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# A new stage in the evolution of the mole rats (Rodentia, Spalacinae) from the Early Miocene of northern Greece

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## ABSTRACT

The cheek teeth of *Debruijnina kostakii* n. sp. from the Early Miocene of Karydia are only slightly smaller than those of the largest extant species of the Spalacinae (*Spalax giganteus*), but show characteristics that are reminiscent of its Paleogene cricetid ancestor. The peculiar combination of large size and primitive dental morphology of this species bridges the gap between *Debruijnina* and *Pliospalax* and thereby supports the hypothesis that these genera form the core of the complex evolutionary history leading to extant *Spalax*.

## ARTICLE HISTORY

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Early Miocene; Greece;  
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species

## Introduction

The fossiliferous lacustrine deposit of Karydia was discovered by Mr. Dimitris Foussekis and the author during a prospection trip in the early nineties of the last century. Karydia 1 refers to the small test sample taken from the, at the time abandoned, quarry on the west side of Karydia Hill. Karydia 2 and 3 refer to lignitic clay beds at the top of two superposed sediment cycles exposed in the quarry on the east side of the hill. Lithostratigraphical correlation of the deposits exposed in these two quarries was impossible due to lack of exposure and the presence of faults. Samples of several tons of matrix from Karydia 2 were collected and wet-screened during three consecutive years. This means that the large spalacine that will be described below occurs at a rate of about four cheek teeth per ton of matrix.

The fossil record of the fossorial muroid rodents assembled in the subfamily Spalacinae can be traced to the Late Oligocene of south eastern Europe (De Bruijn et al. 2013; De Bruijn et al., 2015), but the group is probably much older. The evolutionary history of the mole-rats is largely based on isolated cheek teeth from south eastern European and Middle Eastern localities, that is to say, from the core of the area occupied by the extant representatives (Figure 1). Although the number of sites that have yielded spalacine teeth is quite large the number of specimens per site is usually limited. This makes the evaluation of samples difficult because, in addition to the regular individual variation of details of the occlusal pattern, the morphology of the occlusal surface of these semi-hypsodont teeth changes as a result of attrition (De Bruijn et al., 2015).

The similarity in overall dental architecture of all Spalacinae (rather high-crowned robust teeth with thick enamel, cusps incorporated into the lophs, metaconid of the m1 large and situated at the level of the anteroconid) and the limited geographical range occupied by its representatives through time suggests that it is a very closely knit clade. Representatives from different time-slices

show a, seemingly random, mosaic-like combination of primitive (low-crowned and complex) and derived (high-crowned and simple) dental characteristics. This ‘homogeneity’ and the lack of polarity in the development of the dental features through time resulted in the recognition of only four, poorly delimited, fossil genera (*Vetuspalax*, De Bruijn, Marković & Wessels 2013, *Debruijnina*, Ünay, 1996, *Heramys* Klein Hofmeijer & De Bruijn, 1985 and *Pliospalax* Kormos, 1932 = *Sinapospalax* Sarica & Sen, 2003 see De Bruijn et al., 2013, 2015). Since Spalacine species do not cluster into readily recognizable groups generic allocation remains subjective. This peculiar property is exemplified by the material that will be described below.

## Methods

The material described below is housed in the collections of the department of Earth Sciences of Utrecht University, the Netherlands. Measurements have been taken with an Ortholux microscope with mechanical stage and measuring clocks and are given in 0.1 mm. units. Upper molars are indicated by M1–3, lower molars by m1–3. Specimens are all figured as from the left side. If the original is from the right side its number on the plate has been underlined. All pictures were taken with a Jeol table SEM.

## Systematic paleontology

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Spalacinae Gray, 1821

Extinct genera included: *Vetuspalax*, *Debruijnina*, *Heramys* and *Pliospalax*

Genus *Debruijnina* Ünay, 1996

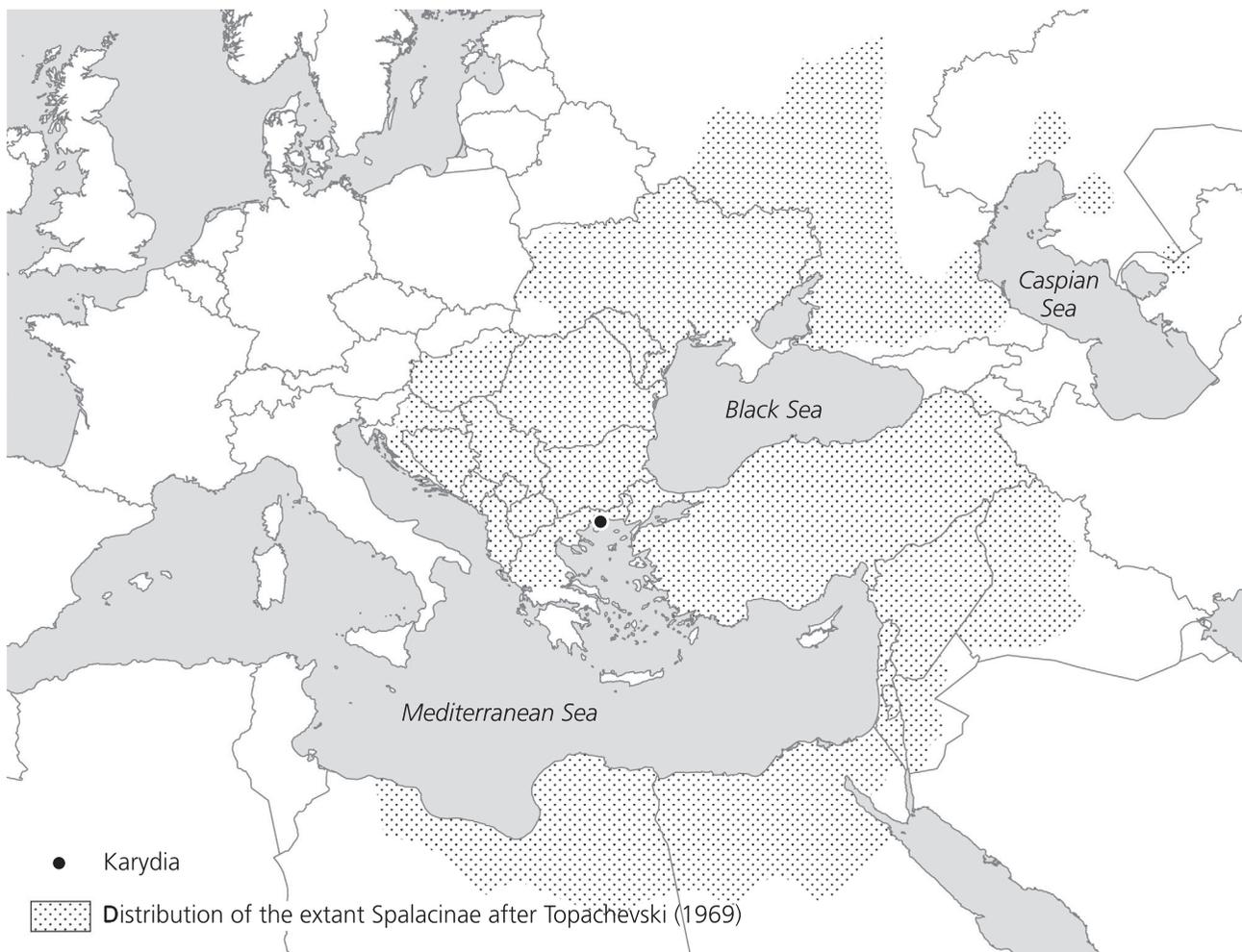
Type species *Debruijnina arpatii* Ünay, 1996

Type locality and level: Keseköy, Anatolia, MN3

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**Figure 1.** Map of Europe, the Middle East and North Africa showing the geographical range of the extant Spalacinae and the position of the locality Karydia.

Other species included: *Debruijnia* sp. (in Ünay and Göktaş, 1999), *Debruijnia kostakii* n. sp.

*Debruijnia kostakii* n.sp.

Figures 2 and 3

Selected reference: *Debruijnia kostakii* n. sp. *Debruijnia* n. sp (large) in Theocharopoulos (2000, p. 86).

Derivatio nominis: I dedicate this species to the late Constantinos D. Theocharopoulos (Kostaki for friends) who showed admirable character and stamina when we collected the Karydia material in the rain.

Holotype: m1 dext. KR 2, nr. 1014, Figure 3(1a & 1b).

Type locality: Karydia 2, (KR 2), Greece, MN4.

Diagnosis: *Debruijnia kostakii* is a large spalacine. The anteroloph of the M1 is separated from the protocone by a shallow notch and the anterior arm of the protocone is either complete or interrupted. The metalophule is transverse in some M1, but connected to the posteroloph in others. The sinus of the five-lobed M3 remains open lingually until an advanced stage of wear. The m1 is elongate and its metaconid does not fuse with the anteroconid until a late wear stage. The protosinusid is progressively less developed from m1 through m3. A long free-ending posterior arm of the hypoconid is present in fresh m1.

Differential diagnosis: Most teeth of *Debruijnia kostakii* are somewhat larger than those of *P. sinapensis* Sarica & Sen, 2003

(MN10), *P. canakkalensis* Ünay, 1981 (MN7/8) and *P. primitivus* Ünay, 1978 (MN7/8). Their dental pattern is in many respects intermediate between the type species of the genus *D. arpatti* and the oldest known *Pliospalax*: *P. marmarensis* Ünay, 1990. The degree of lophodonty and hypsodonty in *D. kostakii* is similar as in *Pliospalax*, but its cheek teeth differ in retaining plesiomorph details such as the presence of the anterior arm of the protocone in the M1 and the free-ending posterior arm of the hypoconid in the m1. In these respects *D. kostakii* it is closer to *Debruijnia* than to *Pliospalax*.

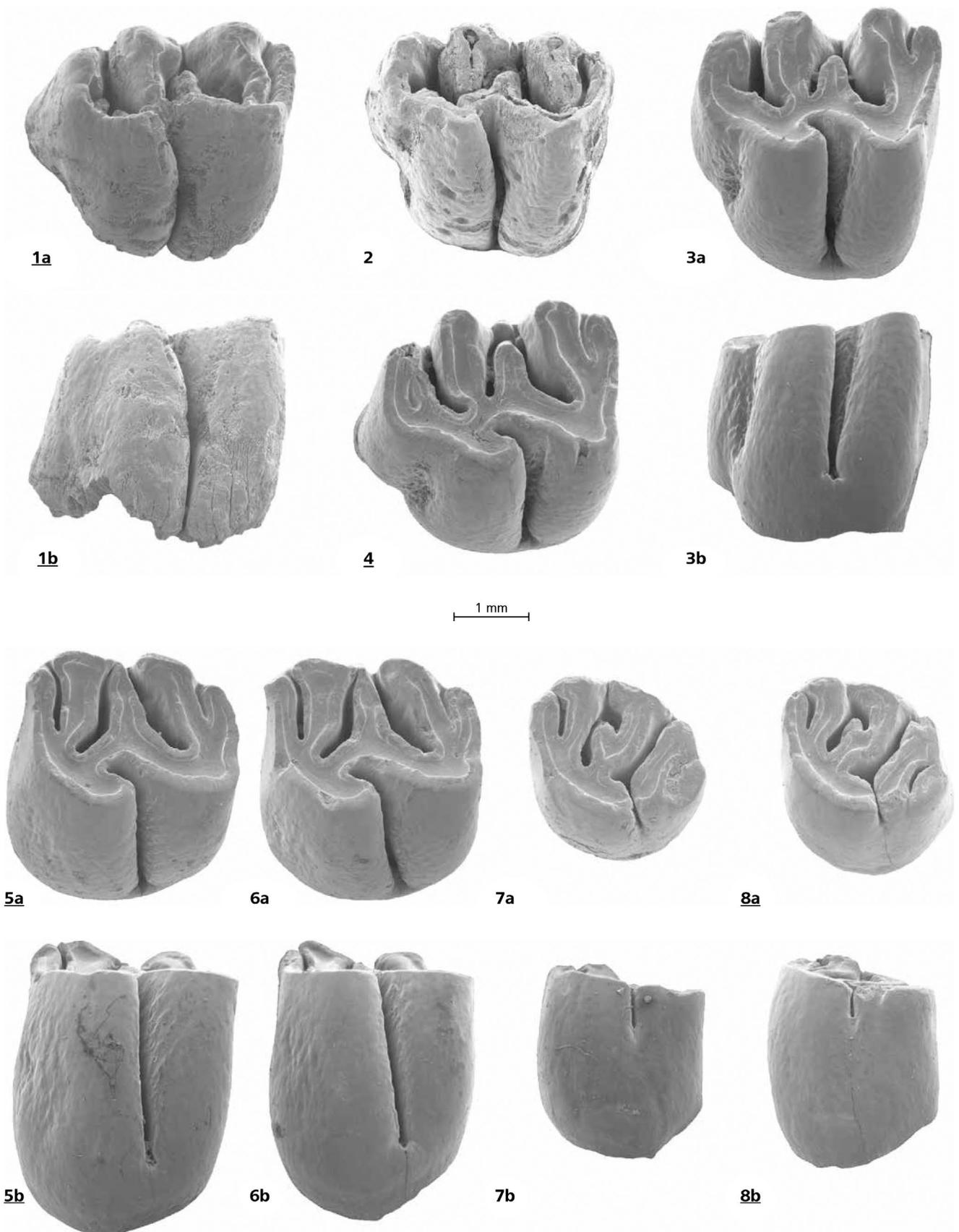
## Materials and measurements

### Karydia 2

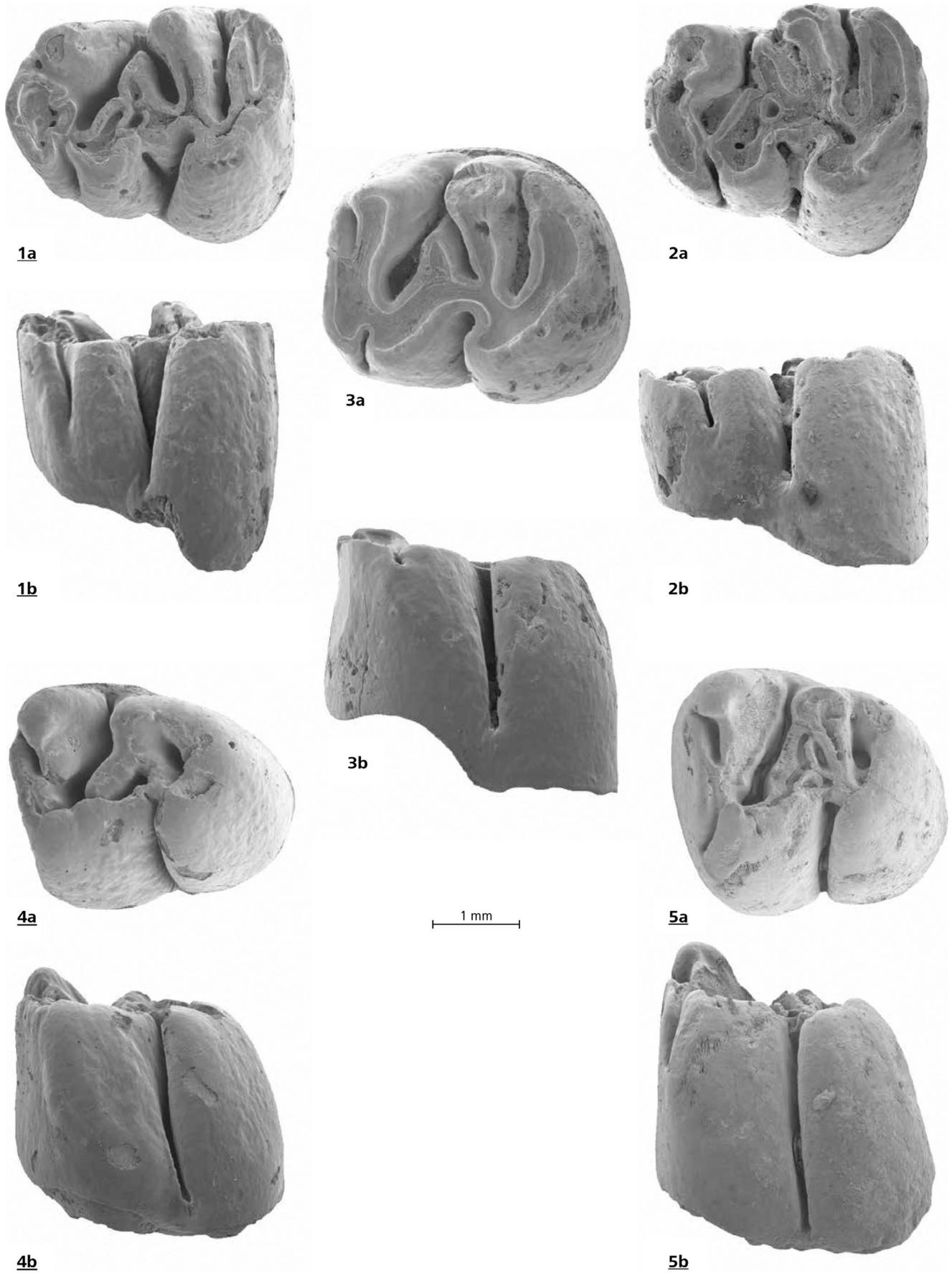
	Length			Width	
	Range	Mean	N	Mean	Range
M1	30.7–32.3	31.6	4	26.3	25.9–27.3
M2	26.7–28.2	27.7	5	26.0	24.1–28.8
M3	21.5–22.2	21.8	2	21.8	21.4–22.3
m1	29.9–32.6	30.7	3/4	24.1	22.9–26.5
m2	30.0–30.5	30.3	2/1	20.7	
m3	29.9–30.3	30.1	2/3	25.7	24.3–26.7

### Karydia 3

1 M1 32.5 × 24.1



**Figure 2.** *Debruijnina kostakii* from Karydia 2: 1 a, b, M1 inverse No. 1027, 3 a, b, M1 No. 1021, 4, M1 No. 1023, 5 a, b, M2 inverse No. 1035, 6 a, b, M2 No. 1031, 7 a, b, M3 No. 1038, 8 a, b, M3 No. 1039. *Debruijnina kostakii* from Karydia 3. Figure 2 M1 No. 1041.  
 Note: Specimens figured inverse are underlined.



**Figure 3.** *Debruijnina kostakii* from Karydia 2: 1 a, b, m1 No. 1014, 2 a, b, m1 No. 1013, 3 a, b m2 No. 1016. 4 a, b, m3 No. 1019, 5 m3 No. 1020. Note: Specimens figured inverse are underlined.

## Description

M1. The depth of the notch that separates the anterocone from the protocone and the development of the anterior arm of the protocone of the M1 show considerable individual differences. The mesoloph is strong, but never reaches the labial edge of the occlusal surface.

M2. All five M2 are similar. Their sinuses reach almost to the base of the crowns, their protolophules are directed forwards and connect to the anteroloph just labially of the protocone while the metalophules are directed posteriorly and connect to the posteroloph just labial of the hypocones.

M3. The two available M3 are very similar, both have five lophes and a sinus that does not reach as close to the base of the crown as in the M1 and M2.

m1. The anterior outline of the m1 is like in most cricetids, because the anteroconid is not fused with the far forwards situated metaconid as in *Pliospalax*. The labially open protosinusid reaches rather far down. The short robust posterior arm of the protoconid ends free. The mesolophid is strong. The long posterior arm of the hypoconid fuses with the posterolophid in a rather early wear stage.

m2. The protosinusid of the m2 does not reach far down. The robust posterior arm of the protoconid ends free and the mesolophid and the posterior arm of the hypoconid are absent.

m3. The protosinus of the m3 is very weak. The posterior arm of the protoconid is directed postero-lingually and may connect to the entoconid. The short, rudimentary hypolophulid is directed towards the hypoconid.

## Conclusions

The age estimate for the Karydia assemblage is late Early Miocene (MN4) (Theocharopoulos, 2000), an age that is intermediate between that for Keseköy (MN3) (Ünay et al. 2003), type locality of the type species of *Debruijnina*, and for Paşalar (MN5) (Ünay et al. 2003), the locality that yielded the oldest *Pliospalax*. The dental morphology of *D. kostakii* bridges the gap between *Debruijnina* and *Pliospalax* which suggests that these are closely related. Its cheek teeth are, however, larger than those of any of the younger species of *Pliospalax*. It seems therefore unlikely that there is a direct ancestor – descendant relationship between *P. kostakii* and a known species of *Pliospalax*. The occurrence of seemingly random combinations of dental characteristics in species of different genera shows that the complex evolution of the Spalacinae is poorly understood. The available record suggests that *Debruijnina* and *Pliospalax* are part of the main lineage leading to the extant Spalacinae, while *Heramys* with its high-crowned cheek teeth and reduced M3, and *Vetusspalax* with its relatively brachyodont simple teeth represent extinct branches.

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## Disclosure statement

No potential conflict of interest was reported by the author.

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