



On the antiquity and status of the Spalacidae, new data from the late Eocene of south-East Serbia

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Abstract

A new blind mole-rat species *Debruijnia tintinnabulus* nov. sp. is described from the late Eocene of south east Serbia. This find is approximately 10 Ma older than the hitherto oldest records of Spalacidae *Vetusspalax* and *Pannoniamys*, both from the late Oligocene of Bosnia and Herzegovina and Serbia. The antiquity of the new species (~34 Ma) is in accordance with recent genetically based age estimates of Spalacidae as an early branch of the Supramyomorpha. A review of the fossil record shows that the Spalacidae are probably not closely related to the Rhizomyinae and Myospalacinae. The spalacid finds from the Paleogene of the Balkans and the Neogene of Anatolia suggests that the family underwent a radiation during the Oligocene involving *Debruijnia*, *Vetusspalax*, *Pannoniamys* and *Heramys*. During the middle and late Miocene *Heramys* evolved into a large number of species, here all tentatively allocated to *Pliospalax*.

Keywords Balkans · Burrowing rodents · Spalacidae · New species · Phylogeny · Rhizomyinae · Myospalacinae · Tachyoryctoidinae

Introduction

The content and phylogenetic position of the family Spalacidae Grey, 1821 is still controversial (reviewed in de Bruijn et al. 2015). The main reason behind differences of opinion on the content of the family is that fossorial rodents belonging to different clades tend to develop cheek teeth with

similar patterns and, seemingly, similar genomes (Flynn, 2009). An additional taxonomic problem is that most Miocene and older genera and species of the Spalacidae are based on a few isolated, rather high-crowned cheek teeth with a dental pattern that changes through wear. A good example of dental similarity causing taxonomic problems is the genus *Rhizospalax* Miller and Gidley, 1919 from the late Oligocene of France. This rodent, now recognised to be a beaver (Hugueney 1969, Hugueney and Mein 1993), has long been considered to be an early spalacid. Stehlin (1922–1923), who considered *Rhizospalax* ancestral to the Spalacidae, identified its first cheek tooth as a premolar, whereas the first cheek tooth is a molar in all muroids. He consequently assumed the dental formula of spalacids to include one premolar and two molars, reason to separate the group from all other muroids and raising it to family rank.

The genus *Prospalax* Mehely (1908) was originally considered ancestral to *Spalax*, but this genus as well as *Miospalax* Stromer (1928), are mostly recognised to be members of the Anomalomyinae Schaub, 1925 (see Bolliger 1996, 1999), but Flynn (2009, fig. 6) links this group to the spalacids. Fejfar (1972) suggested that the Spalacidae and Anomalomyinae might have their ancestors in the supposedly burrowing, central Asian Tachyoryctoidinae, which were poorly known at that time. But this idea has, as far as we know, not been followed in later studies.

Hans de Bruijn is deceased

This is the eighth paper in the series: “The Paleogene rodent faunas from south-east Serbia”.

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After removal of the castorid *Rhizospalax* and the anomalomyines *Prospalax* and *Miospalax* from the Spalacidae, *Heramys* Klein Hofmeijer and de Bruijn, 1985 (early Miocene of Greece, MN4) and *Debruijnia* Ünay, 1996 (early Miocene of Anatolia, MN3) for long remained the oldest records of the family. Recently described older records of the family are the late Oligocene (MP30) genera *Vetusspalax* de Bruijn et al. (2013) from Banovići (Bosnia and Herzegovina) and *Pannoniamys* van de Weerd et al. (2021) from Paragovo (Serbia).

Below we describe a new species from Zvonce, a late Eocene site in southern Serbia (de Bruijn et al. 2017) and include it in the spalacid genus *Debruijnia*. The antiquity of this early spalacid species is in accordance with the recent genetically based age estimates of the Spalacidae as an early branch of the muroids within the suborder Supramyomorpha D'Elia, Fabre et Lessa, 2019. Next, we discuss the content of the Spalacidae in terms of genera and discuss its relationship to the muroid subfamilies Rhizomyinae, Myospalacinae and the Tachyoryctoidinae that have been considered its sister groups (Flynn et al. 2019).

This paper is the eighth in the series "The Paleogene rodent faunas from south-east Serbia". The geological setting and composition of the faunas from southern Serbia (consisting mainly of rodents) have been described by de Bruijn et al. (2017). Rodent groups that have been studied are the Diatomyidae (Marković et al. 2017), the Melissiodontinae (Wessels et al. 2018), the Paracricetodontinae (van de Weerd et al. 2018), the Pappocricetodontinae (de Bruijn et al. 2018), the Pseudocricetodontinae (Marković et al. 2019) and the Dipodidae (Wessels et al. 2019). The distribution of rodent species in these faunas is shown in Wessels et al. (2019, their table 1).

Material and methods

Large samples of the poorly fossiliferous blueish claystone at the Zvonce locality, south eastern Serbia (de Bruijn et al., 2017) produced two lower and one upper molars of a medium-sized muroid with rather high-crowned complex cheek teeth. The three molars (m1, m2 and M1) probably belonged to a single individual; similarly, we suspect that some isolated molars of other taxa collected at this site belonged to one individual as well. Unfortunately, the m1 disintegrated during cleaning and is now only known by a photograph. Although various details of the molar of this photograph were obscured by sedimentary matrix, we have been able to reconstruct most of its dental morphology.

The material from Zvonce (ZV) has been collected by a team of the Museum of Natural History in Belgrade (Serbia) and the University of Utrecht (the Netherlands). The material of *Debruijnia tintinnabulus* is housed in the Natural History Museum in Belgrade under the locality code 036. Unfortunately, further collecting at the site is dangerous, because it requires either further undercutting of the almost vertical

outcrop or the use of explosives to remove the overlying sandstones. Since the locality is situated adjacent to the local grocery shop neither approach is feasible.

Measurements were taken with an Ortholux microscope with mechanical stage and measuring clocks and are given in millimetres. Upper molars are indicated by M, lower molars by m. All specimens are figured as from the right side. If the original is from the left side its figure number has been underlined. The dental elements named in the descriptions *Debruijnia tintinnabulus* nov. sp. are shown in Fig. 1.

Taxonomy

Suborder Supramyomorpha D'Elia, Fabre et Lessa, 2019

Infraorder Myodonta Schaub, 1958

Superfamily Muroidea, Illiger, 1811

Family Spalacidae Grey, 1821

Genus *Debruijnia* Ünay, 1996

Species included: *D. arpati* Ünay, 1996; genotype, early Miocene (MN3), Keseköy Anatolia. *D. kostakii* de Bruijn, 2017; early Miocene (MN4), Karydia Greece.

Debruijnia tintinnabulus nov. sp.

(Figs. 2g, 3g and 3h)

2017 ?Spalacinae nov. gen. 1 sp.A, de Bruijn et al. (2017), Wessels et al. (2019)

Derivatio nominis: Zvonce means little bell in Serbo-Croatian, tintinnabulum = bell in Latin.

Type locality and level: Zvonce, late Eocene (MP 18-19) south/east Serbia.

Holotype: M1 dexZV-571. (Fig. 2g)

Material and measurements: M1 dexZV-571, (2.31 x 1.75 mm); m2 sinZV-577, (1.95 x 1.50mm); m1 sin. lost, photograph available (Fig. 3h).

Diagnosis: The cheek teeth of *Debruijnia tintinnabulus* are semi-hypsodont and show a complex dental pattern; the enamel of the ridges and cusps shows many tiny folds and protuberances. The protocone of the M1 is connected to the lingual part of the anterocone. The long anterior arm of the protocone and the mesoloph reach the lingual border of the occlusal surface. The protolophule of the M1 is double and the metalophule is transverse. The metaconid on the m1 is situated far forward and is confluent with the small anteroconid. The metalophulid on m1 has a posterior position and connects the mesoconid to the metaconid. The lingual part of the mesolophid is split, with one ridge leading to the metaconid and the other to the entoconid. There are two ridges between the entoconid and hypoconid, with the anterior one interpreted to be the mesolophid and the posterior one as the true

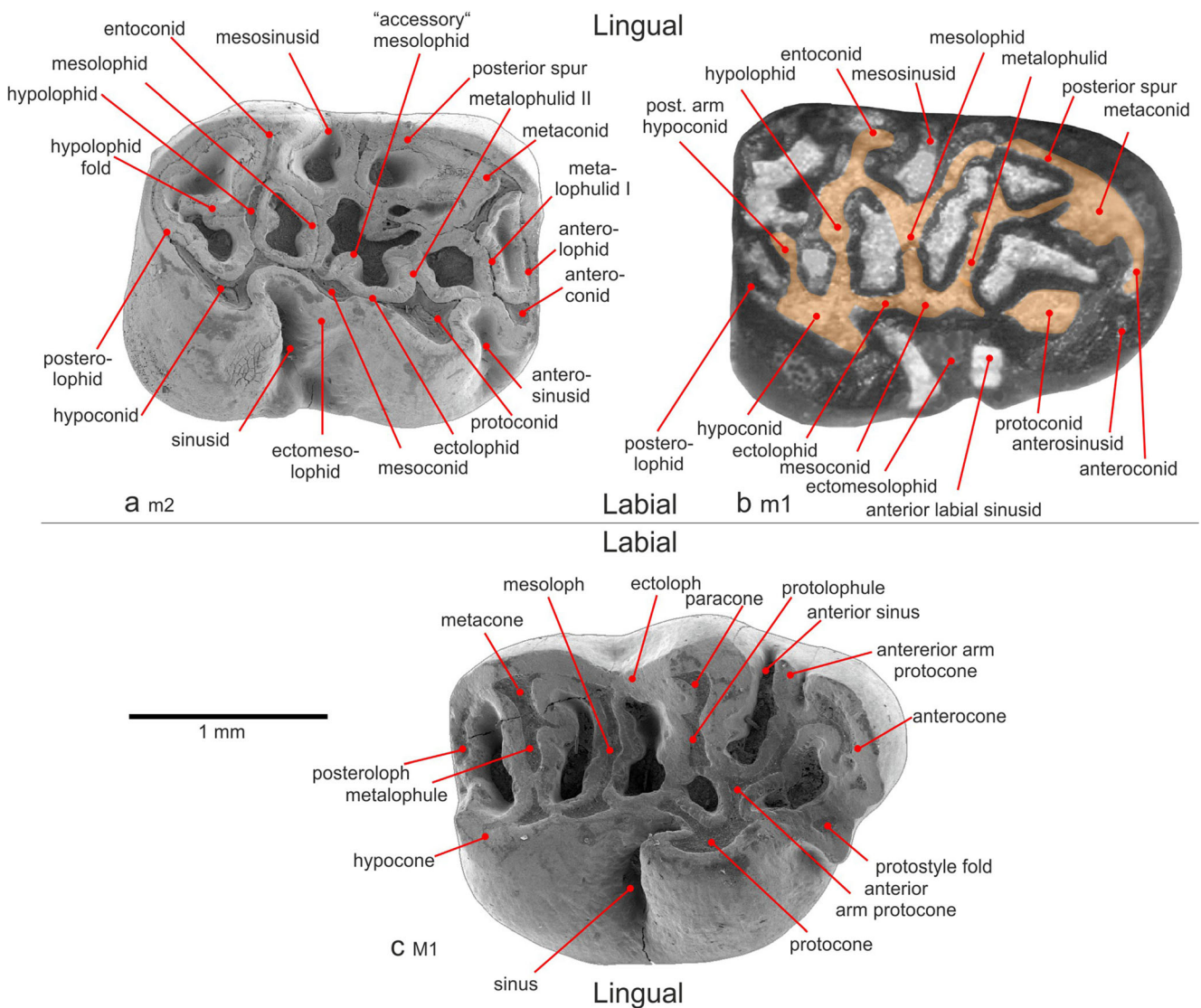


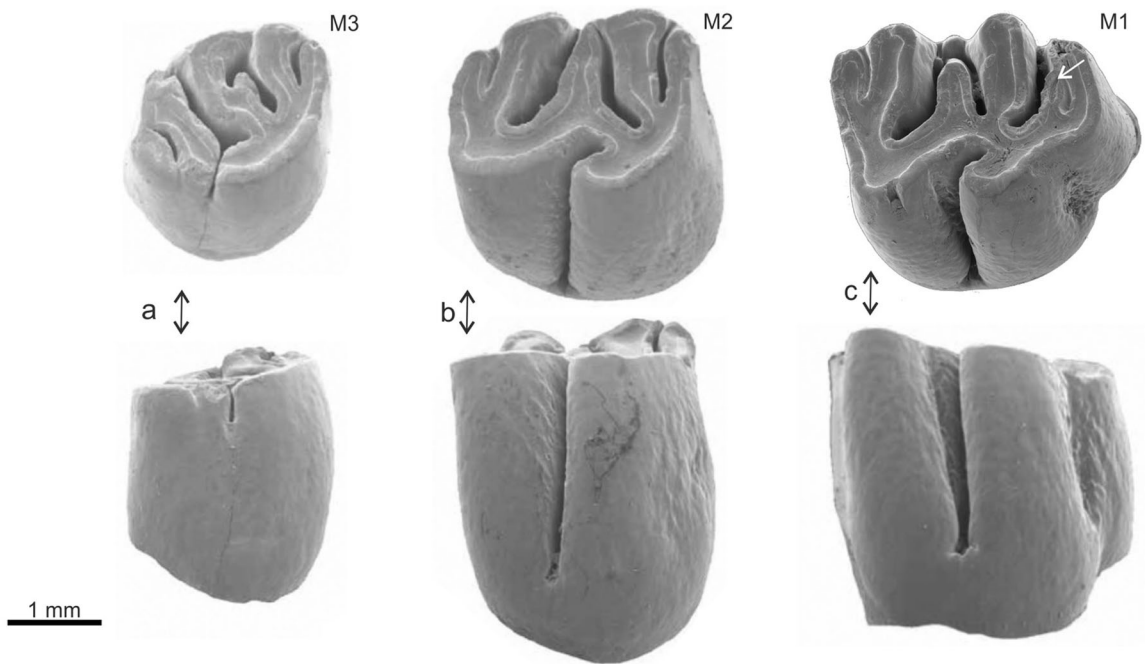
Fig. 1 Nomenclature of dental parts used in the description of *Debruijnia tintinnabulus* nov. sp. Homology of some elements of these complex molars remains uncertain

hypolophid. A free posterior arm of the hypoconid is present in the m1, but not in the m2.

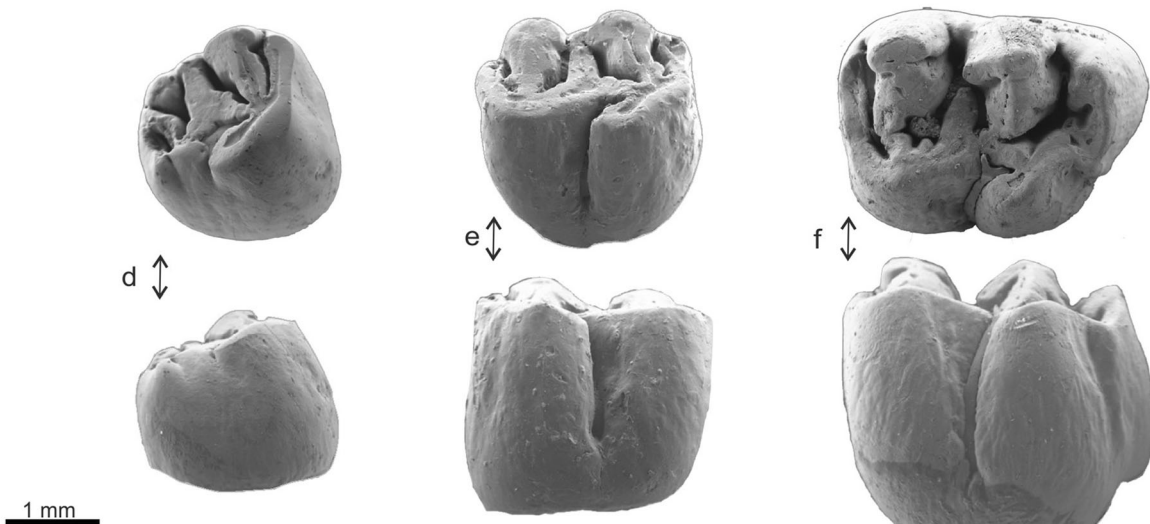
Differential diagnosis: The shape and the general architecture of the cheek teeth of *Debruijnia tintinnabulus* are similar to those in *D. arpati*, but the cheek teeth of *D. tintinnabulus* are smaller, more complex, lower crowned and contain less inflated cusps. The cheek teeth of *Debruijnia kostakii* are larger and much more hypsodont than those of *D. tintinnabulus*. The anterior arm of the protocone of the M1 is long in *D. tintinnabulus*, whereas it is rudimentary in *D. arpati*. The ectoloph in M1 of *D. tintinnabulus* is complete, it is incomplete in *D. arpati* and absent in *D. kostakii*. The m1 and m2 of *D. tintinnabulus* have a well developed posterior spur on the metaconid connecting to the mesolophid, this spur is poorly developed in *D. arpati* and absent in *D. kostakii*.

Description of the material from the type locality

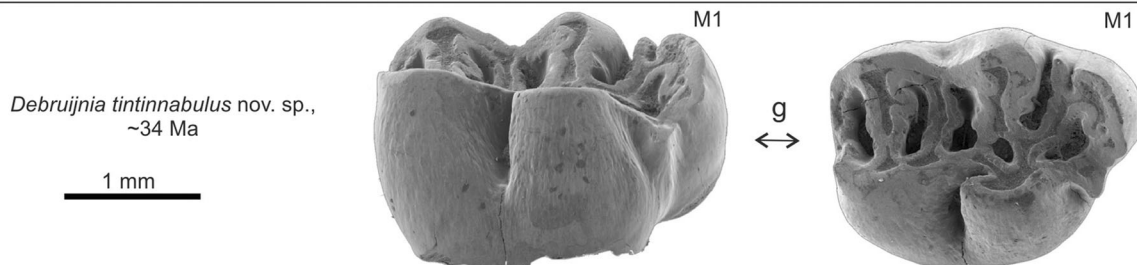
M1 (Figs. 1c and 2g): The wide anterocone is lingually connected to the protocone. A well-developed protostyle-fold is present between the anterocone and the protocone. The anterior arm of the protocone is split. Its anterior part extends to the labial tooth-border and connects to the anterocone and its posterior part is connected to the protolophule. The protolophule is sturdy, splits near the protocone and connects to the anterior and posterior arms of the protocone. The long and sturdy mesoloph connects labially to the complete ectoloph. The transverse metalophule connects the metacone and hypocone. The posteroloph descends from the hypocone and ascends labially to the tip of the metacone.



Debruijnja kostakii de Bruijn, 2017, ~16.8 Ma.



Debruijnja arpati Ünay, 1996, ~18.4 Ma



Debruijnja tintinnabulus nov. sp.,
~34 Ma

Fig. 2 Occlusal and lingual labial views of the upper molars of *Debruijnja kostakii* de Bruijn, 2016, Karydia Greece, early Miocene, *D. arpati* Ünay, 1996 (type species of the genus), Keseköy Anatolia,

early Miocene and *Debruijnja tintinnabulus* nov. sp., Zvonce Serbia, late Eocene, **a-g** occlusal and lingual views. The arrow in fig. **c** points to the relict of the anterior arm of the protoconid

m1 (Figs. **1b** and **3h**): The well-developed metaconid is situated anteriorly of the protoconid, at the expense of the anteroconid and bears a strong posterior spur. Metaconid,

posterior spur and anteroconid are merged to form the rounded anterior side of the molar. A shallow anterosinusid is present. The metalophulid on m1 is positioned posteriorly, it is

connected to the mesoconid, lingually it splits into an anterior and a posterior arm. One arm of the mesolophid connects to the posterior spur of the metaconid, the other to the entoconid. The hypolophid has irregular folds at its anterior and posterior sides. The posterior arm of the hypoconid seems to end free. The posterolophid connects the hypoconid to the entoconid along the posterior edge of the occlusal surface.

m2 (Figs. 1a and 3g): An anteroconid is present. The anterolophid is narrow and straight. The antero-sinusid is well developed. The metaconid has several minor folds and protuberances. The transverse metalophid 1 connects the metaconid complex to the anteroconid and to the anterior arm of the protoconid. The metaconid has a strong posterior spur, which is connected to a central ridge that may be a remnant of the mesolophid. The metalophid 2 is formed by the posterior arm of the protoconid. The mesolophid splits with its posterior branch reaching the entoconid. A short "accessory mesolophid" is present. The transverse hypolophid has folds at its anterior and posterior sides. A posterior arm of the hypoconid is absent. The posterolophid descends from the hypoconid and ascends to the tip of the entoconid.

Discussion

D. tintinnabulus resembles *D. arpati* (the genotype) in its general appearance (Figs. 2 and 3), with both showing the wrinkled irregular enamel. Also, both species have a well-developed protostyle fold and a wide anterocone, but the M1 of *D. arpati* lacks the long anterior arm of the protocone that splits and connects to the paracone and anterocone; it has a shorter mesoloph and its ectoloph is incomplete. The M1 of *D. kostakii*, however, shows a relict of the anterior arm of the protoconid (arrowed in Fig. 2c), but the protostyle fold is absent. Lower molars of the three species resemble each other in their complex appearance, but the details of their dental patterns are difficult to compare due to differences in wear stage. The anteroconid of *D. tintinnabulus* is small, but the stronger rounding of the anterior side of the m1 of *D. tintinnabulus* compared to that of *D. arpati* could also be partly due to a difference in wear stage. The posterior arm of the hypoconid is present in the m1 of all three species, but is absent on the m2 of *D. tintinnabulus* and *D. kostakii*. The mesolophid seems better developed in *D. tintinnabulus*. However, *D. tintinnabulus* shows some plesiomorph features such as the presence of an anterior connection between protocone and paracone and the small anteroconid on m1. The morphology of the cheek teeth of *Debruijnina tintinnabulus* suggest it to be ancestral to *D. arpati*, with *D. tintinnabulus*, *D. arpati* and *D. kostakii* molars showing increase in size and hypsodonty (Table 1, Figs. 2 and 3). Considering the age difference of some 15 Ma between *D. tintinnabulus* and *D. arpati*, the similarity in dental pattern is surprising and documents an exceptionally slow change in morphology through time. We therefore expect that better documentation of our new species will lead to separation

Table 1 Comparison of the measurements of the m2 and M1 of *Debruijnina* species from their type localities. Measurements of *D. kostakii* and *D. arpati* from de Bruijn (2016) and Ünay (1996) respectively

Species		length		N	width		
		range	mean		range	mean	N
<i>D. kostakii</i>	m2	3.00-3.05	3.03	2		2.07	1
<i>D. arpati</i>	m2	2.30-2.58	2.46	8	1.96-2.20	2.07	8
<i>D. tintinnabulus</i>	m2		1.95	1		1.5	1
<i>D. kostakii</i>	M1	3.07-3.23	3.16	4	2.59-2.73	2.63	4
<i>D. arpati</i>	M1	2.56-2.94	2.71	4	1.90-2.10	1.99	4
<i>D. tintinnabulus</i>	M1		2.31	1		1.5	1

on the generic level. The lack of records of *Debruijnina* in the intensively sampled early Oligocene Strelac Formation of south east Serbia (de Bruijn et al., 2017, 2018, Wessels et al. 2018, 2019, van de Weerd et al. 2018, Marković et al. 2017, 2019) may have a palaeoenvironmental origin. All these associations contain abundant crocodile teeth indicating a shallow lacustrine biotope which is probably inappropriate for the (fossorial?) lifestyle of *Debruijnina*.

The allocation of the molars from Zvonce to the genus *Debruijnina* is of special interest, because it supports the hypothesis that the Spalacidae are an old branch of the Muroidea and that the cradle of this family was in South-Eastern Europe and/or the Middle East (de Bruijn et al. 2015). The Paleogene history of the family suggests a radiation leading to the genera *Pannoniamys* van de Weerd et al., 2021, *Vetusspalax*, de Bruijn et al., 2013, and *Heramys* Klein Hofmeijer and de Bruijn, 1985 during the early Oligocene (Fig. 4). The first two of these genera seem to have been short lived local branches. *Debruijnina* and *Heramys* seem to form the basis for a wealth of species in the middle and late Miocene of Anatolia (Ünay 1996, Sarica and Sen 2003, Sen and Sarica 2011), here all tentatively grouped in *Pliospalax* (including *Sinapospalax*). The presence of long-living lineages cannot be demonstrated for middle and late Miocene *Pliospalax*. Instead, data seem to suggest a pattern of mosaic evolution with short branches and rapid replacements.

The Rhizomyinae, Myospalacinae and Tachyoryctoidinae

Studies on the phylogenetic relationships among the burrowing rodent clades Rhizomyinae and Spalacidae on the basis of molecular data and evidence from fossils have led to contradictory conclusions (reviewed in de Bruijn et al. 2015). Most geneticists and some palaeontologists classify these groups as subfamilies together with the Myospalacinae in the family Spalacidae Grey, 1821 (Robinson et al. 1997; Stepan et al.

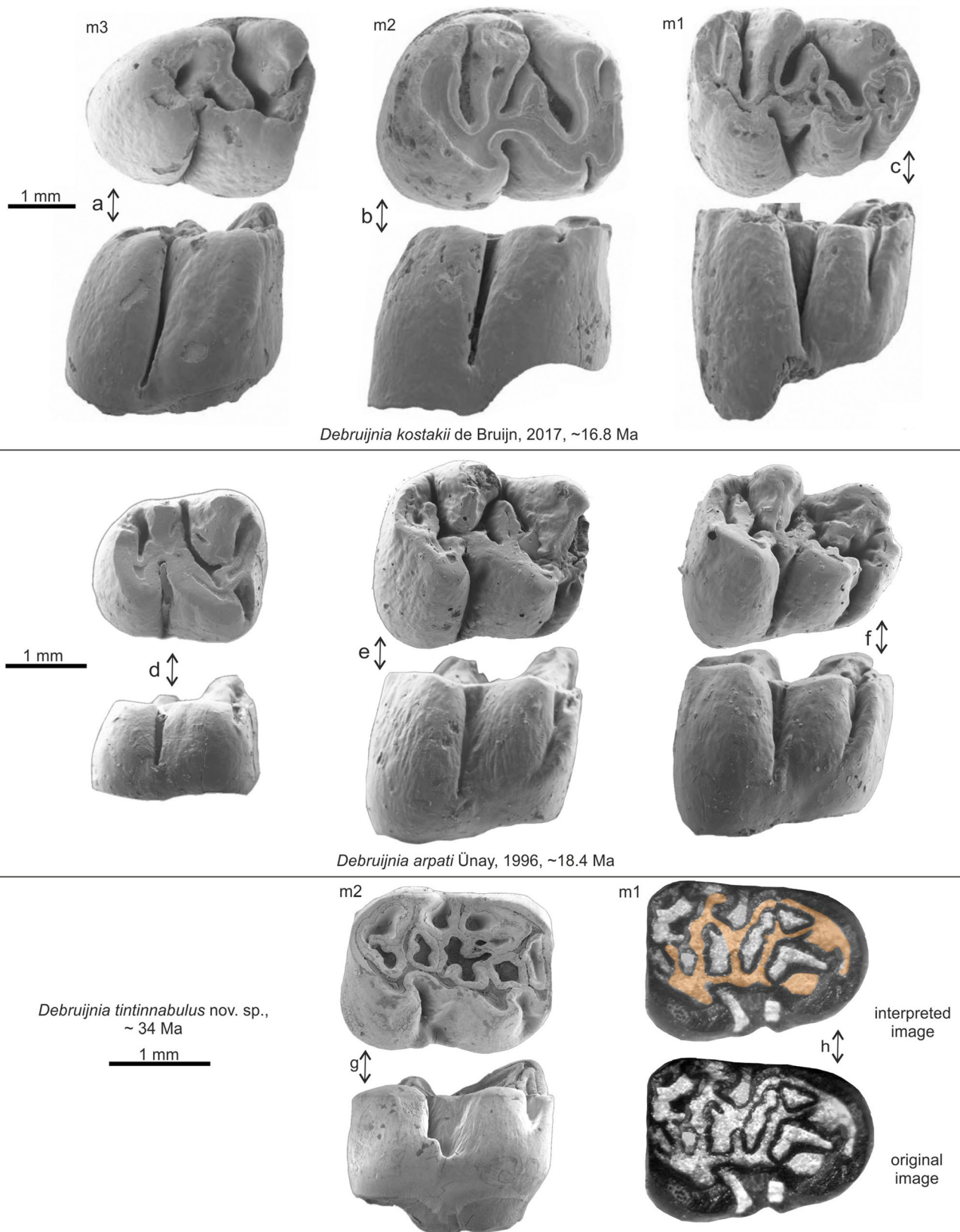


Fig. 3 Lower molars of *Debruijnina kostakii* de Bruijn, 2016, Karydia Greece, early Miocene, *D. arpati* Ünay, 1996 (type species of the genus), Keseköy Anatolia, early Miocene and *Debruijnina tintinnabulus* nov. sp., Zvonce Serbia, late Eocene, **a–g** occlusal en labial views, **h** occlusal view only

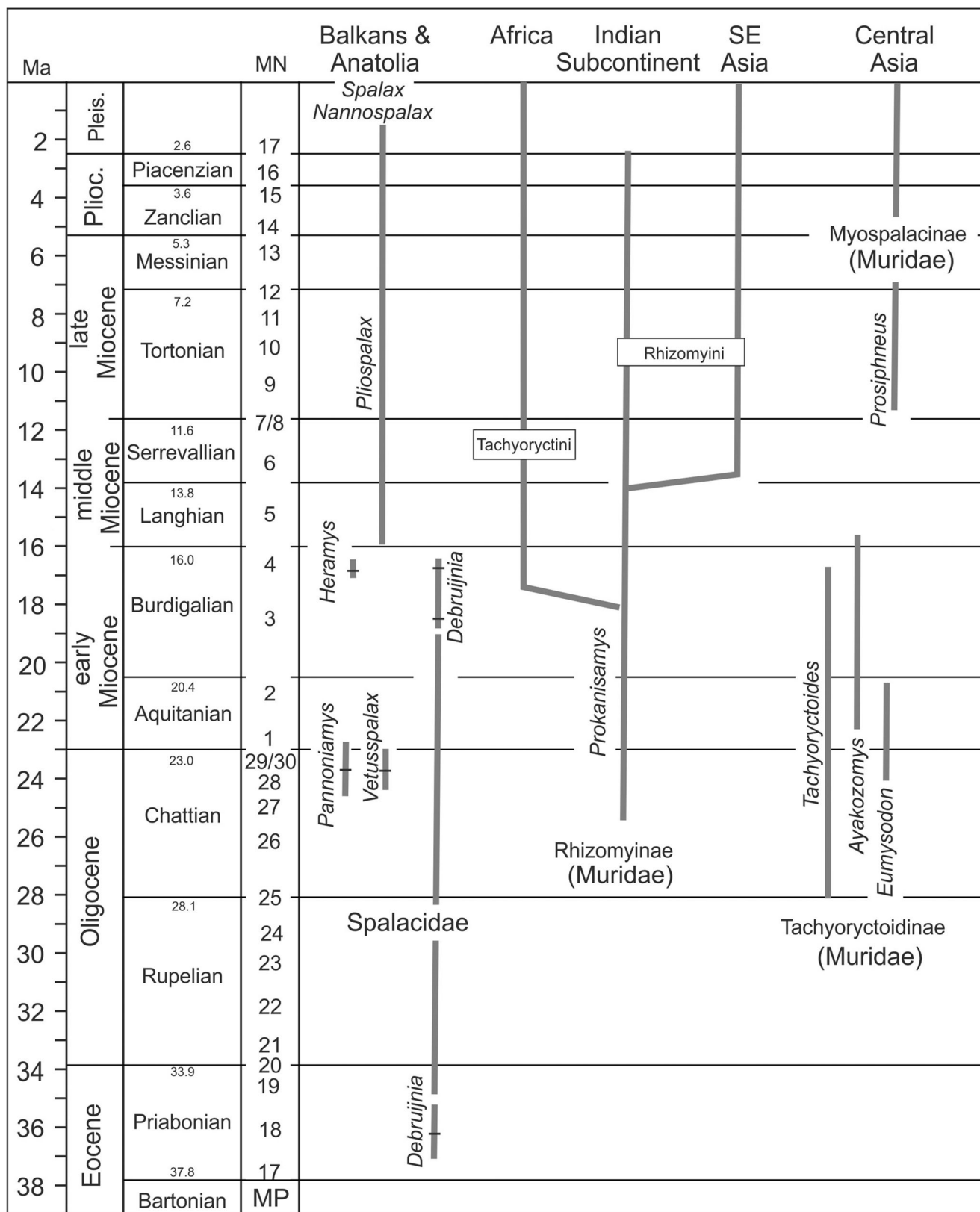


Fig. 4 Distribution in time and place of the Spalacidae and subfamilies of the Muridae (sensu lato) Rhizomyinae, Tachyoryctoidinae and Myospalacinae. Only the oldest genera of the Rhizomyinae and the

Muridae (sensu lato) Rhizomyinae, Tachyoryctoidinae and Myospalacinae are in the figure. In addition, the two tribes of the Rhizomyinae are indicated. MP are European Paleogene mammal zones, MN are Neogene mammal zones

2004; Norris et al. 2004; Wilson and Reeder 2005; Blanga-Kanfi et al. 2009; Gogolevskaya et al. 2010; Steppan and Schenk 2017, Fournier et al. 2021). In an attempt to conjoin the fossil record and molecular data Flynn (2009) hypothesises monophyly of *Spalax*, *Rhizomys* and *Myospalax*. Flynn et al. (2019) included the subfamilies Spalacinae, Rhizomyinae, Myospalacinae and the extinct Tachyoryctoidinae into the Spalacidae. The split of the Spalacidae and the Muridae from the other muroids was assumed by Steppan and Schenk (2017) to have occurred near the Eocene-Oligocene boundary (~ 34 Ma). Considering the age of *Debruijnina tintinnabulus* (~36 Ma, see Fig. 4), however, this split could be much older. Also, de Bruijn et al. (2015) showed that, based on the fossil record, the Spalacidae and the Rhizomyinae originated from distinctly different muroid stocks that were separated in time and space. A major strength of the fossil record is, that it not only provides the age of the appearance of a clade, but also information on their biogeography. All fossil and living spalacids, including the oldest Eocene representative, are exclusively found in the region of the Balkans, the Ukraine, Eastern Mediterranean and adjacent Middle East (this paper; Fig. 4; de Bruijn et al. 2015 and de Bruijn, 2016 show geographic distribution maps).

Flynn (2009) and López-Antoñanzas et al. (2012) recognised the, probably scansorial, *Prokanisamys kowalskii* (Lindsay, 1996) from the late Oligocene - early Miocene of Pakistan as the oldest representative of the subfamily Rhizomyinae. Although the dental pattern of the late Oligocene *Prokanisamys kowalskii* (originally included in *Eumyarion* by Lindsay, 1996) shows incipient rhizomyine characters, it still has a basic cricetine bauplan (Lindsay 1996, Flynn 2009); later species of *Prokanisamys* developed high crowns with a rhizomyine dental pattern (Fig. 5). Rhizomyinae, here ranked as a subfamily in the Muridae (s.l.), thus originated on the Indian subcontinent during the early Oligocene, during the early Miocene they migrated to Africa and during the middle Miocene to South-East Asia (Fig. 4; Lindsay 1996, Wessels and de Bruijn 2001, Flynn 2009, de Bruijn et al. 2015).

The Myospalacinae (zokors) are exclusively known from Central Asia, the earliest representative known is *Prosiphneus qiui* Zheng et al., 2004, from the late Miocene (Fig. 4; Qiu and Li 2016). Flynn (2009) suggests that zokors evolved from later, more derived muroids than the ancestral stock of the spalacines and rhizomyines. Molecular data, however, suggest a relation to spalacids and rhizomyines (Norris et al. 2004, Steppan et al. 2004, Steppan and Schenk (2017). Steppan and Schenk (2017) dated the split of the subfamilies Spalacinae, Rhizomyinae and Myospalacinae from an early muroid stock as late Oligocene (~24 Ma). Flynn et al. (2019) included the subfamily Myospalacinae in the Spalacidae. Li and Wang (2015) and Qiu and Li (2016) reviewed the family attribution of the zokors and suggested an

origin in the Plesiodipinae, a subfamily that we consider a junior synonym of the Cricetodontinae. Plesiodipines are extinct, occurring in the Miocene of central Nei Mongol. The molars of *Prosiphneus qiui*, the oldest species included in the Myospalacinae, dated at ~10.5 Ma, have an incipient microtoid-prismatic pattern resembling the microtoid cricetids, in particular those of Group G of Fejfar et al. (2011) that occur in Europe in MN 13-14 faunal assemblages; later zokors show rapid evolution towards rootless prismatic molars. Thus, there is no palaeontological support for a close relation of the Myospalacinae and the Spalacidae, with the zokors probably evolving from a cricetodontine (=plesiodipine) stock during the early or middle Miocene (Flynn 2009, Qiu and Li 2016).

Extensive new information has become available for the extinct subfamily Tachyoryctoidinae (Wang and Qiu 2012; Däxner-Hock et al. 2015, Qiu and Li 2016). Occurrences of this group are restricted to Central Asia in deposits ranging in age from the early part of the late Oligocene to the early part of the middle Miocene. Three genera may be included (Fig. 4), Qiu and Li (2016) include only *Tachyoryctoides*, *Ayakozomys* and *Eumysodon*, of which *Tachyoryctoides* is best known with a succession of species (Daxner-Höck et al. 2015). The relation of this group to the Spalacidae and Rhizomyinae is discussed by Wang and Qiu (2012), who favoured a family status for the Tachyoryctoidinae next to Spalacidae and Rhizomyidae. The analysis of López-Guerrero et al. (2017) suggests that Spalacidae and *Tachyoryctoides* are not related. The earliest known representative of the Tachyoryctoidinae is from the early part of the late Oligocene; it shows a distinctive tachyoryctoid dental pattern suggesting that its unknown muroid precursor is much older.

Spalacidae split from a muroid (*sensu lato*) stock during the Eocene, whereas the Rhizomyinae and Myospalacinae branched off from different murid stocks (*sensu lato*) during the early Oligocene and (early?) Miocene respectively (Fig. 4). It seems likely that Tachyoryctoidinae represents an early branch splitting too, but without the find of a tachyoryctoid precursor, this hypothesis cannot yet be demonstrated.

Extant Spalacinae and Rhizomyinae are the sole survivors of a large group of otherwise extinct Paleogene clades of muroids and thus these appear close relatives in molecular studies. Assuming that the Myospalacinae evolve from cricetodontines (=plesiodipines) these are likewise survivors from a Paleogene clade. The three surviving subfamilies are thus seemingly close relatives. The genotypic similarity of these survivors is thus, at least partly, a sampling artefact. Spalacidae, Rhizomyinae and Myospalacinae developed their underground lifestyles independently from each other (Flynn, 2009), this lifestyle may have been a decisive factor in their surviving. It may be speculated that adaptive responses to the stresses of

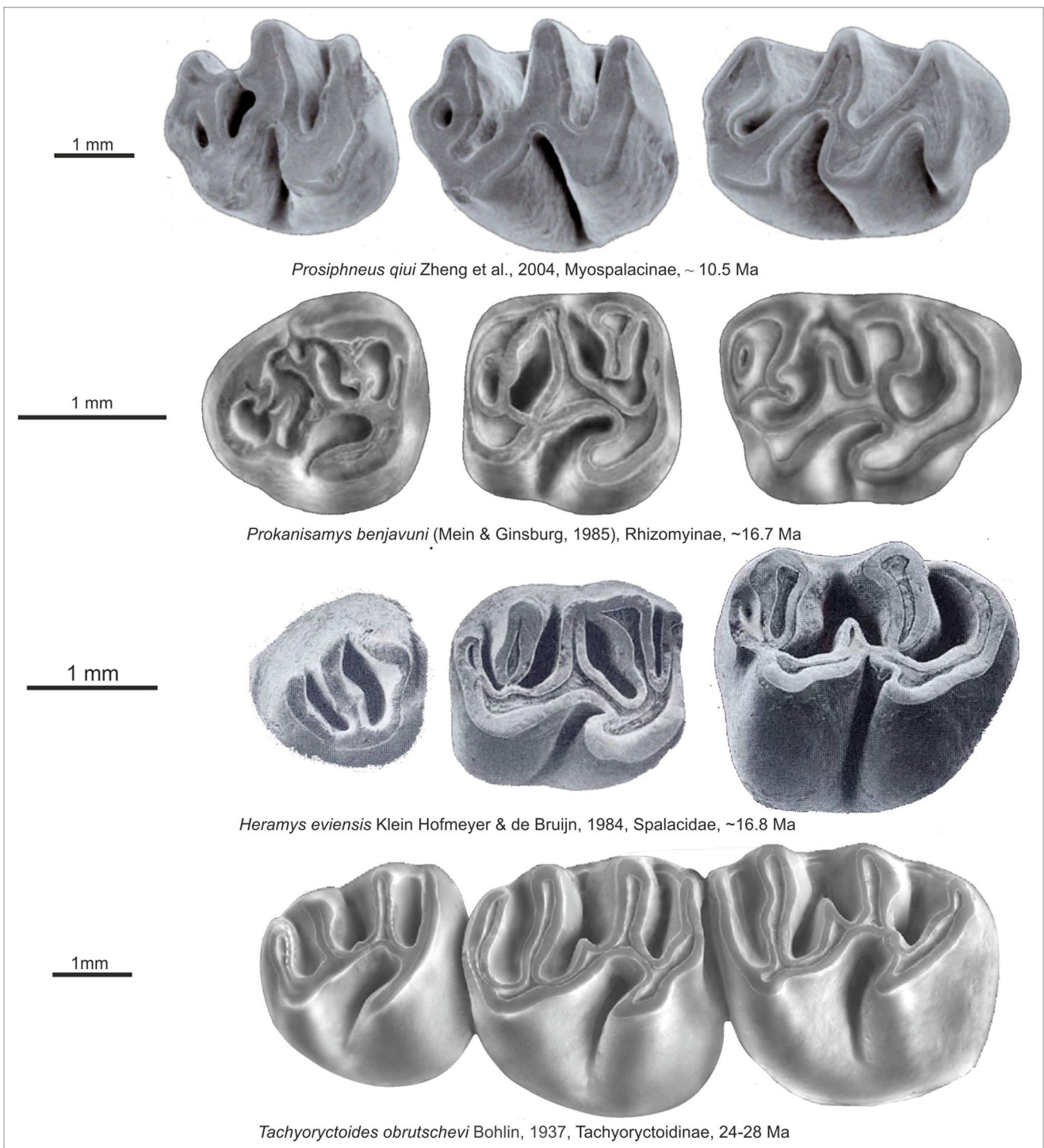


Fig. 5 Upper molars of *Prosiphneus qiui*, Amuwusu, Nei Mongol China, late Miocene, from Zheng et al. (2004); *Prokanisamys benjavuni*, site H-GSP 8114, Pakistan, early Miocene from Wessels and de Bruijn (2001); *Heramys eviensis*, Aliveri; early Miocene from Klein Hofmeijer and de

Bruijn (1984) and *Tachyoryctoides obrutschevi*, Altyn Schokysu Kazakhstan, late Oligocene, from Bendukize et al. (2009). Scales are different

underground life may have resulted in homoplasy and convergence of their genome (Fang et al. 2014).

Similarly, parallelisms occur in dental morphology, in particular in the upper first molar of the Tachyoryctoidinae,

Spalacidae and Rhizomyiinae (Figs. 5 and 6). The M1 of these families resemble each other closely, showing an anteroloph with integrated protocone and anterocone, this evolved independently in the three groups. However, the

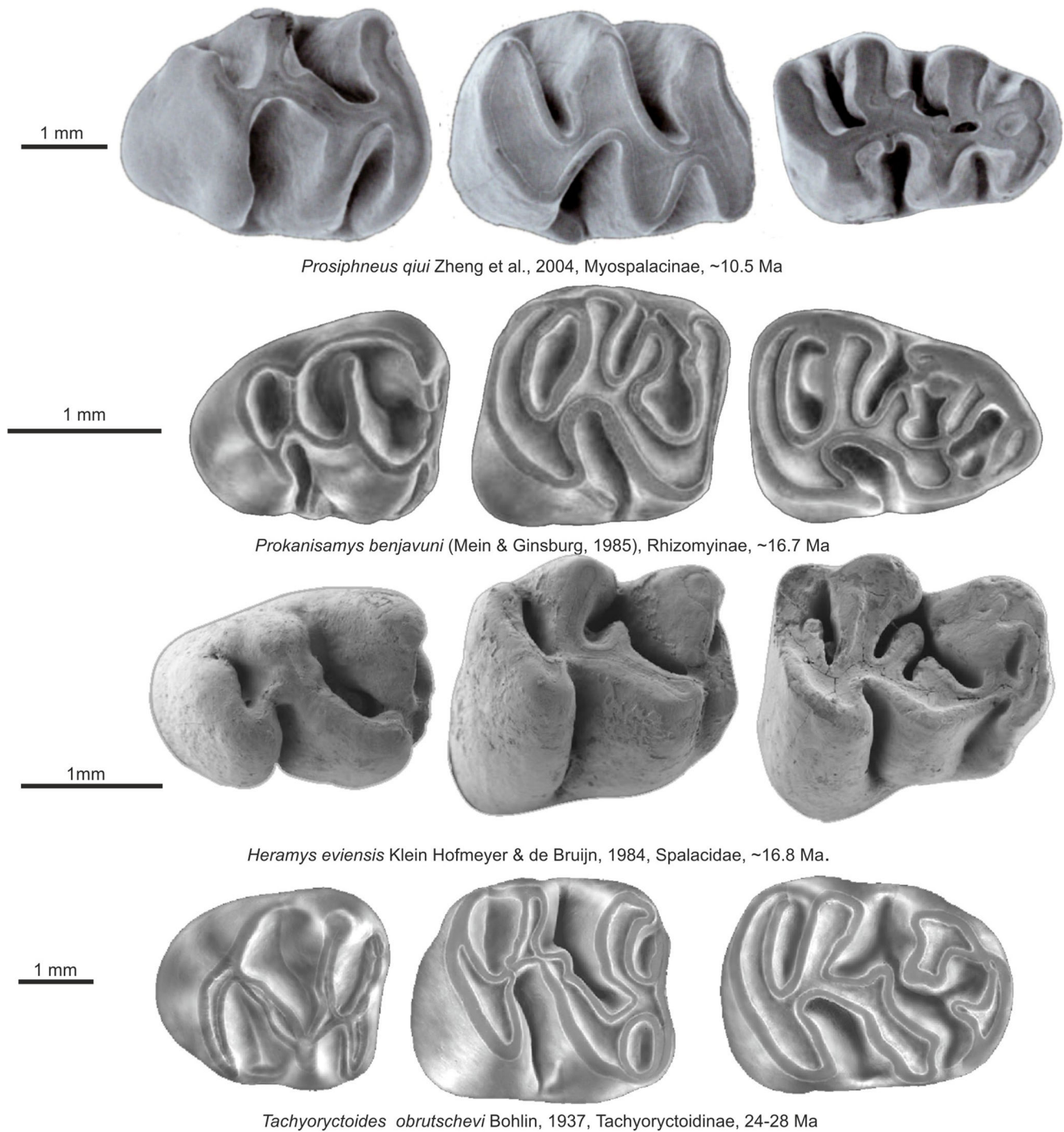


Fig. 6 Lower molars of *Prosiphneus qiu*, Amuwusu, Nei Mongol China, late Miocene, from Zheng et al. (2004); *Prokanisamys benjavuni*, site H-GSP 8114, Pakistan, early Miocene from Wessels and de Bruijn (2001); *Heramys eviensis*, Aliveri, early Miocene, from Klein Hofmeyer and de

Bruijn (1984) and *Tachyoryctoides obrutschevi*, Altyn Schokysu Kazakhstan, late Oligocene, from Bendukize et al. (2009). Scales are different

molars of the Myospalacinae are distinctly prismatic-microtoid (Figs. 5 and 6), thus totally different, showing that the evolution of this group took a different direction. Moreover, extant Myospalacinae are digging with their

front limbs, Spalacidae have reduced fore legs and use their protruding upper incisors and Rhizomyinae use both incisors and fore limbs (Kalthoff, 2000; Norris et al. 2004, Flynn 2009).

Conclusions

The discovery of the late Eocene *Debruijnina tintinnabulus* extends the stratigraphic range of the Spalacidae by about 10 Ma, showing that this family represents an early branch of the Muroidea, with an age much older than that of the Rhizomyinae and the Myospalacinae. Fossils show that Spalacidae, Rhizomyinae and Myospalacinae originated from different muroid and murid stocks, at different time intervals in different areas and are thus not closely related. Spalacidae originated in the late Eocene of what is now SE Europe (East Mediterranean region, this paper), the Rhizomyinae are a branch within the Muridae originating during the Oligocene in the Indian Subcontinent (Flynn 2009, de Bruijn et al. 2015) and the Myospalacinae are a branch in the Muridae originating during the early Miocene in Central Asia (Qiu and Li 2016). The fossil record thus supports genetic studies claiming that Spalacidae are an early branch of the Muroidea (Steppan et al. 2004; Steppan and Schenk 2017), but there is no support from the fossil record for the hypothesis that the Rhizomyinae and the Myospalacinae are part of the same branch and thus part of the same family. Finally, the available data suggests that the presumably fossorial Tachyoryctoidinae, which are exclusively known as fossils, had their roots in another muroid stock.

The so far poorly documented Paleogene history of the Spalacidae suggests presence of an Oligocene radiation leading to the genera *Pannoniamys*, *Vetusspalax* and *Heramys* (Fig. 4). *Debruijnina* and *Heramys* are near the basis of the wealth of the middle Miocene - Pliocene species, here all tentatively allocated to *Pliospalax*.

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Data availability Data sharing not applicable to this article as no datasets were generated or analysed during the current study. The material of *Debruijnina tintinnabulus* is housed in the Natural History Museum in Belgrade under the locality code 036.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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