldeGabriel (Eds.), *Ardipithecus kadabba, Late Miocene evidence from the Middle Awash, Ethiopia* (pp. 105–134). Berkeley: University of California Press.

- Wessels, W. (2009). Miocene rodent evolution and migration. Muroidea from Pakistan, Turkey and Northern Africa. *Geologica Ultraiectina*, 307, 1–290.
- Wessels, W., & Bruijn, H. de (2001). Rhizomyidae from the lower Manchar formation Miocene, Pakistan. *Annals of Carnegie Museum*, 70(2), 143–168.
- Wessels, W., Fejfar, O., Peláez-Campomanes, P., Meulen, A. J. van der, Bruijn, H. de, & El-Arnauti, A. (2003). Miocene small mammals from Jebel Zelten, Libya. In N. López-Martínez, P. Peláez-Campomanes & M. Hernández Fernández (Eds.), *Surrounding Fossil Mammals, Dating, Evolution and Paleoenvironment* (pp. 699–715). Coloquios de Paleontología, Volumen Extraordinario n 1 en homenaje al Dr Remmert Daams.
- Wessels, W., Fejfar, O., Peláez-Campomanes, P., Meulen, A. J. van der, Bruijn, H. de, & El-Arnauti, A. (2008). The age of the small mammal faunas from Jabal Zaltan. *Libia, Garyounis Scientific Bulletin*, 5, 129–138.
- Wilson, D. E., & Reeder, D. M. (2005). *Mammal species of the world. A taxonomic and geographic reference*. Baltimore: Johns Hopkins University Press.
- Winge, H. (1887). Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. *Museo Lundii, Copenhagen*, 1(3), 1–178.
- Wood, A. E. (1937). Fossil rodents from the Siwalik Beds of India. *American Journal of Sciences*, 36, 64–76.
- Wood, A. E. (1965). Grades and clades among rodents. *Evolution*, 19(1), 115–130.
- Zhao, F., Zhang, T., Su, J., Nevo, E., & Lin, G. (2014). Mitochondrial genome of bamboo rat *Rhizomys pruinosus*. *Mitochondrial DNA* 5(5):381–382. doi:10.3109/19401736.2013.809434
- Zheng, S. H. (1980). The *Hipparion* fauna of Bulong Basin, Biru, Xizang. In Qinghai-Tibetan Plateau Comprehensive Scientific Investigation Team of Chinese Academy of Sciences (Ed.), *Paleontology of Tibet, Part 1* (pp. 33–47). Beijing: Science Press.