

*Prospalax priscus* from the upper Pliocene (MN16) of Ridjake,  
Serbia, and its phylogenetic position within Anomalomyinae  
(Rodentia, Muridae)

Nadine Lockett

12/08/2024

MSc thesis Earth, Life and Climate

Utrecht University

Supervisor: Dr. Wilma Wessels

Second supervisor: Dr. Emilia Jarochowska

## LEGEND

<b>Abstract</b>	<b>3</b>
<b>Introduction</b>	<b>4</b>
Ridjake, Serbia	4
Overview list of species within Anomalomyinae	5
<i>Prospalax priscus</i>	6
This research	7
<b>Methods</b>	<b>8</b>
Material	8
Microscopy	8
Nomenclature	8
Phylogenetic analysis	10
<b>Systematic palaeontology</b>	<b>11</b>
<b>Size</b>	<b>16</b>
<b>Phylogenetic analysis</b>	<b>18</b>
Phylogenetic trees	20
Age distribution	20
Geographical distribution	21
<b>Discussion</b>	<b>23</b>
Phylogenetic discussion and geography	23
<i>Eumyarion</i>	25
<i>Anomalospalax</i>	25
Wear and changing morphology	25
<b>Conclusion</b>	<b>27</b>
<b>Acknowledgements</b>	<b>27</b>
<b>References</b>	<b>28</b>
<b>Appendix 1: List of all specimens including size</b>	<b>31</b>
<b>Appendix 2: Morphological characteristics for phylogenetic analysis</b>	<b>35</b>

## ABSTRACT

From Ridjake, Serbia (MN16) 160 molars of *Prospalax priscus* were studied. Together with *Anomalomys* and *Anomalospalax*, *Prospalax* is part of the extinct Anomalomyinae. A phylogenetic analysis was performed comparing the *P. priscus* material from Ridjake, Serbia to literature on *Anomalomys minor*, *A. aliveriensis*, *A. gaudryi*, *A. gaillardi*, *A. grytsivensis*, *P. petteri*, *P. priscus*, *Anomalospalax tardosi* and *Eumyarion bifidus*. This was done to get a better understanding of the relations between species within Anomalomyinae. This is difficult as Anomalomyinae have hypsodont molars which wear down over time. The occlusal pattern of lophes/lophids and cones/conids changes significantly depending on the amount of wear these molars experience. This makes it difficult to find morphological characteristics to compare the different species and requires one to compare molars at the same amount of wear. The resulting phylogenetic tree shows the closeness of *Prospalax* and *Anomalospalax*. This group has likely evolved from *A. gaudryi*, *A. gaillardi* and *A. grytsivensis*, which in their turn evolved from *A. minor* and *A. aliveriensis*. This hypothesis fits well with the different MN-ages of all species. It is hypothesised that two migration events occurred in which Anomalomyinae migrated from Asia into Europe. The first migration brought in *A. minor* and *A. aliveriensis*. The second migration brought in *A. gaudryi*, *A. grytsivensis* and *A. gaillardi*. Although a phylogenetic analysis was performed, the constraints of the molar wear and lack of physical material limited the phylogenetic analysis. To get a full understanding of the changing morphology in Anomalomyinae and the differences between species, Anomalomyinae molars should be x-rayed. Then, the occlusal surface can be studied layer by layer to understand the changing morphology in Anomalomyinae species. This would help solve the question which species are truly distinct and which species may have been mistakenly identified as a new species only due to wear changing the molars' morphology.

## INTRODUCTION

### Ridjake, Serbia

During palaeontological research between 2005 and 2014 near Ridjake, Serbia ( $44^{\circ}39'28''$  N,  $19^{\circ}45'50''$  E; Figure 1), fossilised remains of many different mammal species were found as described in Radović et al. (2019). These fossils were found in red, clayey sand-filled palaeokarst depressions and dated to be of early Villafranchian age (MN16). The identified mammal species showed a heterogeneous composition, meaning they lived in various different habitats (Radović et al., 2019). One of the identified species found is *Prospalax priscus*, of which 160 molar fragments were found.

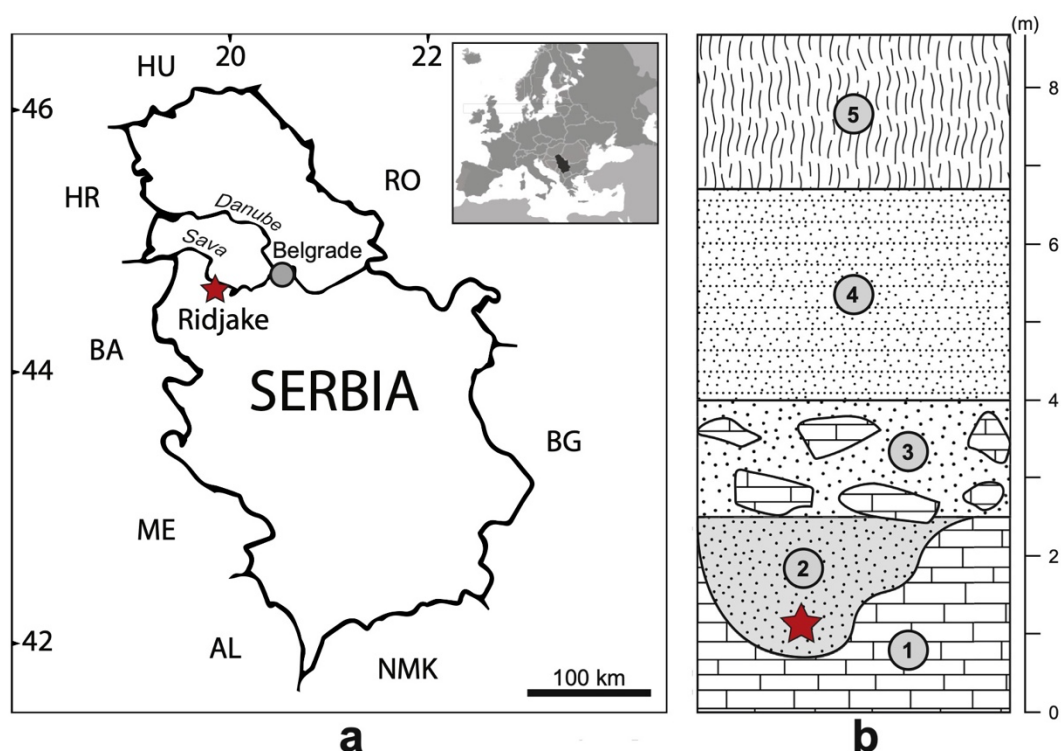


Figure 1 – Location of Ridjake ( $44^{\circ}39'28''$  N,  $19^{\circ}45'50''$  E) in Serbia and the palaeokarst depression in which the *Prospalax priscus* fossils were found. Figure taken from Radović et al. (2019).



## Overview list of species within *Anomalomyinae* SCHAUB, 1925

### *Anomalomys* GAILLARD, 1900

<i>A. aliveriensis</i>	KLEIN HOFMEIJER & DE BRUIJN, 1985	MN4
<i>A. minor</i>	FEJFAR, 1972	MN4-5
<i>A. minutus</i>	BOLLIGER, 1992	MN5
<i>A. gaudryi</i>	GAILLARD, 1900	MN6-9
? <i>A. kowalskii</i>	KORDOS, 1989	MN7/8
? <i>A. rudabanyensis</i>	KORDOS, 1989	MN9
<i>A. grytsivensis</i>	NESIN & KOVALCHUK, 2021	MN9
<i>A. gaillardi</i>	VIRET & SCHAUB, 1946	MN9-11
? <i>A. gernotti</i>	DAXNER-HÖCK, 1980	MN11

### *Prospalax* MÉHELY, 1908

<i>P. petteri</i>	BACHMAYER & WILSON, 1970	MN10-11
<i>P. priscus</i>	(NEHRING, 1897 as <i>Spalax priscus</i> ) MÉHELY, 1908	MN15-16/17
? <i>P. kretzoi</i>	JÁNOSSY, 1972	?
? <i>P. rumanus</i>	SIMIONESCU, 1930	MN16?

### ? *Anomalospalax* KORDOS, 1985

<i>An. tardosi</i>	KORDOS, 1985	MN12
? <i>An. viretschaubi</i>	(KRETZOI, 1971 as <i>Anomalomys viretschaubi</i> ) KORDOS, 1985	MN13

### ***Prospalax priscus***

*Prospalax priscus* is a species of muroid within the extinct Anomalomyidae (Schaub, 1925) family and Anomalomyinae subfamily (De Bruijn, 1984). Anomalomyinae is sometimes considered a subfamily within Spalacidae (Fejfar, 1972) or Cricetidae (López-Guerrero et al., 2017), but these are not popular hypotheses. To avoid making any conclusions, this thesis will use Anomalomyinae as it is also used by De Bruijn et al. (2015) and as it can therefore be considered a subfamily within Anomalomyidae as well as potentially belonging to a different family.

Previously, *Prospalax* was thought to be part of the Spalacinae, another subfamily within the Muridae, due to its relative robustness and simplified molar pattern compared to *Anomalomys* (Fejfar, 1972; De Bruijn, 1984). Some have also considered it as part of the Cricetidae together with *Anomalomys* (Bachmayer and Wilson, 1970; 1978). Later the genus was added to the Anomalomyinae, as the lower dentition of *Prospalax* has many similarities with the lower dentition of *Anomalomys*. Kretzoi (1971) considered *Allospalax*, *Miospalax* and *Pterospalax* to belong to the same family as *Prospalax* and *Anomalospalax*, but most no longer consider these genera to be distinct genera. Thus to summarise, the name *Prospalax* still includes 'spalax' even though it is no longer considered an ancestor of *Spalax* and part of the Spalacidae (De Bruijn, 1984). Many now think that Spalacinae and Anomalomyinae are not closely related (De Bruijn et al., 2015). An ongoing hypothesis is that Anomalomyinae and *Eumyarion* share a common ancestor (Bolliger, 1999). *Eumyarion* is a muroid genus which lived in Europe and Asia during Oligocene and Miocene. Some also hypothesise *Argyromys aralensis*, a cricetid which lived in Kazakhstan during the Oligocene, to be an ancestor of *Anomalomys* and *Prospalax* (López-Guerrero et al., 2017; Czernielewski, 2023).

*Prospalax priscus* is known from the late Pliocene (MN15-16/17). The other two genera within Anomalomyinae are *Anomalomys* and *Anomalospalax*. *Anomalomys* is the ancestor of *Prospalax*, with *Anomalospalax* being intermediate stage between the two. *Anomalomys* is characterised by smaller molars with a more complex enamel pattern, while *Prospalax* has more robust molars and a simplified enamel pattern (Kordos, 1985; Bolliger, 1996). The list on page 5 gives an overview of all species within Anomalomyinae. Question marks indicate uncertainties in both the age as well as uncertainty in if a certain species/genus is truly distinct enough to be considered a separate species/genus. Anomalomyinae are mainly known from

Europe, though the early species of *Anomalomys aliveriensis* (MN4) is also known to have lived in Turkey (Dangremond, 2012).

Anomalomyinae had hypsodont molars which would wear down throughout their life. This created characteristic wear patterns in their molars, which changed over time as they worn down with age. This variability in patterns makes studying the morphology of Anomalomyinae molars difficult, as different occlusal patterns do not automatically indicate a different species. It is therefore preferable to study larger fossil assemblages, to not mistakenly assign one or a few molars to a new species, based on a limited understanding of the variations in the molars' occlusal pattern. This is why some of the species (page 5) have been questioned to be distinct species, as their fossil assemblages are very limited.

### **This research**

This research focusses on getting a better understanding of Anomalomyinae by performing a phylogenetic analysis. This is important as relations within this subfamily are not fully understood. Several questions were asked. How do the species compare based on morphological characteristics? Is *Anomalospalax* so distinct that it warrants its own species? How many potential migrations took place from Asia into Europe? Did all Anomalomyinae species migrate into Europe all at once? And is the link between Anomalomyinae and *Eumyarion* plausible?

To answer these questions a phylogenetic analysis will be done by taking morphological characteristics from several species within this family and comparing them to each other to create a phylogenetic tree. This is important as the relationship between Anomalomyinae species is still a significant point of discussion and no analysis exists in scientific literature.

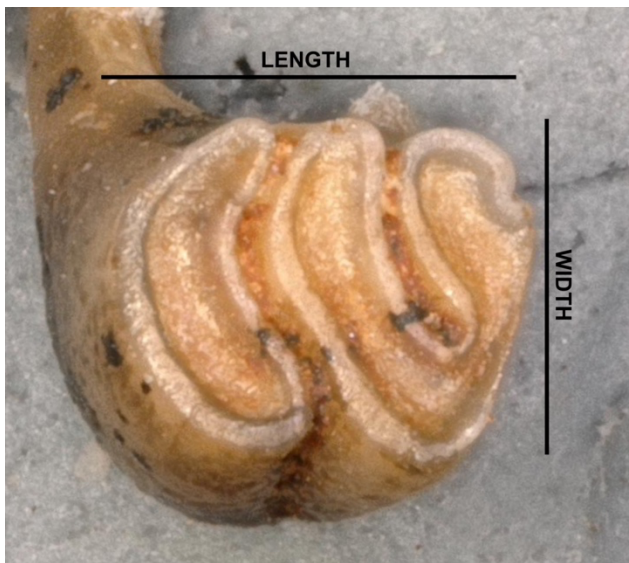
## METHODS

### Material

160 individual molars of *Prospalax priscus* from Ridjake, Serbia, were studied. The code RID- was used followed by a number to identify them. Only 3 left M2/ could be studied as the box with these molars had gone missing.

### Microscopy

To study the material a Leica S9E light microscope was used. Measurements were taken using a Leitz Wetzlar ortholux microscope with mechanical stage and measuring clocks. Measurements were taken of the length and width of molars as shown in Figure 2. A Keyence microscope with a VHZ20R lens (20-200x zoom) was used to take photos.



*Figure 2 – Length measurements were taken along the longest axis; width measurements were taken perpendicular. Measurements were taken of the occlusal area. Molar pictured is RID-003.*

### Nomenclature

Terminology is given in Figures 3 and 4 and was taken from Topachevskii (1976) and Kordos (2005).



### Phylogenetic analysis

The dental characteristics used for phylogenetic analysis were based on medium wear as shown in Figure 5 and 6. *Prospalax priscus* specimens from Ridjake, Serbia were studied under the microscope. The other species' morphology characteristics were taken from the literature: *Anomalomys minor* (Bolliger, 1999); *A. aliveriensis* (Klein Hofmeijer and De Bruijn, 1985), *A. gaudryi* (Bolliger, 1999; Hír and Kókay, 2010), *A. gaillardi* (Bolliger, 1999), *A. grytsivensis* (Nesin and Kovalchuk, 2021), *Prospalax petteri* (Bolliger, 1999; Daxner-Höck, 1980), *Anomalospalax tardosi* (Bolliger, 1999; Kordos, 1985), and as an outgroup species *Eumyarion bifidus* (De Bruijn, 2009). This species was chosen as it is both in age (MN5) and geographical location (Germany) close to the studied Anomalomyinae species, specifically *A. minor* which lived in the same region during the same time. *A. minutus*, *A. kowalskii*, *A. gernoti*, *P. rumanus*, *P. kretzoi* and *An. viretschaubi* were left out of the phylogenetic analysis due to the little number of specimens and/or questionable creation of a new species. W-IQ-TREE (Trifinopoulos et al., 2016; Hoang et al., 2018) was used to create phylogenetic trees of maximum likelihood.

## SYSTEMATIC PALAEOLOGY

Order RODENTIA Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Anomalomyinae Schaub, 1925

Genus *Prospalax* Méhely, 1908

Species *Prospalax priscus* (Nehring, 1897)

First described as *Spalax priscus* by Nehring (1897), from Villány, Hungary.

Later renamed as *Prospalax priscus* by Méhely (1908).

Age: late Pliocene, MN15-16/17 (Bolliger, 1996).

### DESCRIPTION

*Prospalax priscus* molars are hypsodont and the studied specimens show varying degrees of wear (Figure 6). This can influence the pattern of lophs, cones and sinuses or lophids, conids and sinusids as found on the occlusal surfaces of the molars. As wear can cause some molars to look quite similar, the easiest way to differentiate are their shape and number of roots, two in the lower molars and three in the upper molars.

Figure 5 shows an example of the upper and lower molars studied. Sulimski (1964) studied *Prospalax priscus* molars within the lower and upper jaws. Figures 7 and 8 show his pictures.

**Lower molars.** The lower molars have two roots, one on the anterior and one on the posterior side. The molars lean forward in the jaw.

**m/1.** The m/1 is relatively narrow and widens posteriorly. Its shape is rounder on the anterior side and flatter on the posterior side where it sits next to the m/2. Its anterolophid is connected to the protolophid on the labial side. With wear this connection becomes weaker, but never disappears. With extreme wear these two lophs also become connected lingually. A distinction between the mesolophid and entoconid is only seen in one lightly worn molar. The hypolophid is found centrally, though through wear this connection between the metolophid and posterolophid moves to the lingual side. This causes the posterosinusid to disappear.

**m/2.** The m/2 is slightly wider and shorter on average than the m/1. Its shape is more rectangular as it is the middle of the three molars, though it is slightly rounder posteriorly

than anteriorly. The anterolophid and protolophid are connected on the labial side. With extreme wear they will connect on the lingual side as in the m/1. The hypolophid is located centrally in less worn molars and moved further to the lingual side with more wear. With even less wear the hypolophid is not visible as the mesolophid and posterolophid are not connected.

**m/3.** The m/3 is more elongated than the m/2. Its shape is flatter towards the anterior side and rounder towards the posterior side. As in the m/1 and m/2, the anterolophid and protolophid are connected labially. With extreme wear they also connect lingually. The hypolophid connection between the mesolophid and the posterolophid is located centrally, and with wear moved to the lingual side. When little wear has occurred the hypolophid cannot be observed.

**Upper molars.** The upper molars have three roots, one on the lingual side and two on the labial side of the molars. The molars lean backwards in the jaw and are rounded lingually.

**M1/.** The M1/ has a rounder shape than any of the lower molars. Especially with increased wear the molar gets a rounder shape. The posterior side is flatter than the anterior side. Its roots point to the labial side. The anteroloph is not connected to the paraloph unless the molar is very worn, in which case they are connected labially. With extreme wear they also connect lingually and may even start showing a connection centrally. The mesoloph and posteroloph are connected on the lingual side. In minimally worn molars the posteroloph and metacone are distinctly separated.

**M2/.** The M2/ has a rounded shape with, compared to the M1/, two straighter edges anteriorly and posteriorly. Two small roots face the labial side. Just as in the M1/, the anteroloph and paraloph are not connected unless the molar is significantly worn, in which case these lophs connect on the labial side. With extreme wear they also connect lingually.

**M3/.** The M3/ has a round shape and is slightly wider on the anterior side than on the posterior side. One of its roots points posteriorly. The anteroloph and paraloph are connected anterolabially. The mesoloph and posteroloph are connected lingually. With extreme wear these also connect on the labial side.





Figure 5 – Left molars of *Prospalax priscus* from Ridjake, Serbia. Upper row shows upper molars, from left to right: M1/, M2/, M3/. Lower row shows lower molars, from left to right: m/1, m/2, m/3. Sample names in the aforementioned order are: RID-003, RID-071 (mirrored photo), RID-081, RID-121, RID-158, RID-202.

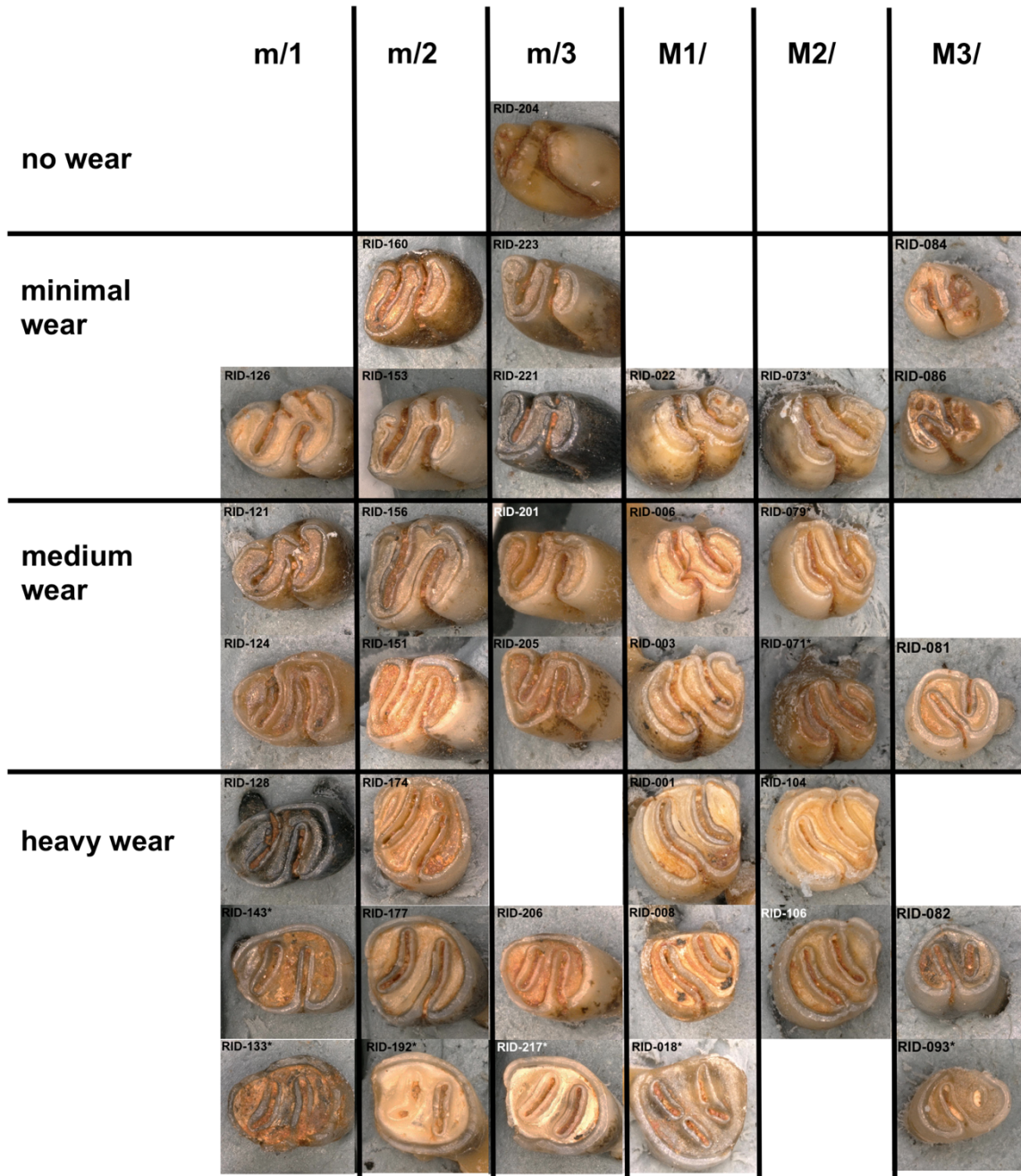


Figure 6 – Stages of wear in *Prospalax priscus* molars from Ridjake, Serbia. All molars are pictured as left molars. An asterisk indicate the photo has been mirrored, and thus is a right molar.

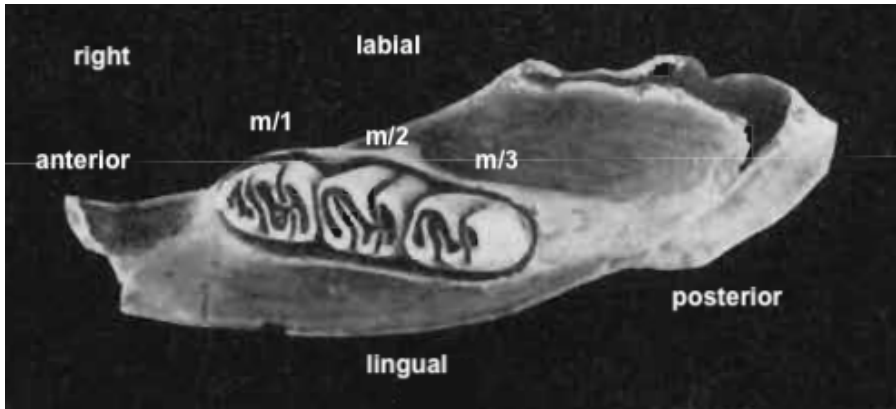


Figure 7 – Lower right jaw of *Prospalax priscus*. Photo taken from Sulimski (1964). Annotations have been added for clarity.

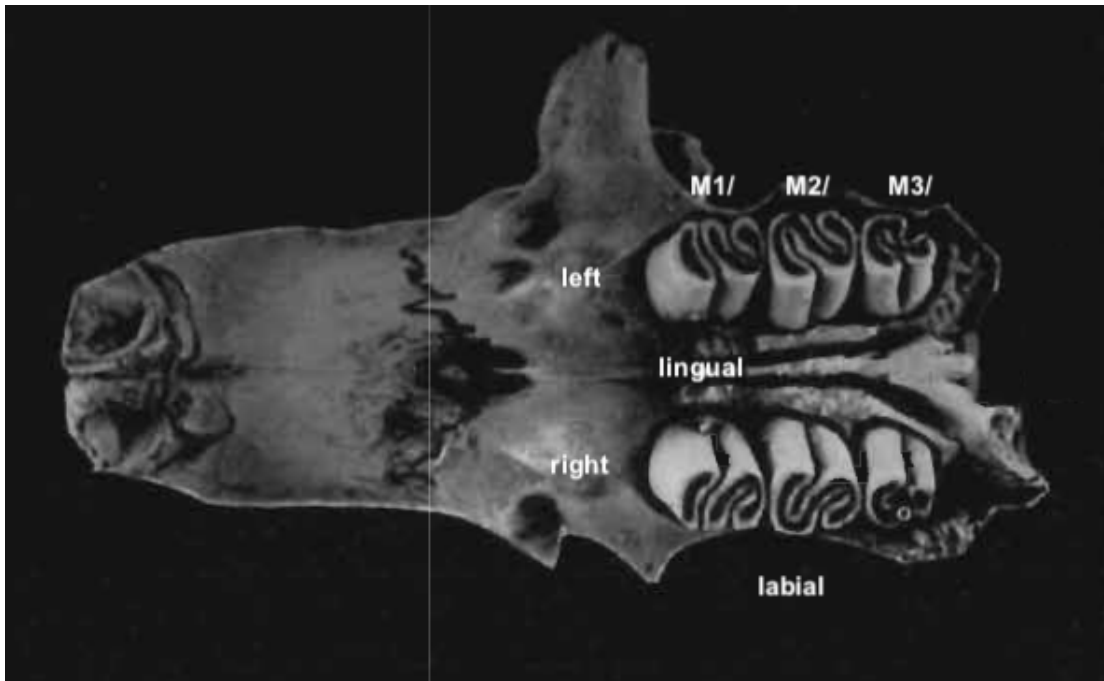


Figure 8 – Upper jaw of *Prospalax priscus*. Photo taken from Sulimski (1964). Annotations have been added for clarity.

## SIZE

Figure 8 shows a size diagram of the studied molars. It shows a relatively wide range of sizes, with m/3 showing the largest size variation and M3/ and m/2 showing the least size variation. It has to be noted that wear over time can cause the occlusal area to become larger as the molars widen from the crown towards the roots. Appendix 1 list the size of every molar individually. Table 1 gives the minimum, maximum and average sizes per molar.

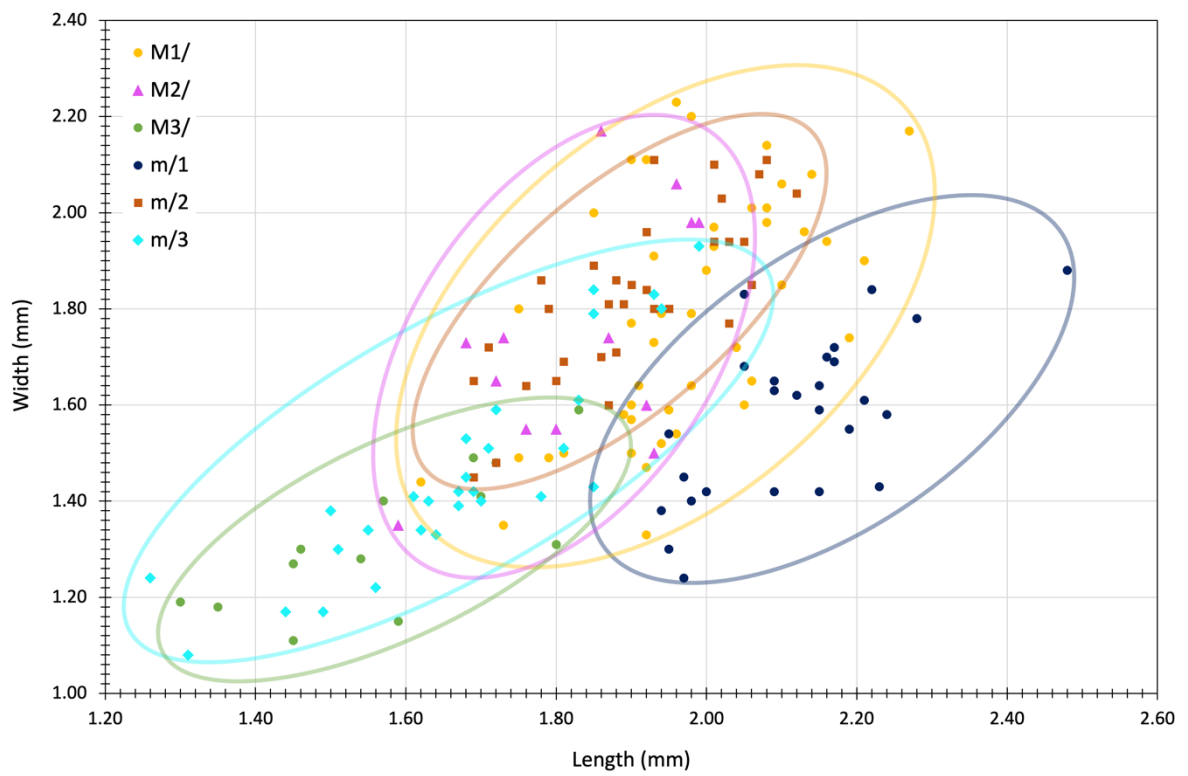


Figure 9 – Size diagram of the studied *Prospalax priscus* molars from Ridjake, Serbia. Individual measurements are given in Appendix 1.

*Table 1 – Number of molars (N) and minimal, average, and maximum length and width in mm of Prospalax priscus from Ridjake, Serbia.*

	N	Length (mm)			Width (mm)		
		min	ave	max	min	ave	max
<b>m/1</b>	45	1.94	2.12	2.48	1.24	1.58	1.88
<b>m/2</b>	13	1.69	1.91	2.12	1.45	1.84	2.11
<b>m/3</b>	13	1.26	1.67	1.99	1.08	1.46	1.93
<b>M1/</b>	26	1.62	1.97	2.27	1.33	1.78	2.23
<b>M2/</b>	33	1.59	1.83	1.99	1.35	1.70	2.06
<b>M3/</b>	29	1.30	1.57	1.83	1.11	1.32	1.59

## PHYLOGENETIC ANALYSIS

Table 2 shows the dental characteristics table used for the analysis. The characteristics are numbered 1 through 19. Differences in characteristics are given numbers of 0 to 3. The detailed list of each characteristic can be found in Appendix 2. All characteristics were judged based on molars which had undergone medium wear (Figures 5 and 6).

*Table 2 – Dental characteristics table used for the phylogenetic analysis (Bolliger, 1996; 1999; Daxner-Höck, 1980; De Bruijn, 2009; Hír and Kókay, 2010; Klein Hofmeijer and De Bruijn, 1985; Kordos, 1985; Nesin and Kovalchuk, 2021). Dental characteristics list: Appendix 2.*

Dental characteristics	<i>Anomalomys minor</i>	<i>Anomalomys aliveriensis</i>	<i>Anomalomys gaudryi</i>	<i>Anomalomys gaillardi</i>	<i>Anomalomys grytsivensis</i>	<i>Prospalax petteri</i>	<b><i>Prospalax priscus</i></b>	<i>Anomalospalax tardosi</i>	<i>Eumyarion bifidus</i>
1	0	0	1	2	1	1	2	1	1
2	0	0	1	2	1	2	2	1	1
3	0	1	0	2	1	1	2	2	1
4	1	1	1	1	2	0	2	2	3
5	2	2	3	0	3	3	3	3	3
6	1	1	1	1	1	2	0	0	2
7	2	2	2	1	1	2	1	2	2
8	0	1	1	1	2	2	2	2	2
9	2	2	2	0	1	1	1	0	2
10	1	2	2	2	1	2	2	2	2
11	2	2	2	1	2	2	2	2	2
12	2	2	2	1	1	0	0	0	2
13	1	1	1	1	1	2	0	2	1
14	1	2	2	1	2	0	1	2	2
15	1	1	1	1	1	0	1	2	2
16	2	2	1	1	0	0	0	0	2
17	1	1	1	3	1	3	3	3	2
18	1	1	1	2	1	0	0	1	1
19	0	0	0	0	0	0	0	0	1

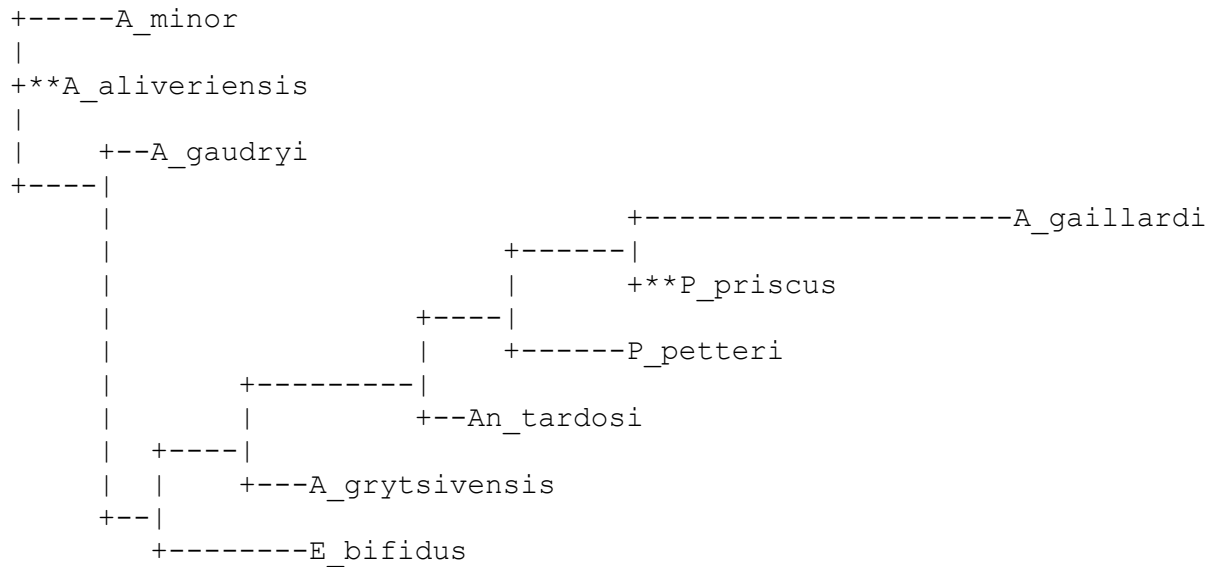


Figure 10 – Maximum likelihood phylogenetic tree based on all dental characteristics as described in Table 2 and Appendix 2. Branches shown as \*\* are uncertain. The length of the branches represents the relative closeness in morphology to the other species.

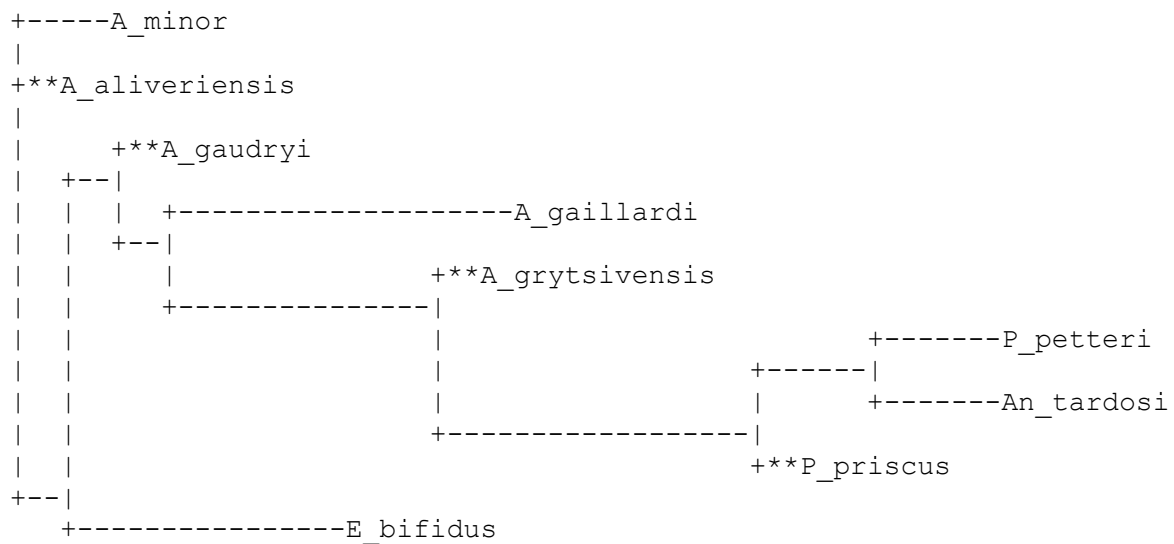


Figure 11 – Maximum likelihood phylogenetic tree based on all dental characteristics except size-based characteristics (1,2,3) as described in Table 2 and Appendix 2. Branches shown as \*\* are uncertain. The length of the branches represents the relative closeness in morphology to the other species.

## Phylogenetic trees

Figure 10 shows a phylogenetic tree of maximum likelihood based on all characteristics as given in Table 2. Figure 11 also shows a phylogenetic tree of maximum likelihood, but the first three characteristics which are size-based, were taken out of the equation. This was done as size is for other species besides *Prospalax priscus* is somewhat uncertain, as most authors do not clarify along which exact axis their measurements were taken. Comparisons of size may therefore be inaccurate. Furthermore, as the molars wear down, the occlusal area becomes larger, meaning sizes are highly variable and can only become somewhat accurate a large number of specimens. Most studies, including this one, do not have enough specimens per molar type to calculate a reliable average size. Differences in age of the species was not accounted for in the analysis.

In both trees *Anomalomys minor* and *A. aliveriensis* are at the base of the tree with *A. gaudryi* showing a close resemblance to both. In Figure 11 *A. gaudryi* shares a common ancestor with the ancestor of *A. gaillardi* and *A. grytsivensis*, which then branches off into *Prospalax priscus*, *P. petteri* and *Anomalospalax tardosi*. Figure 10 however shows *A. gaillardi* in an unlikely position sharing a common ancestor with *P. priscus*. The selected outgroup species of *Eumyarion bifidus* is not regarded as an outgroup in either tree, though in Figure 11 *E. bifidus* is shown to be a separate branch sharing a common ancestor with *A. gaudryi*. In Figure 10 *E. bifidus* is placed after *A. grytsivensis* and ahead of *An. tardosi*, *P. petteri*, *P. priscus* and *A. gaillardi*. *An. tardosi* is similarly linked to *P. petteri* and *P. priscus* in both trees.

## Age distribution

When accounting for the species' ages (page 5) phylogenetic tree which disregards size (Figure 11) shows a more plausible outcome. This could have several causes. Firstly, as previously mentioned, there is an uncertainty in how other studies have taken measurements, which could be different as described in Figure 2. *Anomalomys aliveriensis* (MN4) and *A. minor* (MN4-5) are of the same age and *A. gaudryi* (MN6-9) is younger. *A. grytsivensis* (MN9) and *A. gaillardi* (MN9-11) are even younger in age. *An. tardosi* (MN12) is close in age to *Prospalax petteri* (MN10-11) and *P. priscus* (MN15-16/17) is the most recent species in the tree. Again *Eumyarion bifidus* (MN5) is not seen as an outgroup, as it seems to have more characteristics in common with *Anomalospalax* and *Prospalax* than *Anomalomys*.



### Geographical distribution

Figures 12, 13 and 14 show the geographical distribution of fossil sites for the discussed species. Figure 12 shows the oldest species *Anomalomys aliveriensis* and *A. minor*, the former of which is exclusive to Turkey and Greece, while the latter was only found in Central Europe. Figure 13 shows *A. gaudryi*, *A. gaillardi* and *A. grytsivensis*, of which the first two have a large European distribution, while the latter was only found at one site in Ukraine. Finally, Figure 14 shows the distribution of *Prospalax petteri*, *P. priscus* and *Anomalospalax tardosi*, with the first having a slightly wider distribution reaching into Germany, while the latter two were only found along the border of Central to Eastern Europe.

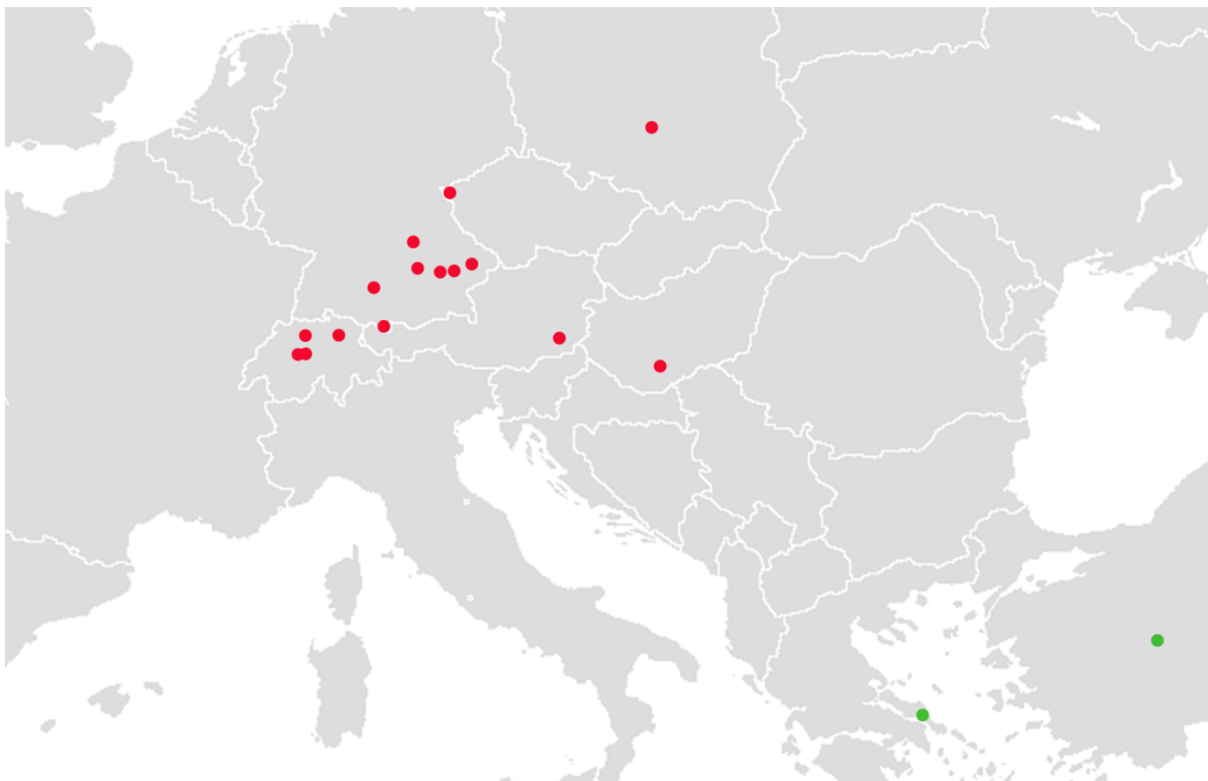


Figure 12 – Map of fossil sites for *Anomalomys aliveriensis* (MN4; green) and *A. minor* (MN4-5; red).

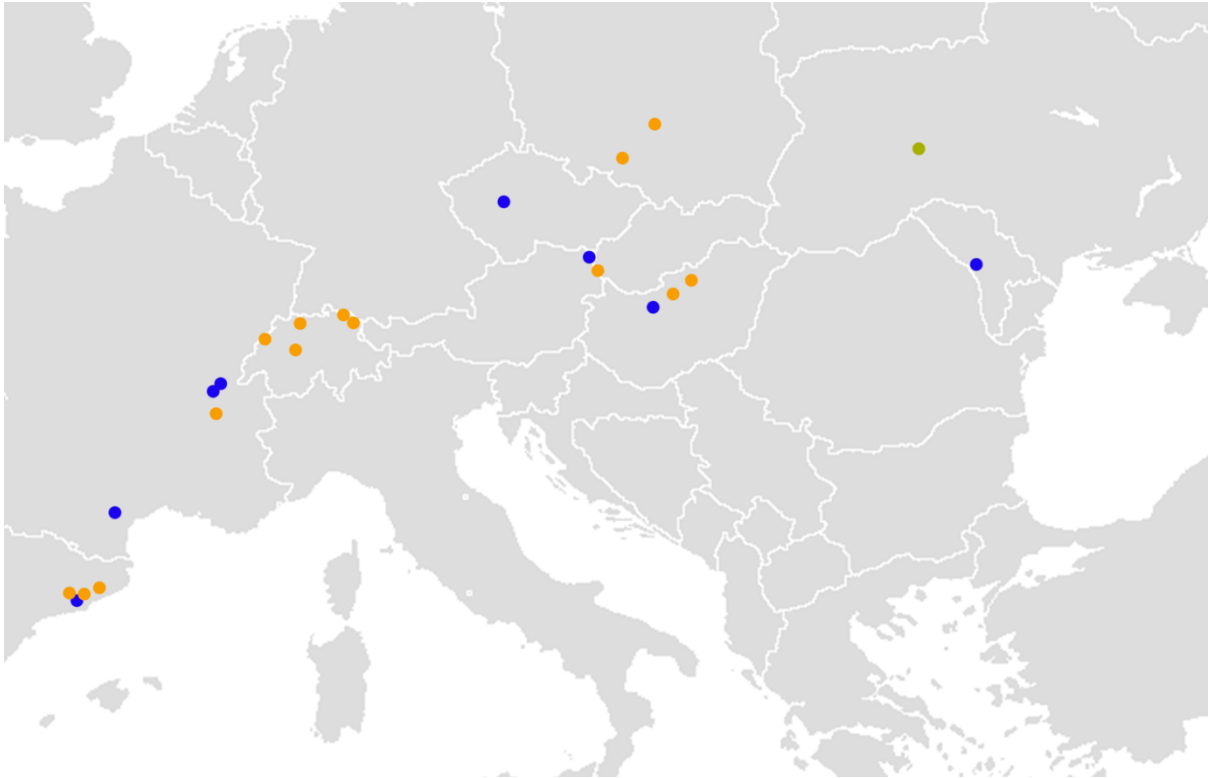


Figure 13 – Map of fossil sites for *Anomalomys gaudryi* (MN6-9; orange), *A. grytsivensis* (MN9; green), and *A. gaillardi* (MN9-11; blue).

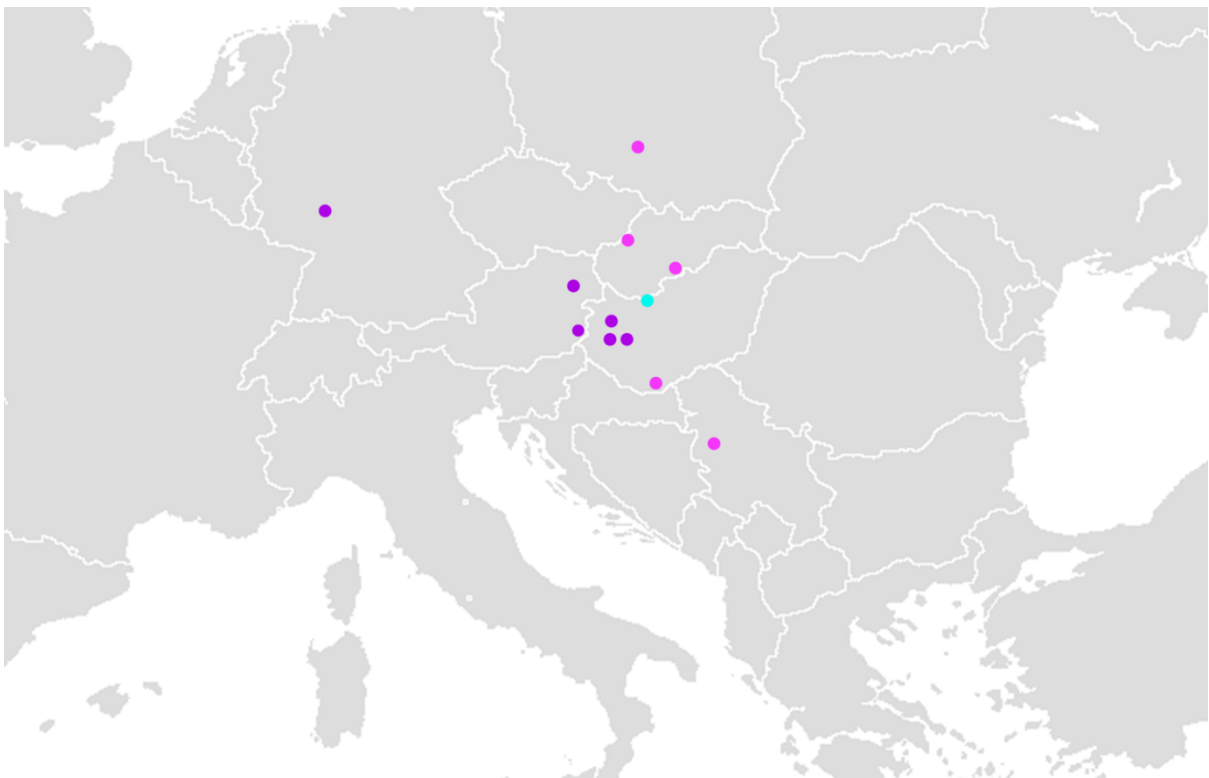


Figure 14 – Map of fossil sites for *Prospalax petteri* (MN10-11; purple), *Anomalospalax tardosi* (MN12; light blue), and *Prospalax priscus* (MN15-16/17; pink).

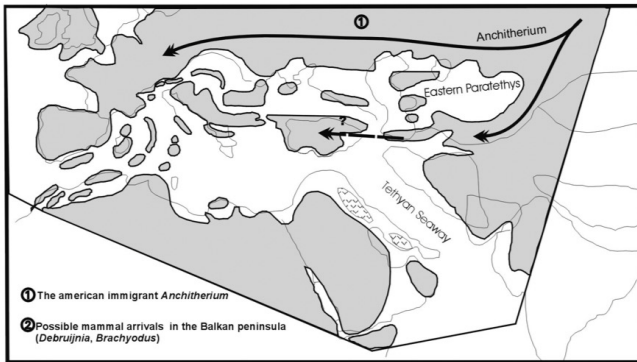
## DISCUSSION

### Phylogenetic discussion and geography

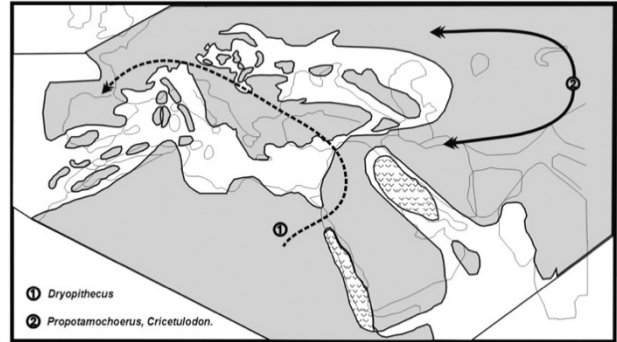
Bolliger (1999) believes in two, or even three, migrations of Anomalomyinae from Asia into Europe. The first migration being that of *Anomalomys aliveriensis*, *A. minor* and *A. minutus*. Koufos et al. (2005) hypothesise such a migration event around MN4 named the Middle Orleanian Migration which primarily re-established a connection between Eurasia and Africa but also reinforced the land bridge between Asia and Europe (Figure 15).

A second hypothesised migration would have brought in *Anomalomys gaudryi*, which then through time evolved into *A. gaillardi* (Bolliger, 1999). Based on the geographical distributions of these species (Figure 13) this could make sense, though a very clear geographical indication of this migration is not present. The fact however that *A. gaudryi* and *A. gaillardi* have similar geographical distribution, does strongly suggest this species evolution through time. The second phylogenetic tree (Figure 11) would agree. A short-term opening of the Tethyan Sea may have occurred during the late Orleanian (MN5) weakening the land bridge between Europe and Asia. Then during the early Astaracian (MN6), when this land bridge was once again fully established, an increase in migration could have occurred (Figure 15; Koufos et al., 2005). However, no remains of a direct ancestor have been found thus far from Asia, hence this migration may have been more of a migration across Europe (Figure 13) as opposed to from Asia.

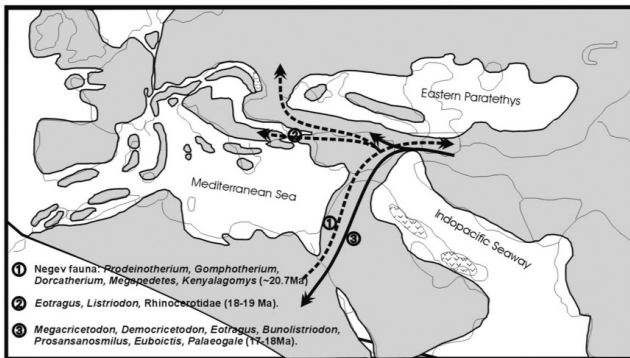
Bolliger (1999) seems unsure of whether a third migration occurred, bringing *Prospalax petteri* and *Anomalospalax tardosi* into Europe, or if these species evolved from *Anomalomys*. Figures 10 and 11 show no indication of a third migration. Rather it seems *Anomalomys* evolved into the *Prospalax-Anomalospalax* lineage. Furthermore, both phylogenetic trees suggest *A. grytsivensis* and the *Prospalax-Anomalospalax* lineage share a common ancestor. This would also make sense timewise as the age of *A. grytsivensis* is MN9 and the age of *P. petteri* is MN10-11.



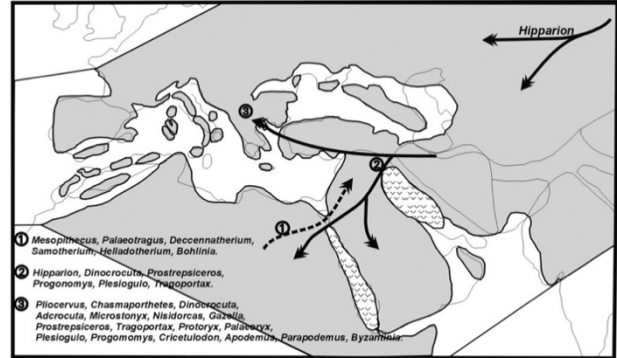
Early Orléanien (MN1-3)



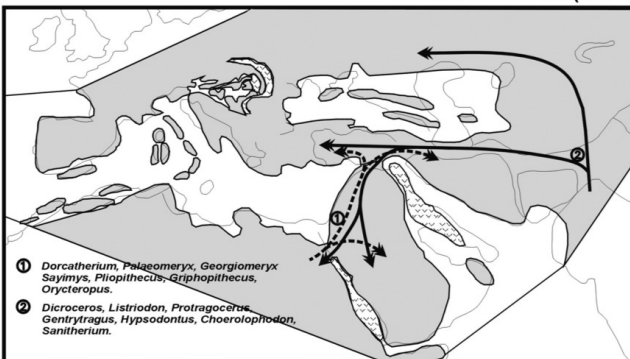
Late Astaracien (MN7+8)



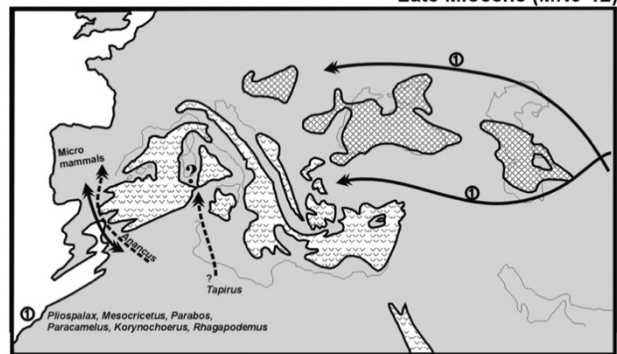
Middle Orléanien (MN 4)



Late Miocene (MN9-12)



Late Orléanien- Early Astaracien (MN5-6)



Latest Miocene (MN 13)

Figure 15 – Hypothesised mammalian migration routes from Asia into Europe during the Miocene. Figure taken from Koufos et al. (2005).

### ***Eumyarion***

The placement of *Eumyarion bifidus* within the phylogenetic trees is inaccurate. This is likely because molar characteristics to distinguish between Anomalomyinae species were used. Most characteristics do not accurately describe *Eumyarion* and its differences to the other species, resulting in a tree where *E. bifidus* was placed right next to the *Anomalospalax-Prospalax* lineage. A distinct feature of *Eumyarion* (Appendix 2: 19) was used in the hopes of avoiding this, however this was not enough. To avoid this in the future, more distinct features within the outgroup should be identified and incorporated into the phylogenetic analysis.

### ***Anomalospalax***

Kordos (1985) came up with the new genus *Anomalospalax*. He mainly saw it as an intermediate stage between *Anomalomys* and *Prospalax*, having the more complicated enamel pattern of the former genus but also possessing the thicker folds of the latter genus. Based on Figure 11 one could argue that *Anomalospalax* does not warrant a distinct species, but rather could be added to *Prospalax*. Furthermore, although Kordos (1985) considered *An. tardosi* (MN12) an intermediate stage, age-wise it sits in between *P. petteri* (MN10-11) and *P. priscus* (MN15-16/17). Based on the phylogenetic analysis (Figure 11), which disagrees with Kordos (1985), it is plausible to reconsider the position of *Anomalospalax* as a distinct genus.

### **Wear and changing morphology**

A big constraint throughout this study has been the changing morphology of Anomalomyinae molars as a result of wear. Though it has been tried to study all molars in a very similar wear-state, the morphological analysis may not be fully accurate. It is not always clear from just studying the literature on different species, which level of wear the molar descriptions have been based on. As seen in the molar descriptions of *Prospalax priscus* and in Figure 6, loph(id)s significantly change over time throughout the species' different ontogenetic stages. And as all other species were only studied based on scientific publications, and not physical specimens, it was impossible to study them as detailed as *P. priscus* was studied. This constraint was further studied by Skandalos and Van den Hoek Ostende (2023), who used x-ray microtomography to fully reconstruct the changes in the occlusal surfaces of several Spalacinae species. Of each molar they made 12 slices to show how the occlusal surface of the molars would change throughout a lifetime. Of two species (*Pliospalax sotirisi* and *Pl.*

*macoveii*) they found that the differences described to be species-specific were just differences in ontogenetic stages. They concluded that these two previously distinct species were so similar they should be considered as one species.

To fully understand the relationships within Anomalomyinae, a similar study should be done of specimens of all different species. This could be especially helpful for the species which are only known from one locality, or from a small number of molars. Ultimately this could determine whether they are fully distinct species, or if they have maybe been studied at different wear-stages and have therefore been wrongfully considered a new species. However, a study like that of Skandalos and Van de Hoek Ostende (2023) would require a lot of time and resources. Molars of all the different Anomalomyinae molars would need to be gathered, 3D scanned and then digitally sliced to create occlusal cross-sections to compare. Although time intensive, this would be the best way to fully understand the molar morphology of Anomalomyinae.

## CONCLUSION

A phylogenetic analysis was performed of Anomalomyinae. Two phylogenetic trees were constructed (Figures 10 and 11), one containing size characteristics, the other not. The latter was considered more accurate, as it grouped *Prospalax* and *Anomalospalax* together, as well as *Anomalomys minor* and *A. aliveriensis*, and *A. gaudryi*, *A. grytsivensis* and *A. gaillardi*. This groupings seem plausible as they also correlate in age. Hypothesised by Bolliger (1999) is that the ancestors of *Anomalomys* species migrated into Europe from Asia in two waves, initially *A. minor* and *A. aliveriensis* (MN3) and later *A. gaudryi*, *A. grytsivensis* and *A. gaillardi* (MN6). Based on the fossil sites (Figure 12) the first migration seems likely, while the second migration (Figure 13) is more of a spread across Europe as opposed to a migration from Asia. *Eumyarion bifidus* was used as an outgroup in the phylogenetic analysis, but not enough distinct *Eumyarion* characteristics were used to create a clear outgroup. Based on the phylogenetic tree (Figure 11) *Anomalospalax*, coined as an intermediate stage between *Anomalomys* and *Prospalax*, may not be distinct enough from *Prospalax* to warrant a separate genus.

As Anomalomyinae molars are hypsodont, the morphology of the occlusal surface is highly variable depending on the level of wear of the molars (Figure 6). This results in various problems when studying these molars. First of all, size increases with increased wear. Secondly, it is difficult to compare species from the literature, as not all species descriptions and images portray the same stages of wear. In order to thoroughly study these Anomalomyinae species, x-ray images should be made so the changing morphology could be studied layer by layer. This could help identify if the more questionable species are truly distinct species or merely existing species which were wrongfully identified as new due to the changing morphology through different stages of wear.

## ACKNOWLEDGEMENTS

Primarily, I would like to thank Wilma Wessels for her patience, help and believe in me, even though it has taken me a long time to finish this thesis. And I would also like to thank Emilia Jarochowska for making the time to read and grade my thesis.

## REFERENCES

- Bachmayer, F., Wilson, R.W., 1970. Small Mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch Fissures of Burgenland, Austria [Die Fauna der altploziänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich)]. *Annalen des Naturhistorischen Museum in Wien* 74:533–587.
- Bachmayer, F., Wilson, R. W., 1978. A second Contribution to the Small Mammal Fauna of Kohfidisch, Austria [Zweiter Beitrag zur Kleinsäugerfauna von Kohfidisch (Burgenland, Österreich)]. *Annalen des Naturhistorischen Museum in Wien* 81:129-161.
- Bolliger, T., 1992. Kleinsäugerstratigraphie in der miozänen Hörnlischüttung (Ostschweiz). Dissertation. ETH Zürich, Zürich, 296 pp. <https://doi.org/10.3929/ethz-a-000666155>
- Bolliger, T., 1996. A current understanding about the Anomalomyidae (Rodentia): Reflections on stratigraphy, paleobiogeography, and evolution, in: Bernor, R.L., Fahlbusch, V., Mittmann, H.-W. (Eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York, pp. 235–245.
- Bolliger, T., 1999. Family Anomalomyidae., in: Rössner, G.E., Heissig, K. (Eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München, pp. 389–394.
- Bowdich, T.E., 1821. An analysis of the natural classifications of Mammalia, for the use of students and travellers. J. Smith, Paris, 115 pp.
- Czernielewski, M. 2023. *Prospalax priscus* jaw from the site of Weże 2 (southern Poland, Pliocene) [Čeljust vrste *Prospalax priscus* iz najdišča Weże 2 (južna Poljska, pliocen)]. *Geologija* 66(2):247-255. <https://doi.org/10.5474/geologija.2023.011>
- Dangremond, A., 2012. Age or paleoenvironment? What is the cause of the differences between two Early Miocene small-mammal assemblages from Kaplangı (Turkey)? Thesis. Utrecht University, Utrecht, 58 pp.
- Daxner-Höck, G., 1980. Rodentia (Mammalia) des Eichkogels bei Mödling (Niederösterreich) 1. Spalacinae und Castoridae 2. Übersicht über die gesamte Nagetierfauna. *Annalen des Naturhistorischen Museum in Wien* 83:135–152.
- De Bruijn, H., 1984. Remains of the mole-rat *Microspalax odessanus* TOPACHEVSKI, from Karaburun (Greece, Macedonia) and the family Spalacidae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 87(4):417–425.
- De Bruijn, H., 2009. The *Eumyarion* (Mammalia, Rodentia, Muridae) assemblage from Sandelzhausen (Miocene, Southern Germany): a test on homogeneity. *Paläontologische Zeitschrift* 83:77–83. <https://doi.org/10.1007/s12542-009-0001-0>
- De Bruijn, H., Bosma, A.A., Wessels, W., 2015. Are the Rhizomyinae and the Spalacinae closely related? Contradistinctive conclusions between genetics and palaeontology. *Palaeobiodiversity and Palaeoenvironments* 95:257–269. <https://doi.org/10.1007/s12549-015-0195-y>



- Fejfar, O., 1972. Ein neuer Vertreter der Gattung *Anomalomys* GAILLARD, 1900 (Rodentia, Mammalia) aus dem europäischen Miozän (Karpat) [A new representative of the genus *Anomalomys* GAILLARD, 1900 from the Miocene (Carpathian) of Europe]. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 141(2):168–193.
- Gaillard, C., 1900. Sur un nouveau rongeur miocène. Comptes Rendus de l'Académie des Sciences 130:191–192.
- Hír, J., Kóky, J., 2010. A systematic study of the middle-late Miocene rodents and lagomorphs (Mammalia) of Felsőtárkány 3/8 and 3/10 (Northern Hungary) with stratigraphical relations. Geodiversitas 32(2):307–329. <https://doi.org/10.5252/g2010n2a5>
- Hoang, D. T., Chernomor, O., Von Haeseler, A., Minh, B. Q., & Vinh, L. S., 2018. UFBoot2: improving the ultrafast bootstrap approximation. Molecular biology and evolution 35(2):518–522. <https://doi.org/10.1093/molbev/msx281>
- Illiger, J.K.W., 1811. Prodrömus systematis mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione germanica. Sumptibus C. Salfeld, Berlin, 302 pp. <https://doi.org/10.5962/bhl.title.106965>
- Jánossy, D., 1972. Middle Pliocene Microvertebrate Fauna from the Osztramos Loc. 1. (Northern Hungary). Annales Historico-Naturales Musei Nationalis Hungarici 64:27–52.
- Klein Hofmeijer, G., De Bruijn, H., 1985. The Mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 4: The Spalacidae and Anomalomyidae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B 88(2):185–198.
- Kordos, L., 1985. Lower Turolian (Neogene) *Anomalospalax* gen. n. from Hungary and its phylogenetic position. Fragmenta Mineralogica et Palaeontologica 12:27–42.
- Kordos, L., 1989. Anomalomyidae (Mammalia, Rodentia) remains from the Neogene of Hungary [Anomalomyidae Maradványok (Mammalia, Rodentia) a Magyarországi Neogén Képződményekből]. A Magyar Állami Földtani Intézet Évi Jelentése az évről 1987:293–311.
- Kordos, L., 2005. *Anomalomys* (Rodentia, Mammalia) from Rudabánya, Hungary (Miocene, MN9): terminology of molars, age categories and phylogenetic interpretations. Fragmenta Palaeontologica Hungarica 23:19–28.
- Koufos, G.D., Kostopoulos, D.S., Vlachou, T.D., 2005. Neogene/Quaternary mammalian migrations in Eastern Mediterranean. Belgian Journal of Zoology, 135(2):181–190.
- Kretzoi, M., 1971. Bemerkungen zur Spalaciden-Phylogenie. Vertebrata Hungarica 12:111–121.
- López-Guerrero, P., Maridet, O., Zhang, Z., Daxner-Höck, G., 2017. A new species of *Argyromys* (Rodentia, Mammalia) from the Oligocene of the Valley of Lakes (Mongolia): Its importance for palaeobiogeographical homogeneity across Mongolia,

- China and Kazakhstan. PLoS one 12(3):e0172733. <https://doi.org/10.1371/journal.pone.0172733>
- Méhely, L., 1908. *Prospalax priscus* (Nhrig), die pliocäne Stammform der heutigen Spalax-Arten. Annales Historico-Naturales Musei Nationalis Hungarici 6:305–316.
- Nehring, A., 1897. Mehrere neue Spalax-Arten. Sitzungs-Berichte der Gesellschaft naturforschender Freunde zu Berlin 10:163–183.
- Nesin, V., Kovalchuk, O., 2021. A new late Miocene *Anomalomys* species from western Ukraine with implications for the diversity and evolution of anomalomyid rodents in Eastern Europe. Historical Biology 33(9):1809–1816. <https://doi.org/10.1080/08912963.2020.1742711>
- Radović, P., Lindal, J., Marković, Z., Alaburić, S., Roksandic, M., 2019. First record of a fossil monkey (Primates, Cercopithecidae) from the Late Pliocene of Serbia. Journal of Human Evolution 137:102681. <https://doi.org/10.1016/j.jhevol.2019.102681>
- Schaub, S., 1925. Die hamsterartigen Nagetiere des Tertiärs und ihre lebenden Verwandten: eine systematisch-odontologische Studie. Abhandlungen der Schweizerischen paläontologischen Gesellschaft 45(3):1–110.
- Simionescu, I., 1930. Vertebratele Pliocene dela Mălușteni (Covurlui). Publications du Fondation Vasile Adamachi, Akademia Romana 9(49):83–151.
- Skandalos, P., Van den Hoek Ostende, L.W., 2023. Wear-dependent molar morphology in hypsodont rodents: The case of the spalacine *Pliospalax*. Palaeontologia Electronica 26(3):a47. <https://doi.org/10.26879/1322>
- Sulimski, A., 1964. Pliocene Lagomorpha and Rodentia from Węże I (Poland). Acta Palaeontologica Polonica 9(2):149–244.
- Topachevskii, V.A., 1976. Fauna of the USSR: Mammals. Mole Rats, Spalacidae. Amerind Publishing Co. Pvt. Lt., New Delhi, 308 pp. <https://doi.org/10.5962/bhl.title.46318>
- Trifinopoulos, J., Nguyen, L.-T., Von Haeseler, A., Minh, B.Q., 2016. W-IQ-TREE: a fast online phylogenetic tool for maximum likelihood analysis. Nucleic Acids Research 44(W1):W232–W235. <https://doi.org/10.1093/nar/gkw256>
- Viret, J., Schaub, S., 1946. Le genre *Anomalomys*, rongeur néogène et sa répartition stratigraphique. Eclogae Geologicae Helvetiae 39(2):342–352.

**Appendix 1: List of all specimens including size**

Code	Molar type	Left/right	Length (mm)	Width (mm)
RID-001	m1/	Left	2.08	2.14
RID-002	m1/	Left	2.01	1.97
RID-003	m1/	Left	2.04	1.72
RID-004	m1/	Left	1.95	1.59
RID-005	m1/	Left	1.89	1.58
RID-006	m1/	Left	1.79	1.49
RID-007	m1/	Left	2.21	1.90
RID-008	m1/	Left	1.90	1.60
RID-009	m1/	Left	2.06	2.01
RID-010	m1/	Left	1.90	1.57
RID-011	m1/	Right	1.94	1.52
RID-012	m1/	Right	1.96	1.54
RID-013	m1/	Right	1.93	1.73
RID-014	m1/	Right	2.08	2.01
RID-015	m1/	Right	2.06	1.65
RID-016	m1/	Right	1.91	1.64
RID-017	m1/	Right	2.14	2.08
RID-018	m1/	Right	2.27	2.17
RID-019	m1/	Right	2.16	1.94
RID-020	m1/	Right	1.94	1.79
RID-021	m1/	Left	2.05	1.60
RID-022	m1/	Left	1.92	1.33
RID-023	m1/	Left	1.90	1.50
RID-024	m1/	Left	1.73	1.35
RID-025	m1/	Left	2.19	1.74
RID-026	m1/	Left	2.00	1.88

Code	Molar type	Left/right	Length (mm)	Width (mm)
RID-027	m1/	Left	1.92	1.47
RID-028	m1/	Left	2.08	1.98
RID-029	m1/	Left	2.01	1.93
RID-030	m1/	Left	2.10	2.06
RID-031	m1/	Right	2.10	1.85
RID-032	m1/	Right	1.98	1.64
RID-033	m1/	Right	1.92	2.11
RID-040	m1/	Left	1.96	2.23
RID-061	m1/	Right	1.98	1.79
RID-062	m2/	Right	1.68	1.73
RID-071	m2/	Right	1.59	1.35
RID-072	m2/	Right	1.92	1.60
RID-073	m2/	Right	1.93	1.50
RID-074	m2/	Right	1.80	1.55
RID-075	m1/	Right	2.13	1.96
RID-076	m2/	Right	1.72	1.65
RID-077	m1/	Right	1.62	1.44
RID-078	m2/	Right	1.87	1.74
RID-079	m2/	Right	1.76	1.55
RID-081	m3/	Left	1.69	1.49
RID-082	m3/	Left	1.72	1.48
RID-083	m3/	Left	1.83	1.59
RID-084	m3/	Left	1.59	1.15
RID-085	m3/	Left	1.35	1.18
RID-086	m3/	Left	1.54	1.28
RID-087	m3/	Left	1.57	1.40

Code	Molar type	Left/right	Length (mm)	Width (mm)
RID-091	m3/	Right	1.70	1.41
RID-092	m3/	Right	1.45	1.11
RID-093	m3/	Right	1.80	1.31
RID-094	m3/	Right	1.30	1.19
RID-095	m3/	Right	1.45	1.27
RID-096	m3/	Right	1.46	1.30
RID-101	m1/	Left	1.98	2.20
RID-102	m1/	Left	1.75	1.49
RID-103	m1/	Left	1.81	1.50
RID-104	m2/	Left	1.98	1.98
RID-105	m2/	Left	1.99	1.98
RID-106	m2/	Left	1.96	2.06
RID-121	m/1	Left	1.97	1.24
RID-122	m/1	Left	2.12	1.62
RID-123	m/1	Left	1.98	1.40
RID-124	m/1	Left	2.09	1.63
RID-125	m/1	Left	2.09	1.42
RID-126	m/1	Left	2.24	1.58
RID-127	m/1	Left	2.15	1.59
RID-128	m/1	Left	2.19	1.55
RID-129	m/1	Left	2.09	1.65
RID-130	m/1	Left	2.23	1.43
RID-131	m/1	Right	2.15	1.64
RID-132	m/1	Right	2.21	1.61
RID-133	m/1	Right	2.22	1.84
RID-134	m/1	Right	2.00	1.42

Code	Molar type	Left/right	Length (mm)	Width (mm)
RID-135	m/1	Right	2.28	1.78
RID-136	m/1	Right	2.48	1.88
RID-137	m/1	Right	2.15	1.42
RID-138	m/1	Right	2.05	1.83
RID-139	m/1	Right	1.95	1.30
RID-140	m/1	Right	1.95	1.54
RID-141	m/1	Right	2.17	1.69
RID-142	m/1	Right	1.97	1.45
RID-143	m/1	Right	2.17	1.72
RID-144	m/1	Right	2.16	1.70
RID-145	m/1	Right	2.05	1.68
RID-146	m/1	Right	1.94	1.38
RID-151	m/2	Left	1.86	1.70
RID-152	m/2	Left	1.87	1.81
RID-153	m/2	Left	1.71	1.72
RID-154	m/2	Left	1.79	1.80
RID-155	m/2	Left	1.78	1.86
RID-156	m/2	Left	2.01	2.10
RID-157	m/2	Left	1.87	1.60
RID-158	m/2	Left	2.06	1.85
RID-159	m/2	Left	1.92	1.96
RID-160	m/2	Left	1.69	1.65
RID-161	m/2	Right	1.93	1.80
RID-162	m/2	Right	1.95	1.80
RID-163	m/2	Right	2.08	2.11
RID-164	m/2	Right	1.90	1.85

Code	Molar type	Left/right	Length (mm)	Width (mm)
RID-165	m/2	Right	1.80	1.65
RID-166	m/2	Right	1.88	1.71
RID-167	m/2	Right	1.88	1.86
RID-168	m2/	Left	1.73	1.74
RID-169	m/2	Right	1.72	1.48
RID-170	m1/	Left	1.90	1.77
RID-171	m/2	Left	2.03	1.77
RID-172	m/2	Left	1.85	1.89
RID-173	m/2	Left	1.81	1.69
RID-174	m/2	Left	1.93	2.11
RID-175	m2/	Right	1.86	2.17
RID-176	m1/	Right	1.90	2.11
RID-177	m/2	Left	2.08	2.11
RID-178	m/2	Left	1.76	1.64
RID-181	m/2	Right	1.92	1.84
RID-182	m/2	Right	2.05	1.94
RID-183	m/2	Right	2.03	1.94
RID-184	m/2	Right	1.69	1.45
RID-185	m1/	Left	1.85	2.00
RID-186	m1/	Left	1.75	1.80
RID-187	m/2	Right	2.07	2.08
RID-188	m/2	Right	1.89	1.81
RID-189	m/2	Right	2.12	2.04
RID-190	m/2	Right	2.01	1.94
RID-191	m1/	Right	1.93	1.91
RID-192	m/2	Right	2.02	2.03

Code	Molar type	Left/right	Length (mm)	Width (mm)
RID-201	m/3	Left	1.85	1.43
RID-202	m/3	Left	1.67	1.42
RID-203	m/3	Left	1.44	1.17
RID-204	m/3	Left	1.26	1.24
RID-205	m/3	Left	1.72	1.59
RID-206	m/3	Left	1.81	1.51
RID-207	?	Left	1.80	1.88
RID-208	m/3	Left	1.78	1.41
RID-209	m/3	Left	1.68	1.45
RID-210	m/3	Left	1.68	1.53
RID-211	m/3	Right	1.64	1.33
RID-212	m/3	Right	1.83	1.61
RID-213	m/3	Right	1.69	1.42
RID-214	m/3	Right	1.50	1.38
RID-215	m/3	Right	1.49	1.17
RID-216	m/3	Right	1.71	1.51
RID-217	m/3	Right	1.99	1.93
RID-218	m/3	Right	1.55	1.34
RID-219	m/3	Right	1.31	1.08
RID-220	m/3	Right	1.67	1.39
RID-221	m/3	Left	1.61	1.41
RID-222	m/3	Left	1.63	1.40
RID-223	m/3	Left	1.51	1.30
RID-224	m/3	Left	1.85	1.84
RID-225	m/3	Right	1.62	1.34
RID-226	m/3	Left	1.85	1.79

RID-227	m/3	Left	1.70	1.40
RID-228	m/3	Left	1.94	1.80
RID-229	m/3	Left	1.93	1.83
RID-230	m/3	Right	1.56	1.22

## Appendix 2: Morphological characteristics for phylogenetic analysis

### 1) m/1 average length

0: 1.0 mm  $\leq$  length < 1.5 mm

1: 1.5 mm  $\leq$  length < 2.0 mm

2: 2.0 mm  $\leq$  length < 2.5 mm

3: 2.5 mm  $\leq$  length < 3.0 mm

4: 3.0 mm  $\leq$  length < 3.5 mm

### 2) m/1 average width

0: 0.5 mm  $\leq$  width < 1.0 mm

1: 1.0 mm  $\leq$  width < 1.5 mm

2: 1.5 mm  $\leq$  width < 2.0 mm

3: 2.0 mm  $\leq$  width < 2.5 mm

### 3) m/1 width/length

0: 0.50 to 0.59

1: 0.60 to 0.69

2: 0.70 to 0.79

### 4) m/1 anterolophid-protolophid/mesolophid connection

0: absent

1: lingual side

2: labial side

3: centrally

### 5) m/1 mesolophid-posterolophid connection

0: absent

1: lingual side

2: labial side

3: centrally

- 6) m/1 anterosinid opening
- 0: lingual side
  - 1: labial side
  - 2: both sides
- 7) m/1 distinction between mesolophid and entoconid
- 0: absent
  - 1: weak
  - 2: present
- 8) m/2 anterolophid-protolophid/mesolophid connection
- 0: absent
  - 1: lingual side
  - 2: labial side
  - 3: centrally
- 9) m/2 distinction between mesolophid and entoconid
- 0: absent
  - 1: weak
  - 2: present
- 10) m/3 anterolophid-protolophid/mesolophid connection is
- 0: always absent
  - 1: sometimes present
  - 2: always present
- 11) m/3 mesolophid/hypolophid-posterolophid connection is
- 0: always absent
  - 1: sometimes present
  - 2: always present



12) M1/ distinction between mesoloph and paraloph

0: absent

1: weak

2: present

13) M1/ anterosinusid opening

0: lingual side

1: labial side

2: both sides

14) M1/ anteroloph-paraloph/mesoloph connection is

0: always absent

1: sometimes present

2: always present

15) M1/ anteroloph-paraloph/mesoloph connection position

0: always absent

1: lingual side

2: centrally

3: labial side

16) M2/ distinction between mesoloph and paraloph

0: absent

1: weak

2: present

17) M2/ anteroloph-paraloph/mesoloph connection position

0: always absent

1: lingual side

2: centrally

3: labial side

18) M3/ anterosinus opening

0: lingual side

1: labial side

2: both sides

19) M1/ double posterolophid

0: absent

1: present