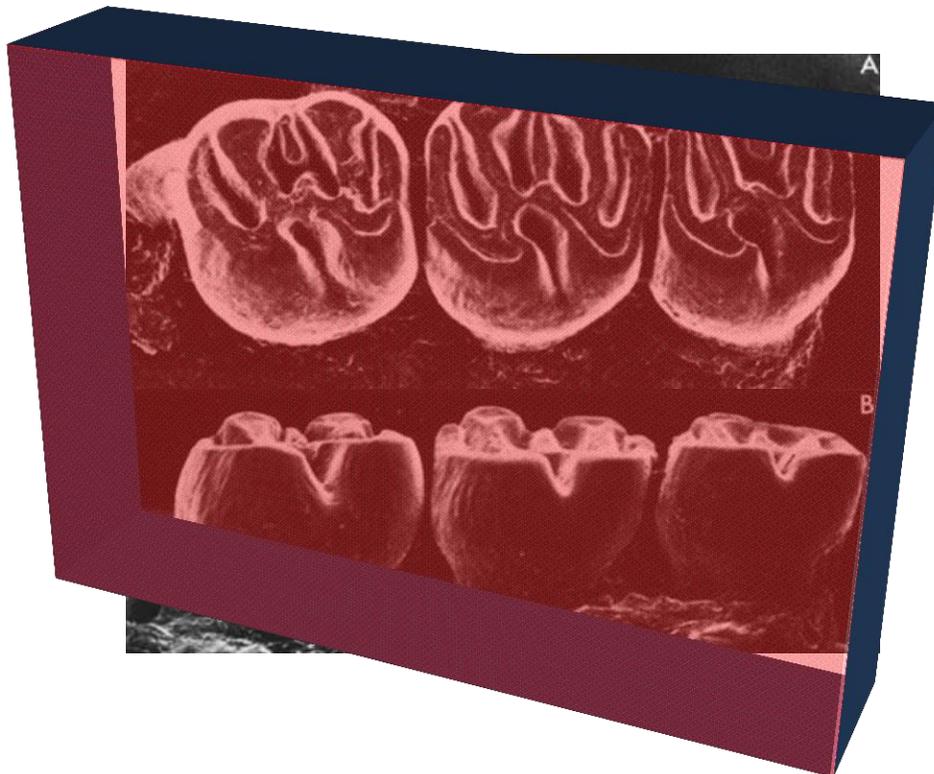




**Universiteit Utrecht**

**THE EARLY MIOCENE SMALL MAMMAL FAUNA FROM KARYDIÁ,  
GREECE:  
Biostratigraphic and Palaeogeographic Implications**



**Master Thesis submitted by:**

**Natalie Duncan**

**Student No: 3434591**

**N.E.Duncan@students.uu.nl**

**First supervisor: Dr W. Wessels**

**Second supervisor: Prof. Dr J. Reumer**

**Department of Earth Science**

**Faculty of Geosciences**

**Utrecht University, The Netherlands**

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## SUMMARY:

The early Miocene was an important period in Eurasian palaeo- and bio-geography. Active tectonism caused the movement and collisions of plate boundaries, orogenesis and sea level changes. This, together with the onset of the Miocene Climatic Optimum, altered land-sea distributions. Various accounts of European palaeo- and bio-geography are available for this time period; however, reconstructions are still speculative. Different regions of the Eurasia, according to their faunal history, give variable amounts of information that may shed light on these processes. Some regions are of particular interest, as they are the places where different faunas came into contact and allowed exchange of members from different ecological environments. The eastern Mediterranean (including Greece, the Balkans and Anatolia) occupies such a key position, located between the European, Asian and African continents. A detailed study of the small-mammals from Karydiá, Greece is essential for understanding early Miocene faunal exchange between Anatolia, Greece and Western Europe.

This research aims to continue the study of the small mammal assemblage from Karydiá, in order to gain further insights into the biostratigraphic position and paleogeography of this location. This research comprised: a detailed analysis and description of the Eomyidae and Cricetidae (*Eumyarion*) material from Karydiá; a comparison of the small mammal species found in Karydiá, with other Greek, European and Anatolian localities; and a re-evaluation of the biostratigraphy of Karydiá and its palaeogeographic implications.

The study led to the identification of the species *Pseudotheridomys* aff. *parvulus* and *Eumyarion* aff. *latior*, which do not serve well as biostratigraphic markers. Based on the presence of the modern Cricetids, the biostratigraphic position of Karydiá is considered to lie within MN4. Based on the stage-in-evolution from *P. parvulus* to *Ligerimys antiquus*, Karydiá is deemed to be younger than Aliveri. The faunal assemblage from Karydiá shows species having affinities with both Central Europe and Turkey, indicating a connection between these areas during and/or before MN4.

## **PREFACE & ACKNOWLEDGEMENTS:**

This thesis provides the results of a graduation project forming part of the Master's programme Biogeology of Utrecht University. This research project lies within the framework of 'Terrestrial Oligocene and Miocene vertebrate Biostratigraphy' and is connected to the project "Age or palaeoenvironment? What is the cause of the differences between two Early Miocene small-mammal assemblages from Kaplang1 (Turkey)?" Dr Wilma Wessels and Prof. Dr Jelle Reumer from Utrecht University, The Netherlands, supervised the work.

Many thanks go out to Wilma Wessels and Hans de Bruijn, who gave me the freedom to find my own way through this subject and were there for me when I got lost. I appreciate the encouragement from Constantin Doukas, gratefully received during the beginning of my research. Thanks to Anne Dangremond, who was good company in the microscope room and who made the most delicious home-made chocolates; and to my friends in Ireland and the Netherlands - you really kept my sane.

Nothing would have been possible without the support of my family. Big hugs and sloppy kisses!

Finally, thanks to the Netherlands, for its generosity and for presenting me opportunities available nowhere else.

"Everything in life is temporary".

Natalie Duncan

Tuesday, 31 January 2012

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### 1. General Introduction

#### *1.1 Context and application*

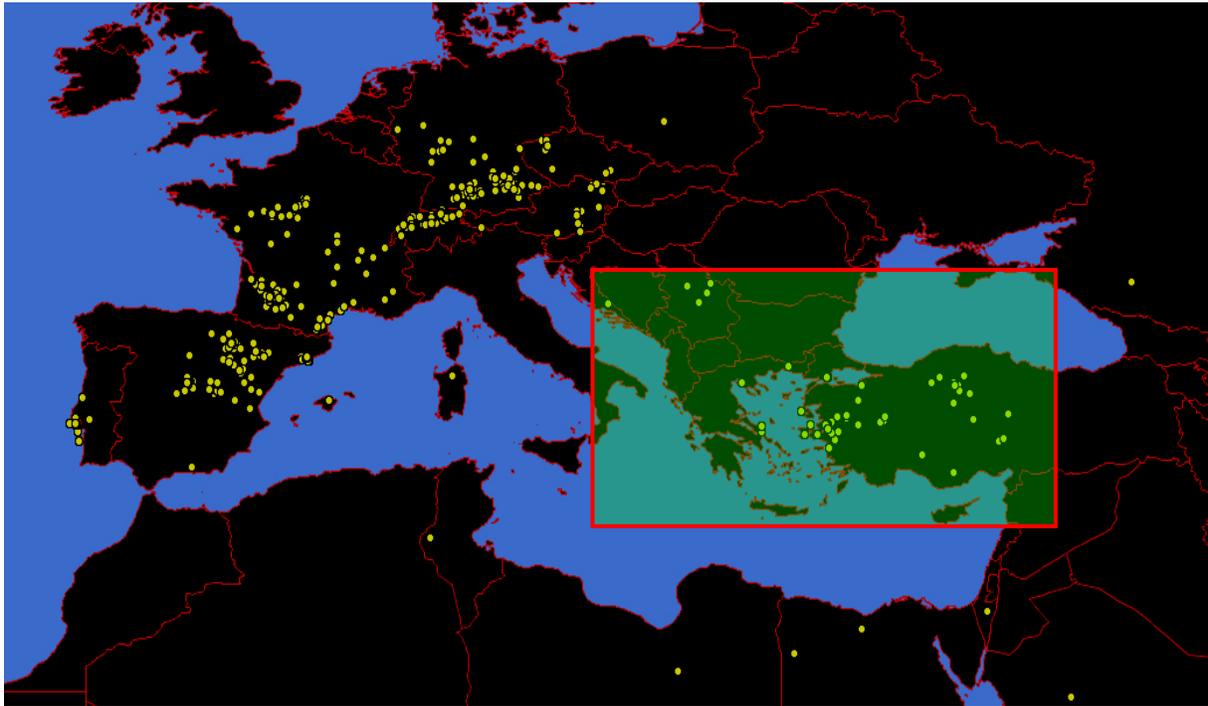
The early Miocene was an important period in Eurasian palaeo- and bio-geography. Active tectonism caused the movement and collisions of plate boundaries, orogenesis and sea level changes. This, together with the onset of the Miocene Climatic Optimum, altered land-sea distributions. Various accounts of European palaeo- and bio-geography are available for this time period; however, reconstructions are still speculative.

One tool that can aid reconstructions is biostratigraphy. For the Miocene period, the Mammalian Neogene (MN) zonation is used for terrestrial mammal biogeography. When correlated with a timescale, MN zonation can chronologically record mammalian migration and diversification patterns; however, these are obscured by geological conditions including a rarity of continental basin deposits, the occurrence of only isolated localities lacking stratigraphic control, the resulting stratigraphic gaps (Agusti 1999) and a rarity of datable sediments (Fahlbusch and Mein 1989). As a result, the fossil record of mammalian distribution and evolution in most regions of Eurasia is discontinuous.

Different regions of the Eurasia, according to their faunal history, give variable amounts of information that may shed light on these processes. Some regions are of particular interest, as they are the places where different faunas came into contact and allowed exchange of members from different ecological environments. The fossil record originating from such regions of intercontinental faunal exchange is of prime importance for the understanding of the evolution of ecosystems. The eastern Mediterranean (including Greece, the Balkans and Anatolia) occupies such a key position, located between the European, Asian and African continents.

Numerous localities for mammal fossils have been uncovered in the eastern Mediterranean (see Figure 1 below); only few Early Miocene mammal faunas are known from Greece and adjacent areas. Each new study from this area contributes to a better understanding of migration patterns, faunal changes and evolutionary history. A detailed study of the small-mammals from Karydiá is essential for understanding early Miocene faunal exchange between Anatolia and Greece (i.e. Western Europe).

**Figure 1: Early Miocene mammal localities of Europe and Anatolia** (Fortelius 2011). Highlighted is the area of interest – the eastern Mediterranean.



### **1.2 Mammalian Neogene (MN) biozonation:**

The Mammalian Neogene (MN) zones are subdivided according to the stage of the evolutionary development of mammalian fossil associations (MN zones). The use of MN zones simplifies the comparison of fossil terrestrial vertebrate faunas. Different parameters, based on the morphology of the organisms, are taken into consideration, allowing certain associations of mammals to be placed in succession. Since its original publication, Mein has revised the MN zones and currently recognizes 17 Neogene zones (13 Miocene, 4 Pliocene) (Table 1.2) and two subzones (2a and 2b). This methodology enables a Neogene fossil record to be assigned to a MN unit, from MN1 to MN17, and, sometimes, to define its position within a MN zone as well. Each of the 17 MN units was characterized by the combination of three criteria (Mein 1990, 1999):

1. the presence of characteristic representatives, generally short-lived, of evolutionary lineages;
2. characteristic associations of temporally short co-occurrences of two or more genera;  
and
3. the first appearances of genera.

Fossil sites with a variety of species, and especially sites having species which are good indicators for certain MN zones, once placed within a zone, and within its geographical position (considering its palaeogeography), may give a lot of information on migrations and the ecology of the specified region. The presence of certain species, and omission of other species, is of major importance for the understanding of the evolution of species and their ecology.

The Early Miocene covers MN1 to MN4 (approximately 17 to 23 million years before present; however, it is important to note that MN zones can be diachronic and can have different durations between regions. The transition between MN zones in Spain (Agusti *et al* 2001, Daams *et al* 1999) occur earlier than in Europe; similarly, but to less of a degree, the transition between MN zones in Switzerland occur earlier than in the rest of Europe (Steininger 1999), especially in the early Miocene.

### **1.3 Palaeo- and bio-geography of the early Miocene:**

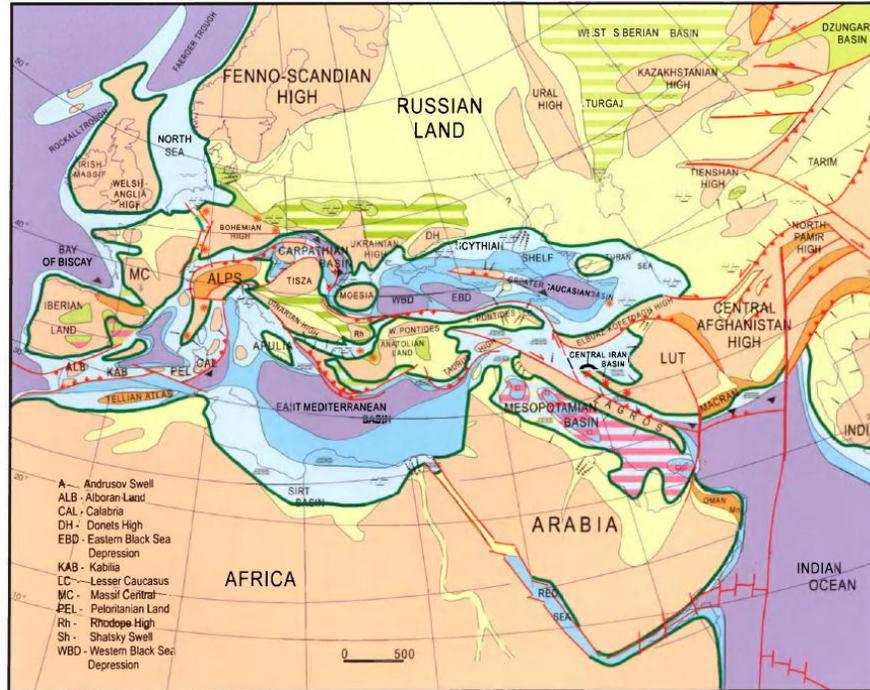
Various palaeo-geographic reconstructions of the Early Miocene have been published to date; those of Popov *et al* 2004 and Cavalier *et al* 1993 are displayed in Figures 2(a-c) below and show the evolution of European geography from approximately 20.5-16 million years before present (corresponding to MN1 – MN4). These, along with bio-geographic reconstructions are still speculative and are summarised below.

Prior to the early Miocene, the Tethys seaway (which joined the Atlantic to the Indo-Pacific Ocean via the Mediterranean) prevented any contact between the African and European continental land masses. The most significant geophysical event during the early Miocene was the collision of the Afro-Arabian and Anatolian tectonic plates. The anticlockwise rotation and northern drift of the Afro-Arabian tectonic plate resulted in collision with Eurasia in the early Miocene (20 - 19Ma). This tectonic movement caused an interruption in the Tethys seaway, and introduced the first land corridor for continental mammal exchange between Eurasia and Africa, known as the “*Gomphotherium* land bridge” (Rögl 1999; Steininger *et al* 1985). During the early-middle Miocene, the Tethys seaway closed and re-opened intermittently, as a result of tectonic activity (Rögl 1999; Steininger *et al* 1985).

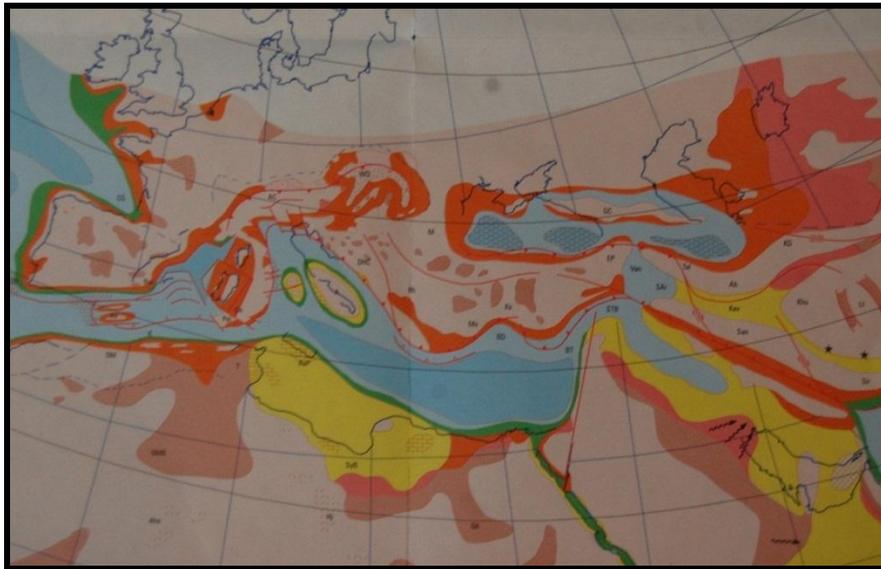
## Early Miocene Small Mammal Fauna from Karydiá, Greece

Figure 2 (a-c): Palaeogeographic maps of the Paratethys

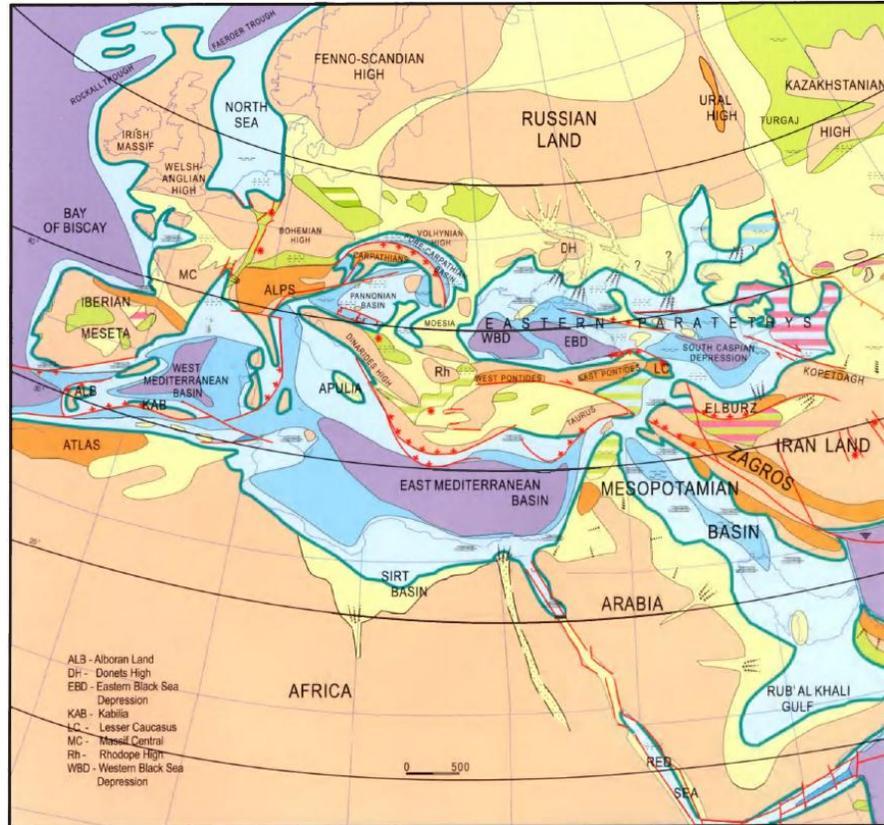
(a) Early Miocene (20.5-19 Ma) (Popov *et al* 2004)



(b) Early Miocene (18-16.5 Ma) (Cavelier *et al* 1993)



(c) Early Middle Miocene (16-15Ma) (Popov *et al* 2004)



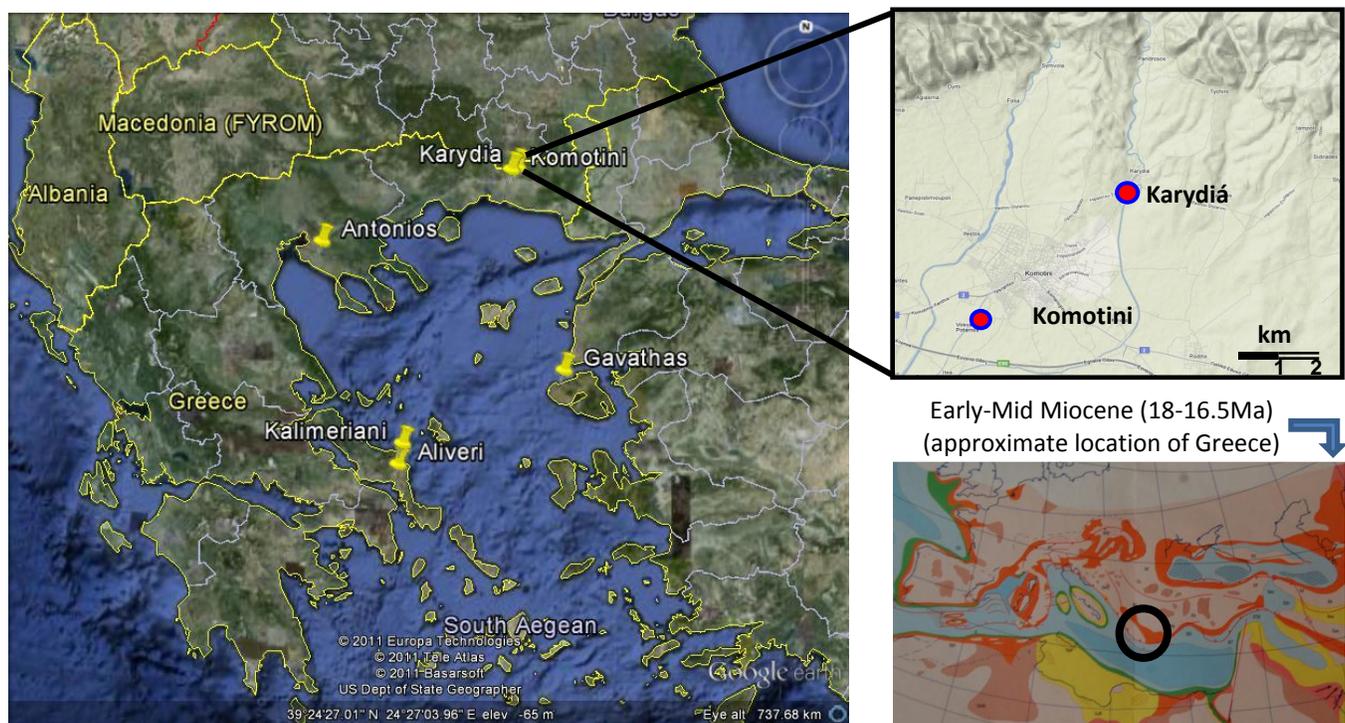
Within Europe, the uplift of mountain chains that could have constituted formidable physical barriers influencing the distribution of mammals included the Pyrenees, Alps, Carpathians and Balkan Mountains. Although many of these topographic features were formed prior to the Neogene, segments of individual mountain chains still experienced orogenic activity during the Miocene (Popov *et al* 2004). Initiating in the Mesozoic due to a collision of the European and Iberian tectonic plates, the Pyrenees experienced maximum uplift in the mid to late Eocene, erecting a potential physical barrier between the Iberian Peninsula and the rest of Europe (Maridet *et al* 2007). The Alps in general began uplifting in the late Cretaceous and Paleocene due to collision of the European and African tectonic plates in addition to other localized factors, and continued their orogeny during the Miocene; the Jura mountains, north-east of France (now incorporated into the Alps), began their uplift in the Oligocene (Stampfli *et al* 2002). The Caucasus Mountains of Georgia also posed a potential physical barrier from Eastern Europe into Asia. These mountains uplifted beginning in the Oligocene/early Miocene (Golonka 2004).

It appears that the main factor affecting migration potential and faunal changes/exchanges during the early Miocene was paleogeography (Koufos *et al* 2005). According to Maridet *et al* 2007, these events led to an emergence of a marked biogeographical pattern and the individualization of biogeographical provinces during biozone MN4.

### 1.4 Early Miocene (MN1-4) of Greece:

The Greek Miocene series of fossil mammal localities is incomplete; the biozones MN1 and MN2 have never been found. The early and early-mid Miocene mammal localities of Greece are displayed in Figure 3 below. These localities are Gavathas, Kalimeriani, Aliveri, Karydiá, Komotini and Antonios. There is little stratigraphic control for these sites (Theocharopoulos 2000), only Gavathas has an absolute age determination (Koufos *et al* 2003).

**Figure 3: Early and Early-Middle Miocene mammal localities of Greece, with location of Karydiá** (adapted from Fortelius 2011, de Bruijn and Saraç 1991 and Cavalier 1993)



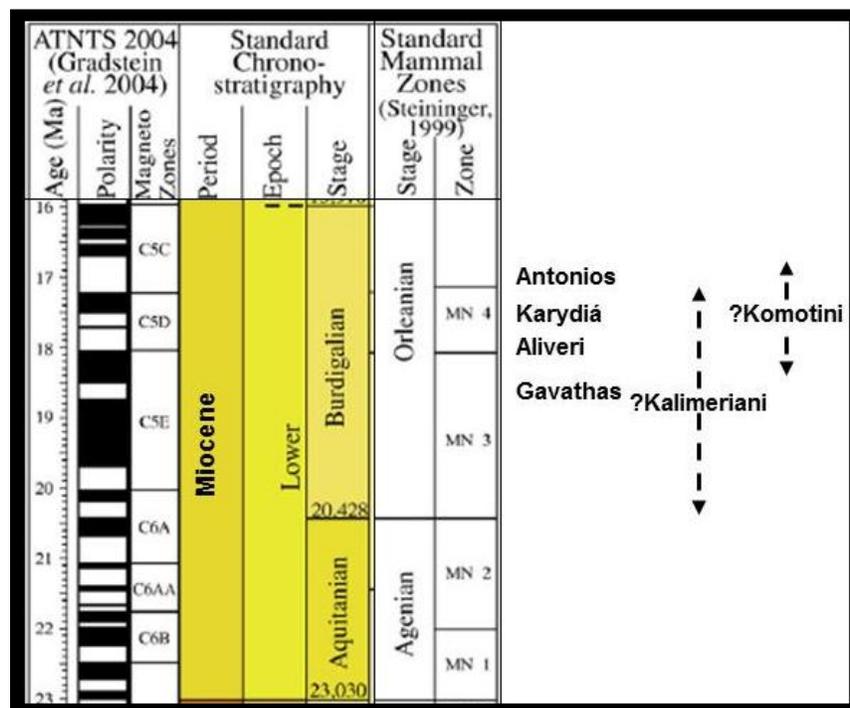
### Biostratigraphy:

The proposed biostratigraphy of Early and Early-Mid Miocene of Greece, according to Koufos (2006) is displayed in Figure 4 below. Kalimeriani is assigned to MN3/4, based on the

## Early Miocene Small Mammal Fauna from Karydiá, Greece

presence of a sole specimen of *Brachyodus* (Bonis & Koufos 1999). Gavathas is assigned to upper MN3 based on the stage-in-evolution of *Prodeinotherium bavaricum* and the radiometric dating of volcanic rocks (Koufos *et al* 2003). Both of these localities, however, did not produce small mammal fossils. The four remaining localities produced mammalian microfossils. The locality of Aliveri produced a substantial amount of small mammal fossils and is allocated to MN4, due to the presence of modern cricetids *Democricetodon*, *Megacricetodon* and *Cricetodon* (Alvarez Sierra *et al* 1987). Antonios and Komotini both produced few micromammal fossil remains and were designated late MN4/early MN5 (Koufos & Syrides 1997, Theocharopoulos 2000).

**Figure 4: Proposed biostratigraphy of Early and Early-Middle Miocene of Greece (Koufos 2006)**



Karydiá lies just west of the Thrace basin, the depositional environment is assumed lacustrine in origin (de Bruijn, pers com.). The Cricetidae (*Democricetodon* and *Karydomys*) were studied by Theocharopoulos (2000), Doukas (2003) reviewed the faunal assemblage, and the Insectivores (Erinaceomorpha, Soricomorpha: Mammalia) were studied by Doukas & Hoek Ostende (2006). A preliminary identification of all the small mammal fauna at Karydiá, based on the literature cited above, is presented in Table 1 below.

## Early Miocene Small Mammal Fauna from Karydiá, Greece

**Table 1: Preliminary faunal assemblage of Karydiá** (adapted from Theocharopoulos 2000 and Doukas & Hoek Ostende 2006). Note 1: N = absolute frequencies of the species = (M1+M2+m1+m2); n.d. = not determined. Note 2: Originally *Mirabella tuberosa* (amended by de Bruijn et al 2007).

Taxa		N <sup>(note 1)</sup>	
Rodentia	Cricetidae	<i>Cricetodon aliveriensis</i>	???
		<i>Democricetodon gracilis</i>	62
		<i>Democricetodon franconicus</i>	57
		<i>Democricetodon anatolicus</i>	9
		<i>Democricetodon</i> cf. <i>gaillardi</i>	7
		<i>Karydomys symeonidisi</i> n.sp.	45
		<i>Karydomys boskosi</i> n.sp.	12
		<i>Eumyarion</i> aff. <i>latior</i>	n.d.
		cf. <i>Deperetomys</i> sp.	n.d.
		<i>Mirabella tuberosa</i> <sup>Note 2</sup>	n.d.
	Sciuridae	<i>Aliveria luteijni</i>	n.d.
		<i>Blackia miocaenica</i>	n.d.
		<i>Palaeosciurus</i> aff. <i>fissurae</i>	n.d.
	Eomyidae	<i>Ligerimys</i> sp.	n.d.
	Anomalomyidae	<i>Anomalomys aliveriensis</i>	n.d.
	Spalacidae	<i>Debruijnina</i> sp.	n.d.
	Gliridae	<i>Glirulus (Glirulus) diremptus</i>	n.d.
		<i>Glirulus (Paraglrulus) agelakisi</i>	n.d.
		<i>Glis galitopouli</i>	n.d.
<i>Glirudinus gracilis</i>		n.d.	
<i>Miodyromys</i> cf. <i>praecox</i>		n.d.	
<i>Seorsumuscardinus alpinus</i>		n.d.	
Insectivora	Erinaceidae	<i>Galerix kostakii</i> n. sp.	23
	Talpidae	<i>Desmanodon antiquus</i>	6
		<i>Myxomygale</i> cf. <i>hutchisoni</i>	1
	Heterosoricidae	<i>Heterosorex</i> sp.	5
	Plesiosoricidae	<i>Plesiosorex</i> sp.	1
	Dimylidae	<i>Plesiodimylus</i> aff. <i>crassidens</i>	5
Soricidae	<i>Lartetium</i> cf. <i>dehmi</i>	5	
	<i>Paenelimnoecus</i> sp.	1	

Theocharopoulos (2000) assigned Karydiá to MN4 on the basis of its fossil content, in particular the presence of the modern cricetids *Democricetodon*, and *Cricetodon*. Compared with the other Greek MN4 locality of Aliveri, Theocharopoulos (2000) considers Karydiá to be younger, on the basis of the stage of evolution of *Cricetodon* and *Anomalomys*. Doukas & van den Hoek Ostende (2006) concur with this suggestion, stating that the Karydiá assemblage contains the same genera as Aliveri, but there are differences on the species level, suggesting a younger age for Karydiá (for example, *Galerix kostakii* is considered a descendent of *Galerix*

*symeonidisi* from Aliveri). Although both localities are referred to MN4, Doukas & Hoek Ostende (2006) suspects a considerable difference in time within these limits.

### *Biogeography:*

The biogeography of the early Miocene of Greece has been covered somewhat by Koufos (2005) and is based on occurrences of individual species. It is summarised as follows: The anthracothere *Brachyodus* from Asia first appeared in Western Europe in MN3 and is also present in Kalimeriani (MN3-4); it is suggested that the migration pathway may have been through the Eastern Mediterranean region indicating a connection between Greece, Anatolia and Asia. The first spalacid *Debruijnina* is known from MN 3 of Asia Minor, while it was also found in Aliveri, Greece, dated at the base of MN 4 (De Bruijn *et al.* 1992). These data suggest an early connection of Asia Minor with the Balkan Peninsula at the end of MN 3. An earlier connection with Asia is suggested, before the closure of the Tethyan Seaway, and is confirmed by the presence of a primitive deinotherium *Prodeinotherium* in Gavathas (dated >18.4Ma). This means that before the final closure of the Tethyan Seaway, there were some early short or temporary landbridges connecting Africa and Eurasia (before 18.0 Ma), allowing the entrance of some mammals. The genera *Megacricetodon*, *Democricetodon* and *Karydomys* are recognized in Aliveri (early MN 4), Komotini (MN 4/5) (Theocharopoulos, 2000). The first carnivores (*Palaeogale*, *Euboictis*) appeared in Aliveri, dated at the base of MN 4 (De Bruijn *et al.* 1992). These are deemed to be immigrants from Asia and Africa. The genus *Euboictis* has possibly a southern Asian origin and the connection of Asia Minor with Europe allowed its migration to the Balkans and Central Europe during MN 4 (Schmidt-Kittler, 1999).

Further studies, based on similarities and differences of fauna assemblages between various European locations or faunal provinces have indicated that the early Miocene mammal assemblages of Greece have an affinity with central Europe; however, the little amount of data available from Greece, for this period, is restrictive for the analysis (e.g. Maridet 2007). Further complications for reconstructions arise due to the lack of fossil localities in the Balkan regions, where an alternative migration pathway may have been possible – from Asia to Europe via north of the present day Black Sea. Fossil localities recently discovered in Serbia may shed light on this and studies have been carried out (for example Marković and Milivojević 2010).

### **1.5 Research Theme:**

This research aims to continue the study of the small mammal assemblage from Karydiá Greece, in order to gain further insights into the biostratigraphic position and paleogeography of this location. It plays a part in the bigger theme of creating a biostratigraphic record for the Eastern Mediterranean region, from which bioprovinces can be deduced, correlations with other European and Asian localities can be made, and paleo- and bio-geographic reconstructions can be updated.

This research comprises:

1. A detailed analysis and description of the Eomyidae and Cricetidae (*Eumyarion*) material from Karydiá
2. A comparison of the small mammal species found in Karydiá, with other Greek, European and Anatolian localities.
3. A re-evaluation of the biostratigraphy of Karydiá and its palaeogeographic implications.

## 2. Materials and Methods

### *Field work:*

The locality of Karydiá was discovered by Dr. H. de Bruijn and Mr. D. Foussekis in 1989. The material was collected from a clay pit 800 m from the village of Karydiá, North-East of Komotini, Thrace, Greece (N 40°08'26" E 25°26') (Doukas, 2005).

Three fossiliferous levels (KR1, KR2 and KR3) were sampled in consecutive years. KR 1 is situated at one side of a hill, KR2 and 3 are situated on the other. All levels are considered synchronous although the lithology would point to a slightly older KR3 (Doukas & Hoek Ostende 2006). Eight and a half tonnes of sediment were washed during the three field campaigns (Doukas 2003). All material was collected by wet screening on a set of sieves; the finest mesh used was 0.5mm (Theocharopoulos 2000). The material from Karydiá is partly housed in the Faculty of Earth Sciences, University of Utrecht and partly housed in the Museum of Geology and Palaeontology of the National and Kapodistrian University of Athens. This study uses material from level KR1, housed in the University of Utrecht.

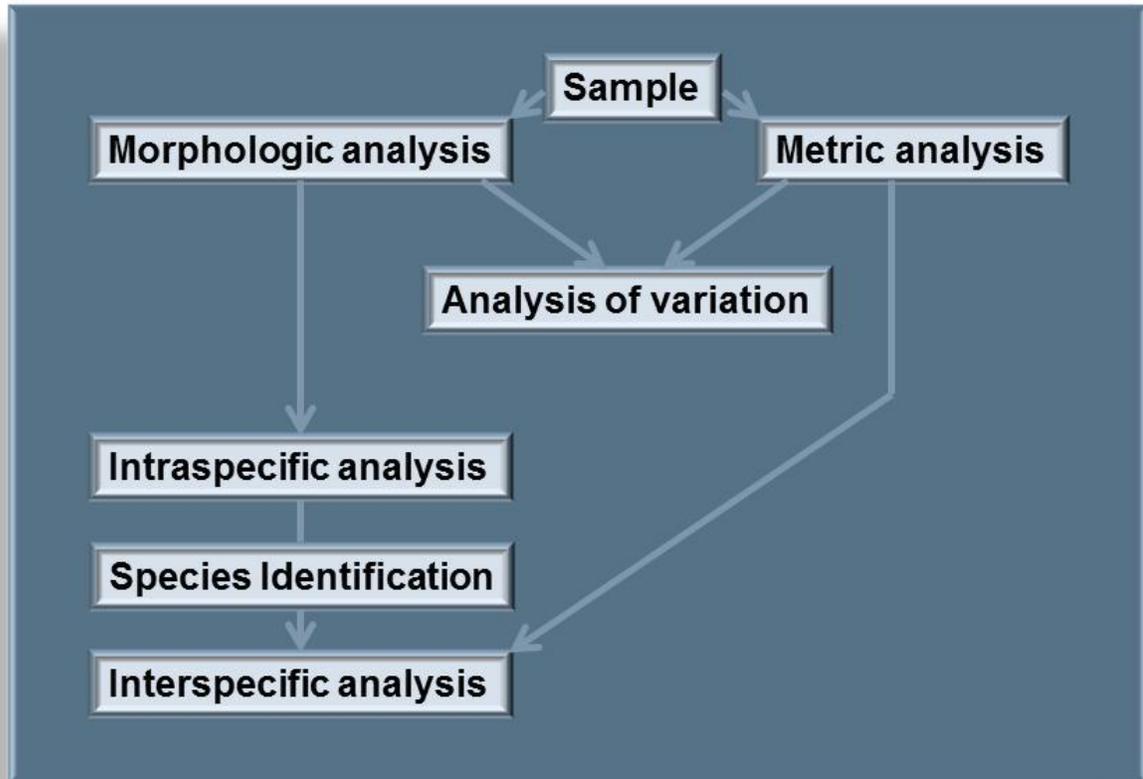
### *Systematics:*

Species and evolutionary stage determination was carried out in a semi-quantitative manner. An outline of the method is shown in Figure 5 below. Specific dental features were selected for quantitative analysis and width and length measurements were obtained. An analysis of the variation within the sample was attempted; however results were treated with caution due to the low number of specimens. The relative frequencies of morphological features in the material were compared with those obtained (through literature and stored, published, material) for similar species in various locations and time intervals in Europe and Anatolia. Once the species were determined, morphological characters and measurements were compared with those species found at other localities. As a result of this, evolutionary patterns were investigated.

This semi-quantitative approach makes the analysis as objective as possible; however, caution must be observed: de Bruijn and Saraç (1991) note that the perception of the observer depends on the quality of the microscope used, the experience of the observer and the mood of the observer. They tested the consistency of results by counting dental features of an association twice, a year apart. The results revealed that the consistencies varied for

different sets of features. This point is of particular importance when comparing features observed first hand with features described in literature. Where inconsistencies are thought to occur, these will be mentioned in the text.

Figure 5: Method used for systematics



*Molar Terminology:*

Molar features are explained in the Introduction section of Family Eomyidae and Family Cricetidae (Chapters 3 and 4), since each Family has its unique characteristics. An explanation of some abbreviations and molar terminology is given below:

- Capital letters and superscript numbers represent upper molars and their position in the maxilla:

P<sup>4</sup>: Upper fourth Premolar;

M<sup>1</sup>: Upper first Molar;

$M^2$ : Upper second Molar;

$M^3$ : Upper third Molar;

$M^{1-2}$ :  $M^1$  and  $M^2$  combined, where a distinction between the two has not been made.

- Small letters and subscript numbers represent lower molars and their position in the mandible:

$p_4$ : Lower fourth Premolar;

$m_1$ : Lower first Molar;

$m_2$ : Lower second Molar;

$m_3$ : Lower third Molar;

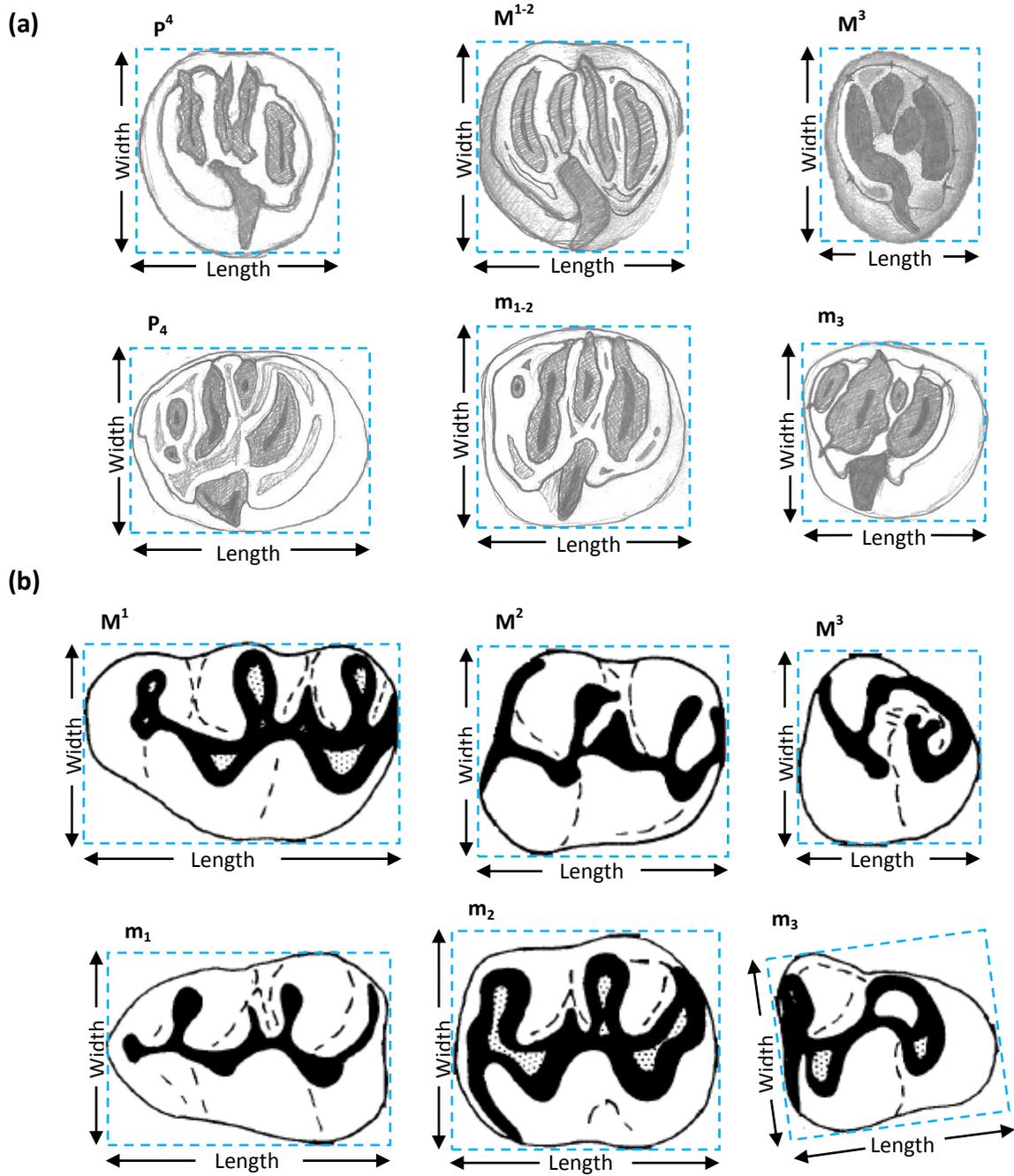
$m_{1-2}$ :  $m_1$  and  $m_2$  combined, where a distinction between the two has not been made.

- The abbreviations sin and dex represent the side of the cranium the specimen is from, i.e. sinistral (left jaw) and dextral (right jaw).
- Dental formulae, for example  $\frac{1013}{1013}$ , shows the number of (from left to right) incisors, canines, premolars and molars, with upper dentition above the line and lower dentition below the line.

#### *Measurements:*

Dental measurements were taken by the author, at Utrecht University, using a Leitz Orthoplan microscope (objective 10x, ocular 4x) with a mechanical stage and measuring clocks. Measurements are given in millimetre units. Maximum lengths were measured in the direction of the tooth row and maximum widths were measured at right angles to the maximum length (refer to Figure 6 below). Measurements were replicated three times; values used for this report are the means of these three measurements, with an accuracy of  $\pm 0.025$  mm. Length:Width ratios of the (pre)molars were calculated using two methods: (1) by averaging the obtained ratios, and (2) by calculating the ratio of the mean values of the molars. Method (2) was applied to data obtained from literature. Tooth row ratios are the ratio of the length of the  $P^4/M^{1-2}$  and  $M^3/M^{1-2}$  (and  $p_4/m_{1-2}$  and  $m_3/m_{1-2}$ ) for the Eomyidae; the length of the  $M^1/M^2$  and  $M^3/M^2$  (and  $m_1/m_2$  and  $m_3/m_2$ ) for the Cricetidae.

Figure 6: Measurement methods for (a) Eomyid (pre)molars, and (b) Cricetid molars.



### 3. Family Eomyidae

#### 3.1 Introduction:

*Evolution and ecology:* (summarised from Engesser, 1999)

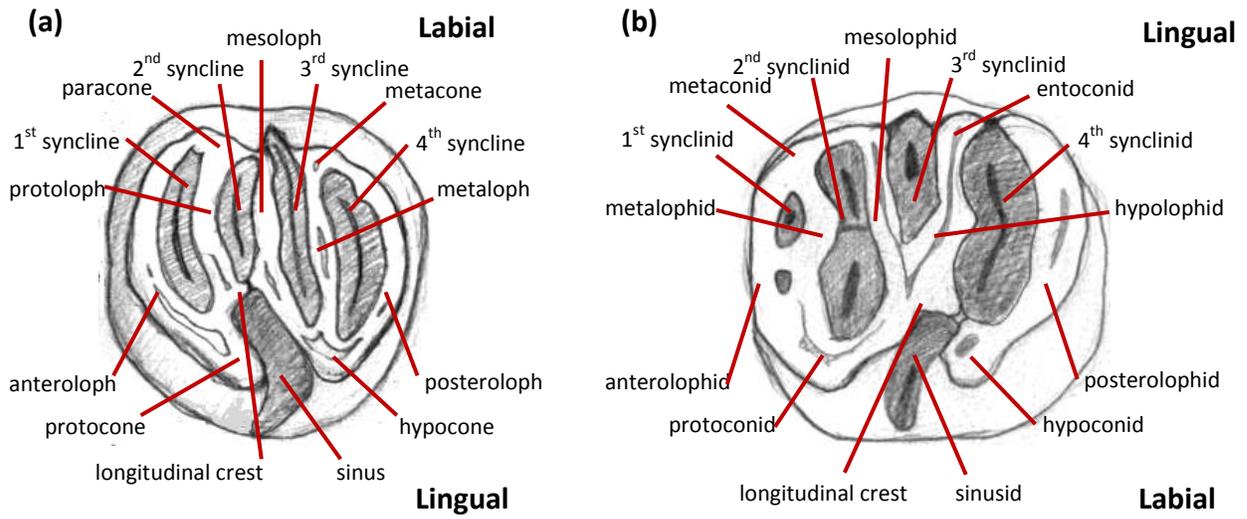
The Eomyidae are an extinct family of myomorph rodents. Almost nothing is known of them outside dentition. Based on frequency curves, their coincidence with gliridae and their absence when ground squirrels (Xerini) persisted, they are generally considered to have dwelled in humid forests. It is likely that they originated in Asia during the Eocene. They first appeared in Europe in the mid-Oligocene (MP21), probably emigrating from North America. Some Eomyid genera may have originated in Europe, where they underwent an independent evolution, whereas especially in the Late Oligocene and Early Miocene some taxa suddenly appeared, without any possible ancestors being known. These latter seem to be immigrants. During the Burdigalian (MN3 and 4), when there was a subtropical or tropical climate, the eomyids obtained their greatest diversity of forms. But at the beginning of MN5 when this warm and humid climate persisted all the existing eomyids disappeared and two new genera immigrated into Europe. They became rare in Europe in the Middle and Late Miocene and finally became extinct in North America and Europe in the Late Pliocene.

*Dentition:*

Family Eomyidae (Deperet and Douxami, 1902) are small rodents with dental formula:  $\frac{1013}{1013}$ .

Molars have differing crown heights, premolars are molariform. The crown displays four lophs, with 5, 4 or 2 transversal ridges of less or equal height as the main lophs. The main lophs are sometimes replaced in favour of reduced transversal ridges. The mesoloph(id) is occasionally missing. The longitudinal crest varies from long to short or can be missing. M3/m3 in the posterior part of the crown is reduced. All upper dentition and lower molars are with 3 roots; the lower p4 is with 2 roots.

Figure 7: Dental terminology for Eomyidae (adapted from Engesser 1999): (a)  $M^{1-2}$ , (b)  $m_{1-2}$



### 3.2 Material and Measurements:

Comparison material:

Table 2: A listing of the comparative material used in the analysis

\*All data, with the exception of Aliveri, has been collected from the literature cited. Data from Aliveri has been collected by the author from material housed in IVAU and was checked with data in the literature cited.

Region	Country	Locality name	Repository	Age (mybp) (NOW db, Fortelius, 2011)	MN zone correlation	References
S.E. Europe	Greece	*Aliveri (N+S)	IVAU	17-18	MN4	Alvarez Sierra <i>et al</i> (1987)
C. Europe	Czech Republic	Dolnice 1-3		17-18	MN4	Fejfar (1974)
C. Europe	Czech Republic	Bohrungen Co+Kr and Tucharice		18-20	MN3	Fejfar (1974)
C. Europe	Germany	Schnaitheim		18-20	MN3	Fahlbusch (1970)
C. Europe	Germany	Wintershof-West		18-20	MN3	Fahlbusch (1970)
C. Europe	Germany	Bissingen		not listed	MN3	Fahlbusch (1970)
C. Europe	Germany	Schaffhausen (1A)		not listed	MN2B	Fahlbusch (1983)
C. Europe	Germany	Schaffhausen (1B)		not listed	MN2B	Fahlbusch (1983)
C. Europe	Germany	Weissenburg 6		22.8-23.8	MN1	Fahlbusch (1970)

*Material and Measurements:*

The material from Karydiá I contains 66 teeth, from which 60 are measurable.

P<sup>4</sup>: 7 (KR 111-112, 116-120) (Plate 1A);

M<sup>1-2</sup>: 14 (KR 91-95, 101-109) (Plate 1B);

M<sup>3</sup>: 11 (KR 71-74, 81-87) (Plates 1A and B);

p<sub>4</sub>: 2 (KR 171-172) (Plate 1C);

m<sub>1-2</sub>: 19 (KR 141-147, 149, 151-161) (Plates 1D and E);

m<sub>3</sub>: 13 (KR 121-127, 131-134, 162-163) (Plate 1C)

**Table 3: Materials and measurements (*Pseudotheridomys aff. parvulus*);** N = total number of samples, n = number of measurable samples.

	Length				Width				L/W				N
	n	min	mean	max	n	min	mean	max	n	min	mean	max	
P <sup>4</sup>	6	1.04	1.06	1.11	6	1.20	1.22	1.24	6	0.85	0.87	0.90	7
M <sup>1-2</sup>	12	0.95	1.06	1.21	11	1.23	1.32	1.42	11	0.70	0.79	0.87	14
M <sup>3</sup>	11	0.79	0.84	0.94	11	1.02	1.08	1.21	11	0.72	0.78	0.88	11
p <sub>4</sub>	2	1.16	1.18	1.20	2	0.98	0.99	1.00	2	1.16	1.19	1.22	2
m <sub>1-2</sub>	16	1.11	1.21	1.33	17	1.07	1.15	1.26	16	0.98	1.05	1.18	19
m <sub>3</sub>	12	0.96	1.06	1.17	12	0.92	1.04	1.15	12	0.97	1.02	1.09	13

*Systematic description:*

Family: Eomyidae (Depéret & Douxami 1902)

Genus: *Pseudotheridomys* (Schlosser 1926)

Species: *Pseudotheridomys (aff) parvulus* (Schlosser 1884)

*Morphological description:*

**Upper dentition**

Present in all specimens are five ridges: the anteroloph, protoloph, mesoloph, metaloph and posteroloph. These ridges are transverse, except for the M<sup>3</sup> molars where a chaotic ridge pattern is observed. For all upper molars, the sinus points obliquely forward and the 2<sup>nd</sup> syncline is the narrowest valley.

**P<sup>4</sup>:** The anteroloph is connected to the paracone in 4 of 7 specimens; however, these are mainly worn specimens. In unworn specimens, the connection is weak. The protoloph and mesoloph meet at the paracone in 3 of 7 specimens. The mesoloph extends from the longitudinal crest to the labial border in 3 of 7 specimens. In four specimens, the mesoloph is a short, labially situated isolated ridge. All specimens display a labial parting between mesoloph and metacone. The longitudinal crest is well developed in 4 specimens. One specimen shows a reduction in this ridge between the sinus and the 1<sup>st</sup> syncline. A further specimen displays a reduction in this ridge between the sinus and the 1<sup>st</sup> syncline and a complete absence of this ridge between the sinus and the 2<sup>nd</sup> syncline. The posteroloph and metaloph form a closed ellipse in 6 of 7 specimens. In 1 specimen there is a weak connection between the posteroloph and metaloph lingually.

**M<sup>1-2</sup>:** In 7 (mostly worn) out of 12 specimens the anteroloph is connected to the paracone labially, and in 10 out of 12 specimens the anteroloph meets the protoloph lingually. The protoloph is connected to the mesoloph at the paracone in 9 out of 12 specimens. The mesoloph is detached from the paracone and metacone in the remaining three cases. The longitudinal crest is complete in 12 of 13 specimens. The mesoloph reaches the labial border in 12 of the 13 specimens; with one specimen the mesoloph is a short, isolated, labial ridge. The mesoloph is connected to the metacone in 9 out of 12 specimens; these are mostly worn specimens. The posteroloph and metaloph form a closed ellipse in all 12 undamaged specimens.

**M<sup>3</sup>:** Four of eleven specimens have a chaotic ridge pattern; the dental pattern of the other seven cases resembles that of M<sup>1-2</sup>. In 6 out of 11 specimens the anteroloph is connected to the paracone labially. The protoloph is connected to the mesoloph at the paracone in 4 out of 11 specimens. The mesoloph reaches the labial border in 8 of the 11 specimens and is connected to the metacone in 9 out of 11 specimens. The 4<sup>th</sup> syncline has a shallow labial opening in 3 specimens. The longitudinal ridge is present in 5 specimens.

### **Lower dentition**

The lower molars show more variance in tooth pattern than the upper molars. Five ridges (the anterolophid, protolophid, mesolophid, metalophid and posterolophid) are present in 27 of 30 intact specimens; for three cases (worn m<sub>3</sub> specimens), the mesolophid is fused with the hypolophid. In general, the anterolophid meets the metalophid labially and lingually and the metalophid meets the mesolophid labially in all lower molars. The sinusid points

obliquely backward in 31 out of 34 specimens, and is transverse in the remaining three (one  $m_{1-2}$  and two  $m_3$  specimens).

**p<sub>4</sub>:** The anterolophid meets the metalophid both labially and lingually in all 2 specimens. There is an incomplete longitudinal ridge between the anterolophid and metalophid in 1 specimen. The metalophid meets the mesolophid labially in both specimens and lingually in 1 specimen. This mesolophid is separated lingually from the hypolophid, but in the more worn specimen the two ridges meet. The mesolophid and hypolophid are parallel in 1 specimen; in the other the mesolophid is transverse and the hypolophid oblique. The longitudinal crest is present between the protoconid and hypoconid in both specimens. In 1 specimen the hypolophid is connected labially to the posterolophid, and in both specimens the hypolophid meets the posterolophid lingually.

**m<sub>1-2</sub>:** The anterolophid meets the metalophid labially and lingually in all 11 intact specimens. In 2 of 14 specimens a short longitudinal spur is present in the 1<sup>st</sup> synclinid. The metalophid is connected lingually to the mesolophid in 12 of 15 specimens and labially in 16 of 16 specimens. The longitudinal ridge, connecting the protoconid to the hypoconid, is present in 16 out of 16 specimens; in 5 cases it situated labially of the midline of the tooth, in 11 cases it has a central position. The lingual parts of the mesolophid and hypolophid are parallel and transverse in 5 of 16 specimens, the mesolophid is transverse and the hypolophid oblique in 4 of 16 specimens. Conversely, the mesolophid is oblique and hypolophid transverse in 5 of 16 specimens and one specimen shows a parallel and oblique mesolophid and hypolophid. The mesolophid and hypolophid meet in the centre of 1 specimen, to form an X-shape. The hypolophid and posterolophid form a closed ellipse in 17 of 19 specimens, with 2 specimens having a shallow opening lingually.

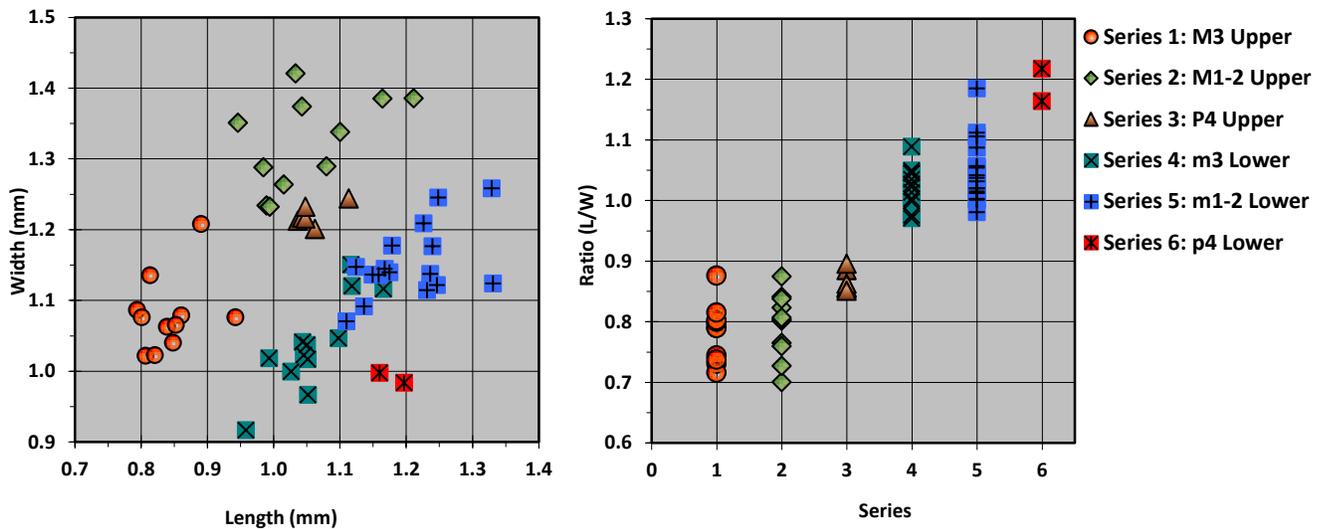
**m<sub>3</sub>:** The anterolophid is present in 9 of 13 specimens, of these the anterolophid is short and 1<sup>st</sup> synclinid shallow in 6 cases and the anterolophid is long in 3 cases. The 1<sup>st</sup> synclinid is closed in all 9 specimens. The mesolophid is long in 9 specimens and has a shallow opening lingually in 2 specimens. The mesolophid is connected lingually to the metalophid in all 13 specimens, and labially in 12 out of 13 specimens (10 of these connections are weak). The longitudinal ridge is absent in 3 of 11 specimens and has a labial position whenever present. In unworn or slightly worn specimens the mesolophid is separated lingually from the hypolophid, 1 specimen has a wide opening between these two ridges. The hypolophid and posterolophid form a closed ellipse in 3 of 11 specimens, with 4 ellipses interrupted lingually

and a further 3 interrupted labially. In 8 out of 11 specimens a short longitudinal spur is present in the 1<sup>st</sup> synclinalid, but this does not reach the hypolophid.

**Special remarks:** An unusual specimen, determined to be M<sup>1-2</sup>, is present in the material from Karydiá (Plate 1B, figure 29). The molar's two anterior roots are fused. In general, this molar has an unusual crown shape.

*Metric analysis:*

Figure 8: Metric analysis of *Pseudotherimyoys* aff. *parvulus* dentition from Karydiá



### 3.3 Comparative Analysis:

A comparison of the morphologies and measurements of the specimens from Karydiá and the comparative material are summarised in Tables 4, 5 and 6, and Figures 9 and 10 below. They are discussed in the subsequent discussion section.

# Early Miocene Small Mammal Fauna from Karydiá, Greece

**Table 4: Morphological analyses of Eomyidae upper (pre)molars, from Karydiá, Aliveri and Central European localities**

Region	M <sup>1-2</sup>										M <sup>3</sup>															
	Development of the Mesoloph					Development of the Longitudinal Crest					Development of the Sinus					Development of Syncline I and IV										
	Country	Locality	MN Zone	Genus	Species	Long spur, detached from Paracone and Metacone	Long spur, connected to Paracone, reduced connection to Metacone	Long interrupted spur, connected to Paracone, reduced connection to Metacone	Half spur, connected to Paracone, reduced connection to Metacone	Half spur, detached from Paracone and Metacone	Short spur, detached from Paracone and Metacone	Absent	Broad	Shallow opening at 2nd Syncline	Open at 2nd Syncline	Shallow opening at 1st Syncline	Open at 1st Syncline	Very oblique, approx. 45 deg angle	Oblique, approx. 20 deg. Angle	Slightly oblique, approx. 10 deg angle	Transverse	Syncline I and IV closed	Syncline I partly open bbibly, Syncline IV closed	Syncline I open bbibly, Syncline IV partly open bbibly	Syncline I and IV open	n
S.E. Europe	Greece	Karydiá	MN4	<i>Pseudotheridomys</i>	<i>(aff) parvulus</i>	17	67	8	8	8	17	54	23	15	8	13	38	62	13	67	33	13	67	33	12	12
S.E. Europe	Greece	Aliveri (M-S)	MN4	<i>Pseudotheridomys</i>	<i>parvulus</i>	18	79	3	8	8	152	63	15	1	21	155	13	81	6	159	95	5	159	95	5	154
C. Europe	Czech Rep.	Dolnice 1-3	MN4	<i>Ligerimys</i>	<i>antiquus</i> (Mt A)	100					2	100			2	50	50	2	100		2	50	50	2	2	
C. Europe	Czech Rep.	Bohrungen Co-Kr and Tuchtovice	MN3	<i>Ligerimys</i>	<i>antiquus</i> (Mt A)	100					2	50			2	100			2	50		2	50	50	2	2
C. Europe	Germany	Erkershofen	MN4	<i>Ligerimys</i>	<i>flavescens</i>	1			1	2	98	400	96	1	2	400	2	6	56	36	400	1	7	44	40	8
C. Europe	Germany	Schnaitheim	MN3	<i>Ligerimys</i>	<i>antiquus</i>	2			2	5	92	242	94	1	4	242	30	40	28	2	242	2	32	34	26	6
C. Europe	Germany	Wintershof-West	MN3	<i>Ligerimys</i>	<i>antiquus</i> (Mt A+B)	3	11	1	2	3	80	166	84	4	1	165	45	37	18	2	242	5	34	31	28	2
C. Europe	Germany	Wintershof-West	MN3	<i>Ligerimys</i>	<i>antiquus</i> (Mt B)	9	35	2	2	2	5	46	382	85	7	2	144	35	43	22	130	2	30	36	30	2
C. Europe	Germany	Wintershof-West	MN3	<i>Ligerimys</i>	<i>antiquus</i> (Mt A)	9	35	2	2	2	5	46	382	85	7	21	100			22	23	54	9	14	22	22
C. Europe	Germany	Bissingen	MN3	P-L transition	Mt (A+B)	20	77	3	4	3	8	84	215	91	3	1	217	42	47	11	212	7	35	35	20	
C. Europe	Germany	Bissingen	MN3	P-L transition	Mt B	20	77	3	4	3	8	84	215	91	3	1	217	42	47	11	212	7	35	35	20	
C. Europe	Germany	Weissenburg 6	MN1	<i>Pseudotheridomys</i>	<i>(aff) parvulus</i>	177	77	13	1	6	3	178	95	5	1	178	95	5	1	178	95	5	1	178	95	3
C. Europe	Germany	Weissenburg 6	MN1	<i>Pseudotheridomys</i>	<i>(aff) parvulus</i>	177	77	13	1	6	3	178	95	5	1	178	95	5	1	178	95	5	1	178	95	3

Region	M <sup>3</sup>										M <sup>3</sup>														
	Development of the Mesoloph					Development of the Anteroloph					Development of the Sinus					Development of Syncline I and IV									
	Country	Locality	MN Zone	Genus	Species	Long	Short	Absent	Short spur, connected to mid-Protoloph	Medium length spur, interrupted, originating from Protoloph	Medium length spur, connected to Protoloph	Medium length spur, attached to Protolone	Long spur, attached to Protolone	La	Lb	Lc	Ld	Le	Lf	n					
S.E. Europe	Greece	Karydiá	MN4	<i>Pseudotheridomys</i>	<i>(aff) parvulus</i>	43	57	7	100	100	7	100	100	100	100	100	100	100	100	11					
S.E. Europe	Greece	Aliveri (M-S)	MN4	<i>Pseudotheridomys</i>	<i>parvulus</i>	89	11	47	100	100	47	100	100	100	100	100	100	100	100	26					
C. Europe	Czech Rep.	Dolnice 1-3	MN4	<i>Ligerimys</i>	<i>antiquus</i> (Mt A)	22	78	9	100	100	9	100	100	100	100	100	100	100	100	26					
C. Europe	Czech Rep.	Bohrungen Co-Kr and Tuchtovice	MN3	<i>Ligerimys</i>	<i>antiquus</i> (Mt A)	67	33	3	100	100	3	100	100	100	100	100	100	100	100	26					
C. Europe	Germany	Erkershofen	MN4	<i>Ligerimys</i>	<i>flavescens</i>	3	97	203	100	100	203	100	100	100	100	100	100	100	100	26					
C. Europe	Germany	Schnaitheim	MN3	<i>Ligerimys</i>	<i>antiquus</i>	4	97	115	100	100	115	100	100	100	100	100	100	100	100	26					
C. Europe	Germany	Wintershof-West	MN3	<i>Ligerimys</i>	<i>antiquus</i> (Mt A+B)	30	5	65	57	2	98	55	2	98	55	2	98	55	2	98	55	2	98	55	2
C. Europe	Germany	Wintershof-West	MN3	<i>Ligerimys</i>	<i>antiquus</i> (Mt B)	42	7	51	215	2	98	215	2	98	215	2	98	215	2	98	215	2	98	215	2
C. Europe	Germany	Wintershof-West	MN3	<i>Ligerimys</i>	<i>antiquus</i> (Mt A)	42	7	51	215	2	98	215	2	98	215	2	98	215	2	98	215	2	98	215	2
C. Europe	Germany	Bissingen	MN3	P-L transition	Mt (A+B)	42	7	51	215	2	98	215	2	98	215	2	98	215	2	98	215	2	98	215	2
C. Europe	Germany	Bissingen	MN3	P-L transition	Mt B	42	7	51	215	2	98	215	2	98	215	2	98	215	2	98	215	2	98	215	2
C. Europe	Germany	Bissingen	MN3	P-L transition	Mt A	42	7	51	215	2	98	215	2	98	215	2	98	215	2	98	215	2	98	215	2
C. Europe	Germany	Bissingen	MN3	P-L transition	Mt B	42	7	51	215	2	98	215	2	98	215	2	98	215	2	98	215	2	98	215	2
C. Europe	Germany	Weissenburg 6	MN1	<i>Pseudotheridomys</i>	<i>(aff) parvulus</i>	91	9	99	100	100	99	100	100	100	100	100	100	100	100	100	100	100	100	100	100



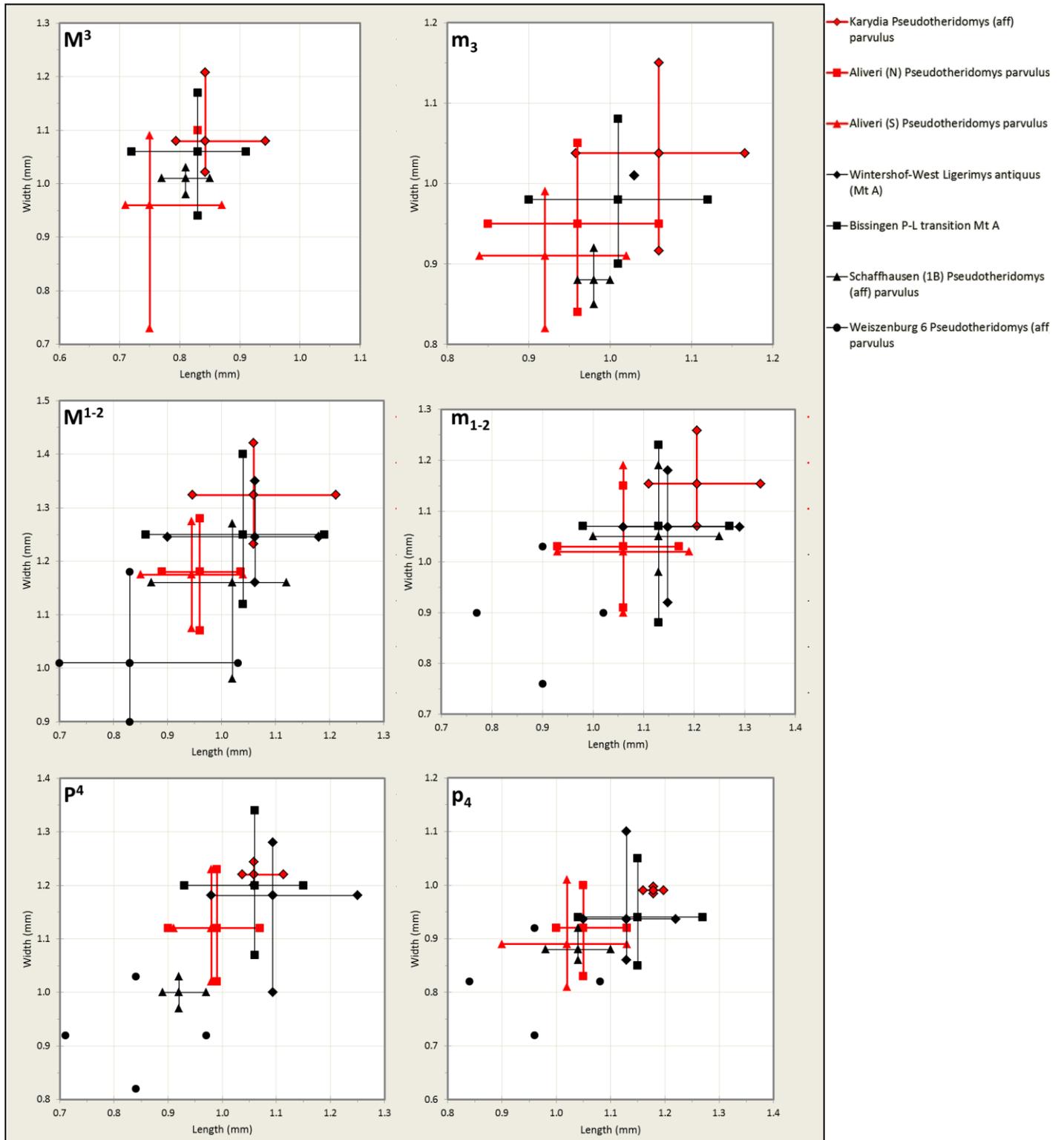
## Early Miocene Small Mammal Fauna from Karydiá, Greece

**Table 6: Length/Width ratios and tooth-row length ratios for Eomyidae (pre)molars, from Karydiá, Aliveri and Central Europe**

Locality	MN Zone	Species	M <sup>1/2</sup>	Length/Width ratios						Tooth row length ratios			
				P <sup>4</sup>	M <sup>1-2</sup>	M <sup>3</sup>	p <sub>4</sub>	m <sub>1-2</sub>	m <sub>3</sub>	P <sup>4</sup> /M <sup>1-2</sup>	M <sup>3</sup> /M <sup>1-2</sup>	p <sub>4</sub> /m <sub>1-2</sub>	m <sub>3</sub> /m <sub>1-2</sub>
Karydia	MN4	<i>P. aff. parvulus</i>	M <sup>1-2</sup>	<b>0.87</b>	<b>0.79</b>	<b>0.78</b>	<b>1.19</b>	<b>1.05</b>	<b>1.02</b>	<b>1.00</b>	<b>0.79</b>	<b>0.98</b>	<b>0.88</b>
Aliveri (S)	MN4	<i>P. parvulus</i>	M <sup>1</sup>	0.88	0.84	0.78	1.15	1.04	1.01	0.99	0.76	0.96	0.87
Aliveri (N)	MN4	<i>P. parvulus</i>	M <sup>2</sup>		0.77					1.09	0.83		
			M <sup>1</sup>	0.88	0.85	0.75	1.14	1.03	1.01	0.99	0.83	0.99	0.91
Dolnice 1-3	MN4	<i>L. antiquus</i> (Mt A)	M <sup>1-2</sup>	x	0.98	x	1.21	x	x	x	x	x	x
			M <sup>1-2</sup>	0.91	x	x	x	x	x	x	x	x	x
Bohrungen Co + Kr and Tucharice	MN3	<i>L. antiquus</i> (Mt A)	M <sup>1-2</sup>	0.91	x	x	x	x	x	x	x	x	x
Schnaitheim	MN3	<i>L. antiquus</i>	M <sup>1-2</sup>	0.99	0.88	0.82	1.22	1.11	1.06	1.03	0.75	0.96	0.80
Wintershof-West	MN3	<i>L. antiquus</i> (Mt A+B)	M <sup>1-2</sup>	0.96	0.86	x	1.18	1.09	1.08	0.99	x	0.93	x
Wintershof-West	MN3	<i>L. antiquus</i> (Mt B)	M <sup>1-2</sup>	x	x	x	x	x	x	x	x	x	x
Wintershof-West	MN3	<i>L. antiquus</i> (Mt A)	M <sup>1-2</sup>	x	x	x	x	x	x	x	x	x	x
Bissingen	MN3	P-L transition Mt (A+B)	M <sup>1-2</sup>	0.91	0.84	0.80	1.20	1.07	1.04	1.01	0.79	0.97	0.85
Bissingen	MN3	P-L transition Mt B	M <sup>1-2</sup>	0.95	0.85	0.82	1.18	1.10	1.07	1.01	0.78	0.93	0.83
Bissingen	MN3	P-L transition Mt A	M <sup>1-2</sup>	0.88	0.83	0.78	1.22	1.06	1.03	1.02	0.80	1.02	0.89
Schaffhausen 1A	MN2b	<i>P. (aff) parvulus</i>	M <sup>1-2</sup>	0.93	0.87	0.81	1.20	1.07	1.09	0.99	0.78	0.89	0.88
Schaffhausen 1B	MN2b	<i>P. (aff) parvulus</i>	M <sup>1-2</sup>	0.92	0.85	0.80	1.21	1.08	1.11	0.90	0.79	0.92	0.87
Weissenburg 6	MN1	<i>P. (aff) parvulus</i>	M <sup>1-2</sup>	x	0.82	x	x	x	x	x	x	x	x

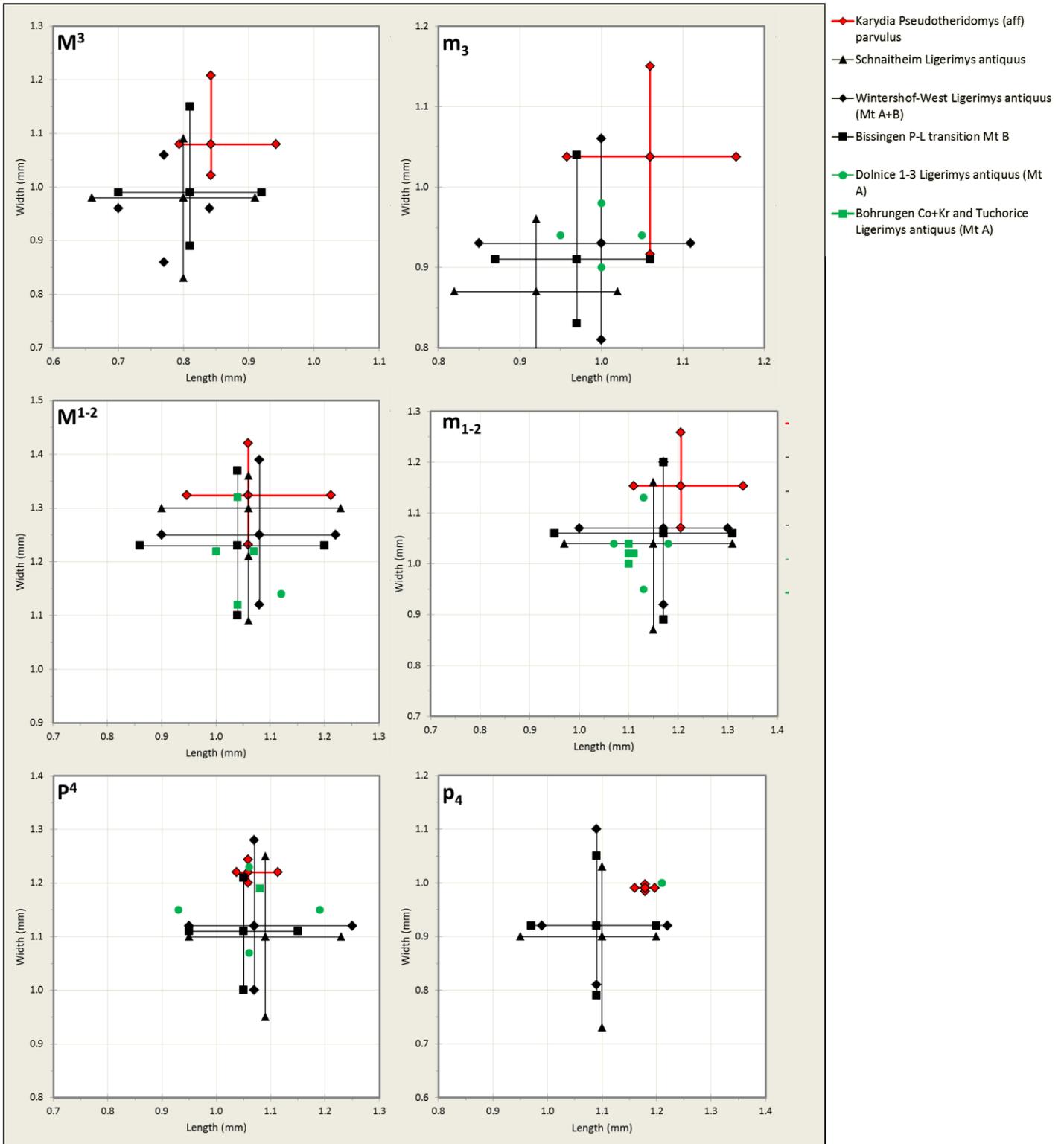
## Early Miocene Small Mammal Fauna from Karydiá, Greece

**Figure 9: Metric comparisons of Eomyidae: Morphotype A (pre)molars, from Karydiá, Aliveri and Central European localities**



## Early Miocene Small Mammal Fauna from Karydiá, Greece

**Figure 10: Metric comparisons of Eomyidae: Morphotype B (pre)molars, from Central European localities. Measurements from Karydiá are included for comparative purposes.**



3.4 Discussion

Species designation:

In order to explain the designation of the Karydiá dentition to the species *Pseudotheridomys* (aff) *parvulus*, it is necessary to discuss the model for the evolution of the genus *Pseudotheridomys* to the genus *Ligerimys* in the Bavarian Freshwater Molasse of southern Germany, described by Fahlbusch (1970, 1979, 1983). An overview of this model is displayed in Figure 11 below.

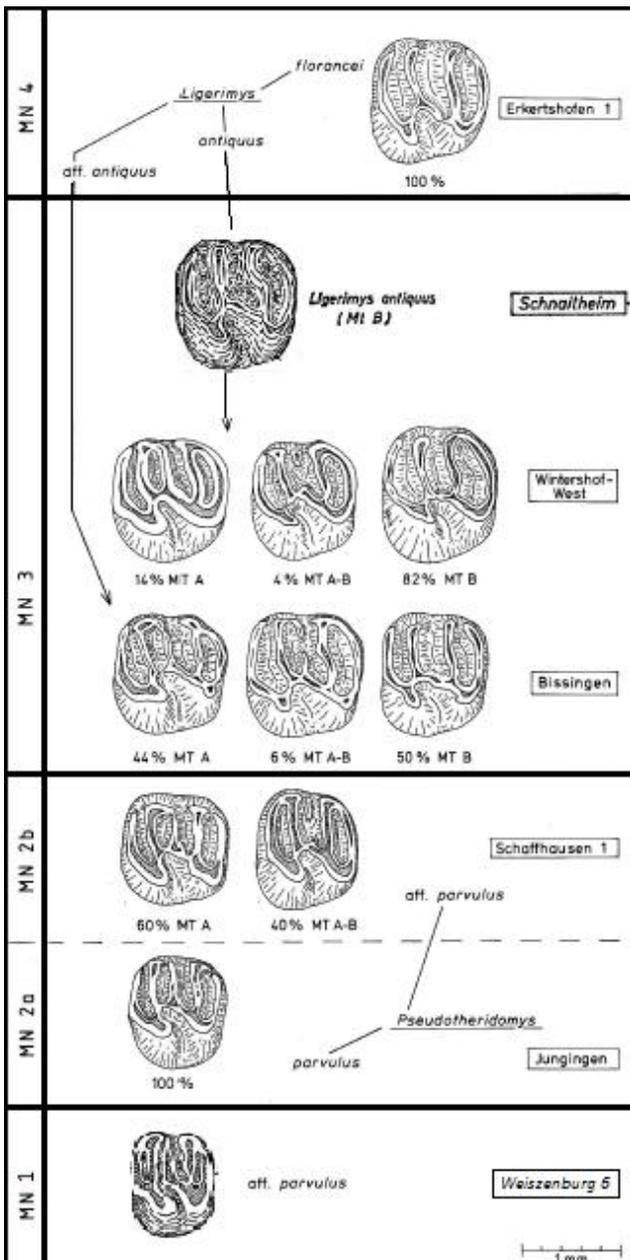


Figure 11: Evolution of the Genus *Pseudotheridomys* to *Ligerimys* with the percentage abundances of the morphotypes. Pictured are examples of M<sup>1/2</sup> from the Agenium and Orleanian (MN 1-4) of Southern Germany (adapted from Fahlbusch 1970, 1979, 1983).

The first signs of the emergence of genus *Ligerimys* from genus *Pseudotheridomys* is during MN1, at Weissenburg 6, when *P. pusillus* has a direct descendent in *P. aff. parvulus*. The species *P. parvulus* can be seen in MN2a of Jungingen, from which *Pseudotheridomys aff. parvulus* develops as seen in the populations of Schaffhausen 1. The second part of the transformation is documented in the fauna from Bissingen, Wintershof-West and Schnaitheim, which show a continuous development to *Ligerimys* until the upper Burdigal *Ligerimys florangei* at Erkertshofen 1.

From the analysis of numerous morphological characteristics and measurement indices of the transitional populations of Bissingen and Wintershof West, significant differences could be seen within the population of each location. These differences divided the molars into two groups (morphotype A and morphotype B). Morphotype A matches the Aquitanian *P. parvulus*; morphotype B is similar to the upper Burdigalian *L. florangei*. The remaining molars were ascribed as an intermediary between the two groups (morphotype A-B). Morphotypes A and B were designated the characteristics displayed in Table 7 below:

**Table 7: Morphological parameters used to differentiate between Morphotype A and Morphotype B of the Pseudotheridomys to Ligerimys lineage** (adapted from Fahlbusch 1983)

Morphological parameter		Morphotype A	Morphotype B
Upper dentition	Synclines	Narrow and deep	Wide and deep
	Mesoloph	Long, rarely interrupted	Absent, rarely a short spur from the longitudinal ridge and/or labial crown edge
	Longitudinal Crest	Occasionally interrupted	Rarely interrupted
	Sinus	Strongly bent to the anterior	Not so strongly bent to the anterior
	Outer synclines	Outer synclines I, II and IV mostly labial, syncline III seldom open.	Outer synclines I and IV often have a shallow opening or are fully open, synclines II and III are mostly joined and labially open.
Lower dentition	Orientation of mesolophid and hypolophid	Almost parallel, transverse crests, directed toward the anterior	Often diverge from the longitudinal crest, lingually
	Synclinids	Narrow and deep	Wide and deep
	Anterolophid of m <sub>1-2</sub>	Located lingually or missing	Mostly long
	Longitudinal Crest	Often interrupted, situated labially	Seldom interrupted, situated lingually or on midline
	Transversal ridges	Parallel	Form an X-shape
	Inner synclinids	Inner synclinids I, II and IV are lingually situated and closed, inner synclinid III is closed or has a shallow opening, rarely fully open	Inner synclinid III is mostly open, rarely has a shallow opening; inner synclinid IV often has either a shallow opening or is fully open

In the stratigraphic succession of the localities Schaffhausen 1, Bissingen, Wintershof-West, Schnaitheim, Fahlbusch describes a gradual shift in the relative frequencies of morphotype A molars to morphotype B molars. The proportion of morphotype A:B in the population shifts from 60%:0% (Schaffhausen 1) 44%:50% (Bissingen) through 14%:82% (Wintershof West) to 0.5%:97% (Schnaitheim), with transitional forms constituting 40%, 6%, 4% and 2.5% of the populations respectively. These locations show a continuous evolutionary progression, which shows the transition from the genus *Pseudotheridomys* to the genus *Ligerimys*, beginning in the Aquitanian, concluding in the lower Burdigalian. Morphotype A, with high proportion of Mt A-B was designated *P. aff. parvulus*; where the proportion of Mt B was greater than Mt A, these were designated as transitional species; a new species, *Ligerimys antiquus*, was introduced to accommodate the assemblages with a greater proportion of Mt B than Mt A (pre)molars.

Morphological analysis (Tables 4 & 5 above, Appendix 1) revealed Karydiá molars to be a combination of morphotype A and intermediate morphotype A-B, with a proportion of 93% and 7% respectively. There were no morphotype B molars detected. This morphology agrees well with *Pseudotheridomys aff. parvulus* from Schaffhausen, although the proportions are different. Metric analysis (Table 6 and Figures 9 & 10 above) showed a similarity with the morphotype A molars of Bissingen and Wintershof-West. The Schaffhausen material had higher L/W ratios, much like the morphotype B (pre)molars. It may be that this is due to the higher proportion of intermediate morphotypes (A-B) in the collection. It is thought that this intermediate morphotype is metrically similar to morphotype B; however, there were no morphotype A-B measurements available in the literature and therefore this proposition could not be proven. The metric analysis of the Karydiá collection showed no such differentiation, but this is deemed to be a result of insufficient samples. Interestingly, the *Ligerimys antiquus* morphotype A (pre)molars from the Czech localities of Tuchorice and Dolnice show similar width/length ratios as the morphotype B molars from Germany, possibly an indication that these evolved directly from morphotype B populations.

### *Comparison with Aliveri:*

Alvarez Sierra *et al* (1987) concluded that the assemblage from the Greek locality of Aliveri consists entirely of type A (pre)molars, which agree in size and morphology with those from Bissingen, Wintershof-West, Schnaitheim, Tuchorice and Dolnice 1, 2 and 3. The molars were subsequently designated as *Pseudotheridomys parvulus*. A detailed study of the assemblage, for the purpose of this thesis, was carried out and concurs with this designation. The

specimens from Karydiá differ from Aliveri, by morphology (through the existence of a reduced mesoloph in a small proportion of Karydiá specimens) and by size (the width/length ratios are similar, but the dentition of the Karydiá assemblage are generally larger). These differences are reflective of the early stages of the transition from *Pseudotheridomys* to *Ligerimys* described by Fahlbusch (1970, 1983).

#### 4. Family Cricetidae, Genus *Eumyarion*

##### 4.1 Introduction:

*Evolution and ecology:* (summarised from Kälin, 1999 and De Bruijn and Sarac, 1991)

The modern Cricetidae, of which *Eumyarion* is a part, appeared in Europe in several immigration waves, for the first time during the latest early Micoene MN4. They are separated from the ancient cricetids of Europe by a temporal gap of approx 2 million years ("Cricetid vacuum", Daams & Freudenthal 1988). The *Eumyarion* are small to medium sized cricetids. The immigration of *Eumyarion* probably took place from Asia Minor, where stratigraphically older species are known (De Bruijn and Sarac, 1991). They are recorded in western and central Europe for the first time in MN4, approximately contemporaneous with the immigration waves of *Megacricetodon* and *Democricetodon*. From MN5, however, it is absent from southeastern Europe and Turkey. In central Europe, the stratigraphically oldest species (*E. weinfurteri*) is the smallest and a considerable size increase seems to have taken place during the Middle Miocene. On the other hand, investigations in the Swiss Molasse Basin showed no uniform trend in size increase, it seems to have taken place in jumps. Therefore, it may be concluded that *Eumyarion* was an ecologically highly adapted and fast reacting cricetid. In Spain, Weerd and Daams (1978) suggested wet/wooded habitats for *Eumyarion*. The associations in which they occur and the sedimentary environment in which they are found suggest that all of the known species lived in a rather similar biotope (wet-forest or reed land).

Their systematic position is not clear, De Bruijn and Saraç (1991) group of species assigned to genus *Eumyarion* as follows:

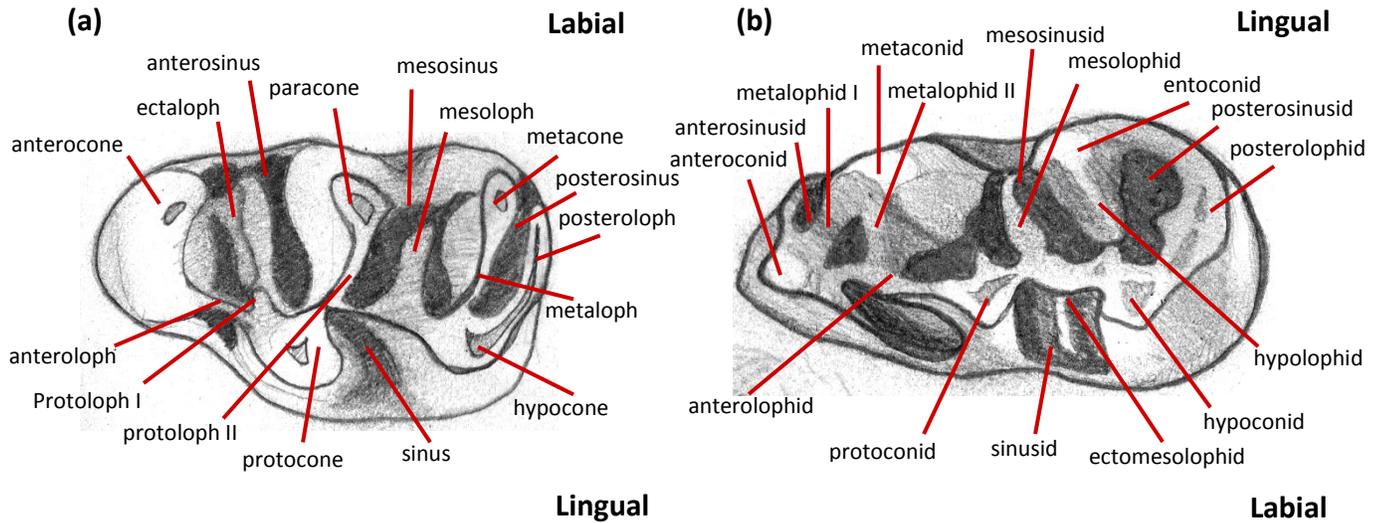
1. Two species of small sized *Eumyarion* (*E. microps* and *E. intercentralis*) that are considered to be members of the lineage leading to *Anomalomys*,
2. Seven species of medium sized *Eumyarion* including the European *E. medius*, *E. bifidus*, *E. latior* and *E. leemanni* as well as *E. orhani*, *E. carbonicus* and *E. montanus* from Anatolia.

*Dentition:*

The dental morphology for all cricetids is  $\frac{1003}{1003}$ . All molars are rooted. The first molar is largest, elongated by the development of the labially situated anterocone/centrally situated

anteroconid. The 3<sup>rd</sup> molar is the smallest, being reduced posteriorly. Primitively, the occlusal pattern of the molars consists of opposing pairs of cusps, lingual cusps being situated slightly more anteriorly than the labial cusps.

**Figure 12: Dental terminology for Cricetidae** (adapted from Daams & Freudenthal 1988): (a) M<sup>1</sup>, (b) m<sub>1</sub>



**4.2 Material and Measurements:**

*Comparison material:*

**Table 8: A listing of the comparative material used in the analysis of *Eumyarion***

\*All data, with the exception of Aliveri, has been collected from the literature cited. Data from Aliveri has been collected by the author from material housed in IVAU and was checked with data in the literature cited.

Region	Country	Locality name	Repository	Age (mybp) (NOW db, Fortelius, 2011)	MN zone correlation	References
S.E. Europe	Greece	*Aliveri (N+S)	IVAU	17-18	MN4	Klein Hofmeijer & Bruijn de (1988), Bruijn de & Sarac (1991)
C. Europe	Germany	Puttenhausen			MN5/6	Wu (1982)
Anatolia	Turkey	Sabuncubeli			MN3	Bruijn de, et al (2006)
Anatolia	Turkey	Kasekoy			MN2/3	Bruijn de & Sarac (1991)
Anatolia	Turkey	Harami 3			MN1/2	Bruijn de & Sarac (1991)
Anatolia	Turkey	Harami 1			MN1/2	Bruijn de & Sarac (1991)

*Material and Measurements:*

The material from Karydiá contains 47 teeth, from which 42 are measurable.

M<sup>1</sup>: 9 (KR 1-4, 6-10) (Plate 2A);

M<sup>2</sup>: 8 (KR 11-13, 16-20) (Plates 2A and B);

M<sup>3</sup>: 8 (KR 21-24, 26-29) (Plate 2B);

m<sub>1</sub>: 6 (KR 31-34, 36-37) (Plates 2B and C);

m<sub>2</sub>: 8 (KR 41-42, 45-50) (Plate 2C);

m<sub>3</sub>: 8 (KR 51-53, 56-60) (Plates 2C and D)

**Table 9: Materials and measurements (*Eumyarion aff. latior*);** N = total number of samples, n = number of measurable samples.

	Length				Width				L/W				N
	n	min	mean	max	n	min	mean	max	n	min	mean	max	
M <sup>1</sup>	8	1.85	1.96	2.13	8	1.28	1.34	1.41	8	1.36	1.46	1.56	9
M <sup>2</sup>	8	1.37	1.47	1.57	7	1.32	1.34	1.40	7	1.04	1.09	1.16	8
M <sup>3</sup>	8	1.01	1.10	1.23	8	1.04	1.12	1.20	8	0.94	0.99	1.03	8
m <sub>1</sub>	3	1.69	1.79	1.90	4	1.08	1.13	1.20	3	1.52	1.56	1.58	6
m <sub>2</sub>	7	1.37	1.45	1.50	8	1.15	1.22	1.31	7	1.14	1.21	1.28	8
m <sub>3</sub>	8	1.24	1.32	1.45	8	1.04	1.10	1.16	8	1.07	1.21	1.30	8

*Systematic description:*

Family: Cricetidae (Fischer von Waldheim 1817)

Genus: *Eumyarion* (Thaler 1966)

Species: *Eumyarion (aff) latior* (Schaub and Zapfe 1953)

*Morphological description:*

**Upper dentition**

For all upper molars, the sinus points obliquely forward and the cones are arranged obliquely, with the lingual cones placed anterior relative to the labial cones. The mesoloph, in all specimens, is either medium or long. In general, the ridge patterns are inconsistent; one M<sup>1</sup> molar does not contain an anteroloph, the protoloph II and metaloph are oblique in some cases and transverse in others.

**M<sup>1</sup>:** The anterocone is compound. It is attached lingually to the anteroloph (which leads to the protocone) and labially to the transverse ectaloph. A labial spur of the anterocone, in 6 of 9 specimens, reaches the base of the paracone. The ectaloph is long, and connects to the anteroloph (3 of 7 specimens) or the anterior side of the protocone (3 of 7 specimens); in 1 specimen it is free lingually. A short spur, the protoloph I, develops from the anterior, lingual side of the protocone in 2 of 9 specimens. The posterior arm of the protocone connects with the paracone forming the protoloph II. A posterior spur of the paracone is present; this spur is attached to the mesoloph in 8 of 9 specimens; it is free in 1 specimen. The curved mesoloph extends from the longitudinal crest (which connects the protocone to the hypocone) to the labial edge of the metacone. In 1 of 9 specimens the mesoloph does not reach the metacone. The metaloph points obliquely forward in 4 specimens, connecting the metacone to the anterior of the hypocone; it curves backward in 5 specimens, connecting the metacone to the posterior of the hypocone. In 1 specimen, there is an extra spur of the metacone extending to the lingual end of the mesoloph. The posteroloph is connected to the base of the metacone in 4 of 7 specimens, thus enclosing the posterosinus; it is open labially in 3 of 7 specimens.

**M<sup>2</sup>:** The anteroloph connects the protocone to the base of the paracone. In 1 specimen the anteroloph is free labially. There is a lingual spur of the anteroloph in 2 of 8 specimens. The protoloph, connecting the posterior arm of the protocone to the paracone, is oblique in 2 specimens, transverse in 6 specimens. A posterior spur of the paracone is attached to the mesoloph in all 8 specimens. The mesoloph extends from the longitudinal crest to the anterior spur of the metacone in 7 of 8 specimens; in 1 of 8 specimens the mesoloph is separate from the metacone. The metaloph points obliquely forward in all unworn specimens and is transverse in worn specimens. The posteroloph connects to the base of the metacone in 6 of 8 specimens, thus enclosing the posterosinus; it is open labially in 2 of 8 specimens. Two molars have a short longitudinal ridge connecting the posteroloph to the metaloph.

**M<sup>3</sup>:** The molar is rounded and the ridges are erratic; the protocone and paracone are present, the other cusps are integrated in a crest surrounding the M<sup>3</sup>. The anteroloph extends labially from the protocone and connects to the base of the paracone. The protoloph, connecting the protocone to the paracone, is oblique in 2 specimens, transverse in 6 specimens. The mesoloph extends from the longitudinal ridge and is present in all 8 specimens; in 6 of 8 specimens, it is attached to the metacone, in 1 specimen it is free standing labially. The metaloph points obliquely forward in all specimens. The posteroloph

connects the hypocone to the metacone. A single specimen has an extra free-ending spur extending obliquely backward from the protoloph. The sinus of the  $M^3$  is closed along the lingual margin, but in some unworn specimens this new connection is lower than the other ridges.

### **Lower dentition**

For all lower molars, the sinusid points obliquely backward and the conids are arranged obliquely, with the lingual conids placed anterior relative to the labial conids. The mesoloph, in all specimens, is either medium or long. The ridge patterns are more consistent than those observed in the upper molars.

**$m_1$ :** In all 5 undamaged specimens there is a free-ending labial spur of the anteroconid; additionally there is a free-ending lingual spur in 2 of the 5 specimens. The anteroconid is connected to the metaconid by the metalophid I in all 6 specimens and to the protoconid by the anterolophid in 3 of 5 specimens. In 1 specimen, the anterolophid is interrupted; in 1 specimen it is absent. The metaconid has a second ridge, the metalophid II, which connects to the anterolophid; in 4 of 6 specimens, this connection is interrupted. The protoconid connects to the hypoconid through a well-developed longitudinal crest. In 4 of 6 specimens, the protoconid also has a lingual spur. This spur connects to the metaconid in 3 of the 4 cases. The mesolophid is oblique and extends from the longitudinal ridge to the posterior spur of the metaconid. In 4 of 5 specimens, the posterior spur of the metaconid extends as far as the entoconid. The hypolophid is transverse and is connected to the longitudinal crest, adjacent to the hypoconid, in 4 of 4 specimens. In two relatively unworn specimens, there is a second ridge leading from the hypoconid to the posterior spur of the entoconid. The posterolophid is connected to the posterior spur of the entoconid lingually, thus enclosing the posterosinusid.

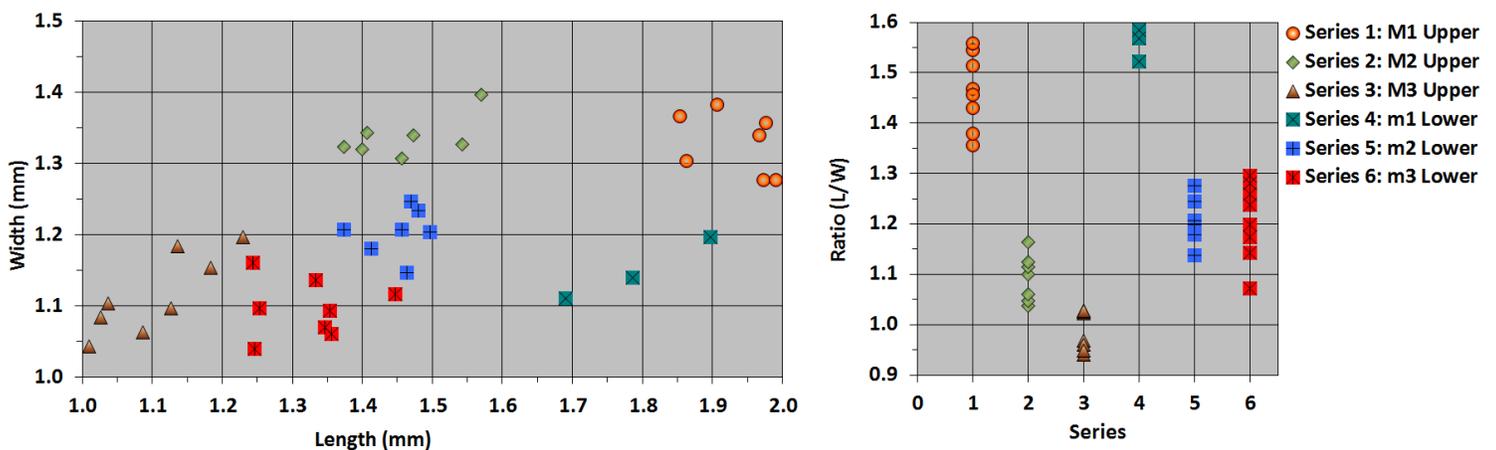
**$m_2$ :** The anterolophid extends from the protoconid and has a labial and lingual spur. The lingual spur connects to the base of the metaconid. The labial spur bends backward and is free-ending. The metalophid connects the anterior spur of the protoconid to the metaconid, it is oblique and points forward in all specimens. The metaconid is connected to the entoconid by a low lingual ridge in 4 of 8 specimens. The longitudinal crest is well developed in all specimens. The mesolophid, extending lingually from the posterior of the protoconid, is present in all specimens; it is long in 7 of 8 specimens, medium length in 1. It is free at the lingual end in 7 of 8 specimens and attached to the base of the metaconid in 1 specimen. The mesolophid is oblique in 3 specimens, transverse in 5 specimens. The ectomesolophid is

present in 7 of 8 specimens, of these 7 specimens, 5 have an extension of the ectomesolophid lingually of the longitudinal crest. The hypolophid is transverse and extends from the posterior end of the longitudinal crest to the entoconid. In all relatively unworn specimens (5 of 7 cases), there is a posterior arm of the hypoconid leading to the posterior of the entoconid. The posterolophid extends from the hypoconid to the base of the entoconid, enclosing the posterosinusid.

**m<sub>3</sub>**: The molar is similar to the M<sup>3</sup>, but the ridges are less erratic. The anterolophid extends from the protoconid and has a labial spur in all 8 specimens. The labial spur bends backward and is free-ending. The anterolophid has a lingual spur in 6 of 8 specimens and is connected to the base of the metaconid in 3 of these. The metalophid is oblique and connects the metaconid to the anterolophid. In 7 of the 8 specimens, there is a low ridge connecting the metaconid to the entoconid. A well-developed longitudinal ridge exists between the protoconid and hypoconid. The mesolophid extends lingually from the longitudinal ridge; it is of medium length in 7 specimens and long for 1 specimen. In 2 specimens it is attached to the entoconid, in all other specimens it is free lingually. In 5 of 8 specimens, the mesolophid is oblique; it is transverse in the remaining specimens. The posterolophid connects the hypoconid to the metaconid. A single specimen contains a posterior arm of the hypoconid, which extends obliquely forward from the posterolophid. The sinus is open labially.

*Metric analysis:*

Figure 13: Metric analysis of *Eumyarion aff. latior* dentition from Karydiá



4.3 Comparative Analysis:

A comparison of the morphologies and measurements of the specimens from Karydiá and the comparative material are summarised in Tables 10, 11 and 12, and Figure 14 below. They are discussed in the subsequent discussion section.

Table 10: Morphological analysis of *Eumyarion* upper molars, from Karydiá, Aliveri, Central European and Anatolian localities

		M <sup>1</sup>										M <sup>2</sup>										M <sup>3</sup>									
Region	Country	Locality	MN Zone	Genus	Species	Development of the protoloph I		Development of the posterior spur of the paracone		Development of the post spur of the paracone		Length of the mesoloph		Lingual spur of the anterocone		Connection between the mesoloph and the metacone		Development of the posterior spur of the paracone		Length of the mesoloph		Configuration of the protoloph		Connection between the metacone and the mesoloph		Number of lingually situated enamel lakes					
						Separated from the metaclaph	Connected to the metaclaph	Separated from the metaclaph	Connected to the metaclaph	Separated from the metaclaph	Connected to the metaclaph	Medium	Long	Absent	Present	Absent	Present	Double	Single	Absent	Present	Two or more	One								
S.E. Europe	Greece	Karydiá	MN4	<i>Eumyarion</i>	<i>aff. latior</i>	11.1	22.2	66.7	9	0	11.1	88.9	9	88	12	8	88.9	11.1	0	100	8	12	88	8	0	100	8	8	8		
S.E. Europe	Greece	Aliveri	MN4	<i>Eumyarion</i>	<i>latior</i> **	33	8	59	12	0	100	0	12	92	8	12	67	33	12	80	20	5	50	50	5	50	50	5	6		
C. Europe	Germany	Putzshausen	MN5/6	<i>Eumyarion</i>	<i>latior-bifidus intercentralis</i> **	8	18	74	78	3	37	60	78	95	5	78	9	91	78												
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>orhani</i> n. sp.	x	x	x		x																					
Anatolia	Turkey	Sabuncubeli	MN2/3	<i>Eumyarion</i>	<i>montanus</i>	5	63	32	65	63	32	5	65	100	0	65	100	0	65	100	0	65	100	0	65	100	0	65	100	0	65
Anatolia	Turkey	Kasekoy	MN1/2	<i>Eumyarion</i>	<i>montanus</i> n. sp.	25	75	12	8	0	75	25	8	88	12	8	75	25	8	88	12	8	75	25	8	88	12	8	75	25	8
Anatolia	Turkey	Harami 3	MN1/2	<i>Eumyarion</i>	<i>aff. carbonicus</i>	3	60	37	62	6	79	15	62	87	31	62	89	11	62												
Anatolia	Turkey	Harami 1	MN1/2	<i>Eumyarion</i>	<i>carbonicus</i> n.sp.	3	60	37	62	6	79	15	62	87	31	62	89	11	62												
S.E. Europe	Greece	Karydiá	MN4	<i>Eumyarion</i>	<i>aff. latior</i>	0	0	100	8	14.3	87.5	7	0	100	8	0	100	8	12	88	8	0	100	8	12	88	8	0	100	8	
S.E. Europe	Greece	Aliveri	MN4	<i>Eumyarion</i>	<i>latior</i> **	0.0	75	25	20	75	25	20	85	15	20	0	100	8	25	75	8	0	100	8	25	75	8	0	100	8	
C. Europe	Germany	Putzshausen	MN5/6	<i>Eumyarion</i>	<i>latior-bifidus intercentralis</i> **	4	23	73	77	55	45	77	19	81	77	85.7	14.3	14													
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>orhani</i> n. sp.	x	x	x		x																					
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>montanus</i>	54	36	10	57	90	10	57	95	5	57	90	10	57	95	5	57	90	10	57	95	5	57	90	10	57	
Anatolia	Turkey	Kasekoy	MN2/3	<i>Eumyarion</i>	<i>montanus</i> n. sp.	0	75	35	8	75	25	8	63	86	8	63	86	8	63	86	8	63	86	8	63	86	8	63	86	8	
Anatolia	Turkey	Harami 3	MN1/2	<i>Eumyarion</i>	<i>aff. carbonicus</i>	3	75	24	68	94	6	68	75	23	68	94	6	68	75	23	68	94	6	68	75	23	68	94	6	68	
Anatolia	Turkey	Harami 1	MN1/2	<i>Eumyarion</i>	<i>carbonicus</i> n.sp.	3	75	24	68	94	6	68	75	23	68	94	6	68	75	23	68	94	6	68	75	23	68	94	6	68	

# Early Miocene Small Mammal Fauna from Karydiá, Greece

**Table 11: Morphological analysis of *Eumyarion* lower molars, from Karydiá, Aliveri, Central European and Anatolian localities**

Region		Country	Locality	MN Zone	Genus	Species	ms.																
							Development of the anterolophid		Development of the metaalophid I		Development of the metaalophid II		Development of the posterior arm of the hypocond		Connection between the posterior arm of the protocond and the mesolophid								
							Absent	Interrupted	Complete	n	Absent	Interrupted	Complete	n	Absent	Interrupted	Complete	n	Absent	Interrupted	Complete	n	
S.E. Europe	Greece	Karydiá	MN4	<i>Eumyarion</i>	<i>aff. latior</i>	20	20	60	5	0	60	40	6	0	66.7	33.3	6	33.3	66.7	3	75	25	4
S.E. Europe	Greece	Aliveri	MN4	<i>Eumyarion</i>	<i>latior</i> **	0	8	92	13	8	46	13	0	70	30	13	39	61	13	86	14	7	
C. Europe	Germany	Puttendhausen	MN5/6	<i>Eumyarion</i>	<i>latior - bifidus intercentrale**</i>	1	9	90	76	45	22	33	76	1	4	95	76	17	83	76			
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>orkani n. sp.</i>																		
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>montanus</i>	2	12	87	52	35	30	35	52	14	31	55	52	17	83	52			
Anatolia	Turkey	Kasekoy	MN2/3	<i>Eumyarion</i>	<i>montanus n. sp.</i>	0	0	100	12	66	26	8	12	8	42	50	12	8	92	12			
Anatolia	Turkey	Harami 3	MN1/2	<i>Eumyarion</i>	<i>aff. carbonicus</i>	2	21	77	64	23	58	19	64	0	34	66	64	0	100	64			
Anatolia	Turkey	Harami 1	MN1/2	<i>Eumyarion</i>	<i>carbonicus n. sp.</i>																		

Region		Country	Locality	MN Zone	Genus	Species	ms.																
							Development of the posterior arm of the hypocond		Connection between the posterior arm of the protocond and the mesolophid														
							Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present					
S.E. Europe	Greece	Karydiá	MN4	<i>Eumyarion</i>	<i>aff. latior</i>	28.6	71.4	7	100	0	8												
S.E. Europe	Greece	Aliveri	MN4	<i>Eumyarion</i>	<i>latior**</i>	47	53	15	100	0	7												
C. Europe	Germany	Puttendhausen	MN5/6	<i>Eumyarion</i>	<i>latior - bifidus intercentrale**</i>	27	73	70															
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>orkani n. sp.</i>																		
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>montanus</i>	100	13																
Anatolia	Turkey	Kasekoy	MN2/3	<i>Eumyarion</i>	<i>montanus n. sp.</i>	8	92	63															
Anatolia	Turkey	Harami 3	MN1/2	<i>Eumyarion</i>	<i>aff. carbonicus</i>	0	100	8															
Anatolia	Turkey	Harami 1	MN1/2	<i>Eumyarion</i>	<i>carbonicus n. sp.</i>	1	99	72															

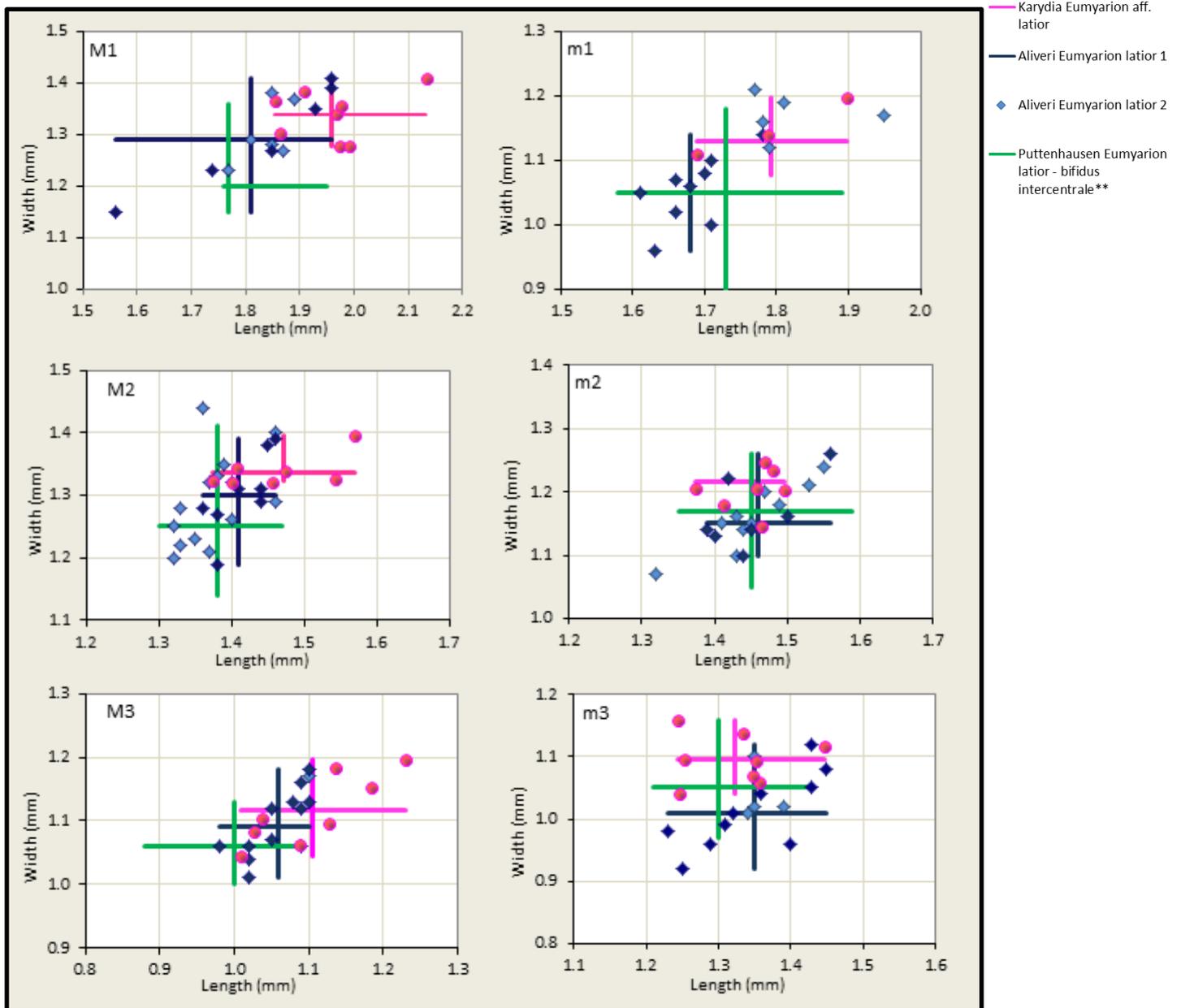
Region		Country	Locality	MN Zone	Genus	Species	ms.																
							Development of the posterior arm of the hypocond		Configuration of the mesolophid														
							Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present	Absent	Present					
S.E. Europe	Greece	Karydiá	MN4	<i>Eumyarion</i>	<i>aff. latior</i>	87.5	12.5	8	0	100	8												
S.E. Europe	Greece	Aliveri	MN4	<i>Eumyarion</i>	<i>latior**</i>	93	7	15	0	100	10												
C. Europe	Germany	Puttendhausen	MN5/6	<i>Eumyarion</i>	<i>latior - bifidus intercentrale**</i>	87	13	63															
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>orkani n. sp.</i>	76.9	23.1	13	92.9	7.14	14												
Anatolia	Turkey	Sabuncubeli	MN3	<i>Eumyarion</i>	<i>montanus</i>																		
Anatolia	Turkey	Kasekoy	MN2/3	<i>Eumyarion</i>	<i>montanus n. sp.</i>	68	32	37															
Anatolia	Turkey	Harami 3	MN1/2	<i>Eumyarion</i>	<i>aff. carbonicus</i>	82	18	11															
Anatolia	Turkey	Harami 1	MN1/2	<i>Eumyarion</i>	<i>carbonicus n. sp.</i>	38	62	58															

## Early Miocene Small Mammal Fauna from Karydiá, Greece

**Table 12: Length/Width ratios and tooth-row length ratios for *Eumyarion* molars from Greece, Central Europe and Anatolia**

Locality	MN Zone	Species	Length/Width ratios						Tooth row length ratios			
			M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	m <sub>1</sub>	m <sub>2</sub>	m <sub>3</sub>	M <sup>1</sup> /M <sup>2</sup>	M <sup>3</sup> /M <sup>2</sup>	m <sub>1</sub> /m <sub>2</sub>	m <sub>3</sub> /m <sub>2</sub>
Karydia	MN4	<i>Eumyarion aff. latior</i>	1.46	1.09	0.99	1.58	1.19	1.21	1.33	0.56	1.23	0.74
Aliveri	MN4	<i>Eumyarion latior 1</i>	1.41	1.09	0.97	1.60	1.25	1.33	1.27	0.59	1.16	0.80
Aliveri	MN4	<i>Eumyarion latior 2</i>	1.40	1.08	0.97	1.60	1.27	1.34	1.28	0.59	1.15	0.80
Puttenhamen	MN5/6	<i>Eumyarion latior-bifidus</i>	1.48	1.10	0.94	1.65	1.24	1.24	1.28	0.56	1.19	0.75
Sabuncubeli	MN3	<i>Eumyarion orhani</i>	1.46	1.10	0.93	1.60	1.19	1.19	1.35	0.58	1.20	0.74
Sabuncubeli	MN3	<i>Eumyarion montanus</i>	1.42	1.06	0.93	1.54	1.22	1.17	1.36	0.56	1.26	0.71
Kasekoy	MN2/3	<i>Eumyarion montanus</i>	1.49	1.09	0.95	1.62	1.24	1.26	1.39	0.55	1.20	0.79
Harami 3	MN1/2	<i>Eumyarion aff. carbonicus</i>	1.50	1.06	1.00	1.58	1.32	1.25	1.39	0.59	1.13	0.80
Harami 1	MN1/2	<i>Eumyarion carbonicus</i>	1.61	1.08	0.99	1.59	1.23	1.27	1.34	0.59	1.16	0.80

**Figure 14: Metric comparisons of *Eumyarion* molars**



#### 4.4 Discussion:

##### *Species designation:*

The metric analysis of the *Eumyarion* specimens indicates that the specimens from Karydiá are a medium sized *Eumyarion* species. De Bruijn and Saraç (1991) acknowledge seven species of medium sized *Eumyarion* including the European *E. medius*, *E. bifidus*, *E. latior* and *E. leemanni* as well as *E. orhani*, *E. carbonicus* and *E. montanus* from Anatolia. They consider *E. valencianum* to be a nomen dubium, *E. helveticum* to be synonymous with *E. medius* and *E. candeloni* and *E. weinfurteri* to be synonymous with *E. latior*. For the purpose of this study, specimens from the locality of Aliveri are designated *E. latior* 1 and *E. latior* 2, which correspond to previous identifications of *E. weinfurteri* and *E. latior* respectively (Klein Hofmeijer & de Bruijn 1988 and De Bruijn & Saraç 1991).

Medium sized *Eumyarion* show wide intraspecific variation in size and morphology, making it difficult to determine whether associations from a particular locality are homogeneous if there are a limited number of specimens. The specimens from Karydiá show large variation in morphology (refer to Appendix 2 and Tables 10 and 11 above), with morphologies and measurements having most affinity with the species *E. latior*. Significant differences, however, are observed:

- For most specimens from Karydiá, the length of the mesoloph in upper molars is long, with a connection occurring between this ridge and both the paracone and metacone. This is in contrast with specimens from Aliveri and (to a lesser degree) Puttenhamen.
- For most specimens from Karydiá, the anterocone in M<sup>1</sup> molars is relatively long compared with those from Aliveri and Puttenhamen. This does not seem to correspond with an increase in width of the specimens. The metric analysis (Table 12 and Figure 14) shows a higher Length/Width ratio for Karydiá M<sup>1</sup> molars than for those from Aliveri and Puttenhamen.
- The M<sup>2</sup> molars from Karydiá show a larger Length/Width ratio (Table 12 and Figure 14) than Aliveri and Puttenhamen.

It is due to these differences, that the specimens from Karydia are assigned to *Eumyarion* (aff) *latior*. It may be that there exists more than one morphotype in the Karydiá population,

however the number of samples is insufficient to carry out a comprehensive analysis; therefore it is considered that the population from Karydiá consists of one morphotype with large interspecific variation.

## 5. Discussion of Biostratigraphic and Palaeogeographic implications

### 5.1 Biostratigraphic implications:

*Pseudotheridomys* (aff) *parvulus*:

If the study by Fahlbusch (1970, 1983), of the Eomyidae in Germany, is taken into consideration, the specimens from Karydiá correspond the evolutionary stage of *Pseudotheridomys* (aff) *parvulus* found at Schaffhausen during zonation MN2b. This is older than the proposed zonation of MN4 for Karydiá (Theocharopoulos 2000), however; various alternative theories exist for the transition of *Pseudotheridomys* to *Ligerimys* populations and are reviewed by Fahlbusch (1983); these include:

1. *Pseudotheridomys* evolved in the upper Aquitanian, *Ligerimys* developed in another area and immigrated to Central Europe in the lower Burdigalian,
2. A mixture of two different geological ages,
3. The two genres lived two different, but still not all too separate ways of life, in neighbouring biotopes, forest or steppe, or undertook temporally differentiated activities,
4. Sexual dimorphism,
5. Wintershof West and Schnaitheim can be regarded as different stages of one phylogenetic development process from the genus *Pseudotheridomys* to the genus *Ligerimys*, beginning at Bissingen

Fahlbusch (1983) argues that these morphotypes must be considered as belonging to a single population due to the presence of the intermediate forms (morphotype A-B).

Alvarez Sierra et al (1987) took the punctualistic view, that *Ligerimys* originated somewhere at the periphery of its geographic range from *Pseudotheridomys* and later ousted the latter genus gradually. For Spain Alvarez Sierra (1987) sees the evolution from *P. parvulus* to *P. fejfari*, with the possibility of a separate evolution occurring between *Pseudotheridomys* and *Ligerimys*. It was argued that *P. parvulus* does not represent a time-bound step in the evolution from *Pseudotheridomys* to *Ligerimys*. The stratigraphic range of *P. parvulus* was reconsidered and the species was said to range from MN zone 2A to MN zone 4, since the composition of the Aliveri fauna as a whole agrees better with MN4.

It is agreed, in this paper, that the stratigraphic range of *Pseudotheridomys parvulus* should be extended to MN4, as suggested by and based on the arguments of Alvarez Sierra *et al* 1987. As such, the punctualistic view of the evolution of *P. parvulus*, suggested by Alvarez Sierra *et al* (1987) is accepted here. It is suggested that there was an advantage for the evolution of morphotype B populations, which gradually replaced the morphotype A populations. This occurred earlier in Central Europe than in the Czech Republic and in Greece. The Aliveri and Karydiá locations shows this transition in Greece during MN4, with Karydiá being considered younger than Aliveri, based on the presence of the transitional morphotype A-B in Karydiá.

### *Eumyarion (aff) latior*:

The stratigraphic range of *Eumyarion latior* is from MN4 to MN9 (Fortelius 2011). They do not show any consistent change in their dental patterns through time, but show a mosaic of combinations of primitive and derived characteristics. De Bruijn and Saraç (1991) suggest that this represents various evolutionary stages and probably lineages, but these lineages cannot be reconstructed on the basis of material available to date. They continue, stating that the lack of evolutionary trends combined with the long stratigraphic range may mean that there were several migrations into Western Europe instead of in situ evolution. It is therefore, not possible to place Karydiá in an MN zonation based on this species, except that it is limited to between MN4 and MN9. Further, it is not possible to determine its relationship with *Eumyarion latior* from Aliveri.

Since both *Pseudotheridomys (aff) parvulus* and *Eumyarion (aff) latior* are not good indicators of biostratigraphic position, Karydiá is placed in MN4, as already suggested, on the basis of the presence of modern Cricetidae *Democricetodon* and *Cricetodon*. The stage-in-evolution of *Pseudotheridomys parvulus* suggests a younger age for Karydiá than Aliveri.

### **5.2 Palaeogeographic implications:**

Based on the evidence gathered so far, Karydiá can be placed in biozone MN4. The implications of this for the stratigraphic ranges and the geographic ranges of its species are summarised in Figure 15:



Karydiá shares some of the same species with both the MN4 of Turkey and of Central Europe and Spain, for example *Democricetodon franconicus*. This suggests that a land connection did exist between these areas, during and/or before MN4. Insectivores from Turkey are not found in the Karydiá faunal assemblage, suggesting that there may have been an ecological barrier between these areas. The assemblage, as a whole, has not been compared with that of other fossil localities from the early Micoene, as a part of this thesis. It is suggested that this be carried out in order to determine whether differences/similarities are age related or palaeoanvironment related.

## 6. Conclusions and Outlook

### *Conclusions:*

This study, of the Families Eomyidae and Cricetidae (*Eumyarion*) from Karydiá, has led to the identification of the species *Pseudotheridomys* aff. *parvulus* and *Eumyarion* aff. *latior*.

- *Pseudotheridomys parvulus* and *Eumyarion latior* do not serve well as biostratigraphic markers, due to their long stratigraphic ranges; *Eumyarion latior* shows large intraspecific variation, with a complex mosaic of derived and primitive characters showing no evolutionary trend. Based on the presence of the modern Cricetids, the biostratigraphic position of Karydiá is considered to lie within MN4.
- Based on the stage-in-evolution from *P. parvulus* to *Ligerimys antiquus*, Karydiá is deemed to be younger than Aliveri.
- *Pseudotheridomys parvulus* and *Eumyarion latior* are only known from European localities and are unknown in Turkey; however, the faunal assemblage from Karydiá shows species having affinities with both Central Europe and Turkey, indicating a connection between these areas during and/or before MN4.

### *Outlook:*

The ultimate goal is to establish a local biostratigraphy for Greece localities, and then to correlate and compare this with other Anatolian and European stratigraphies. From this biogeography, faunal bioprovinces and migration routes can be ascertained and any asynchrony between locations can be determined. Figure 16 below reviews the current understanding of the early/mid Miocene Greek micromammal fossil localities; it includes the stratigraphic range of the micro-mammal fauna (identified to species level) within Spain, Central Europe, Turkey and Greece. It is plain to see that the early Miocene of Greece is poorly expressed in the fossil record; however, insights and questions arise based the data gained thus far:

- The Greek MN4-5 contains species found in both Anatolia and Central Europe, indicating a connection between these areas during that period. When did this connection occur

and was it temporary or permanent? Did faunal exchange also occur due to environmental factors?

- The Greek sites of Karydiá and Aliveri are designated MN4 based on the presence of the modern-type Cricetidae which arrived to Europe during MN4 (Daams & Freudenthal 1988). Is this really the case for Greece and Anatolia, or did they arrive to these areas earlier?
- MN1-4 of Greece is not well known and not calibrated to a time scale. Does asynchrony exist in the MN zonations between Greek localities and central Europe/Anatolia?
- A thorough study has not been carried out on the Early Miocene Greek localities' fossil assemblages, as a whole, to determine whether there are similarities or differences between locations and areas. Are there geographical barriers or environmental or ecological differences between these localities?
- The insectivores from Karydiá and Aliveri have been studied by Doukas & Hoek Ostende (2006) and Doukas (1986). Why are the insectivores present in Karydiá and Aliveri only known from Europe? Was there an ecological barrier between Greece and Anatolia which prevented their migration?





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**Appendix 1: Eomyidae from Karydiá raw data**





**Appendix 2: *Eumyarion* from Karydiá raw data**



M <sup>3</sup>		Number of lingually situated enamel lakes
Reference	Wear level	
KR-21	Worn	One
KR-22	Fresh	Two or more
KR-23	Worn	
KR-24	Damaged, very worn	
KR-26	Fresh	
KR-27	Fresh	
KR-28	Worn	
KR-29	Fresh	

M <sup>3</sup>		Development of the posterior arm of the hypoconid	Configuration of the mesolophid
Reference	Wear level		
KR-51	Fresh	Present	Present
KR-52	Worn	1	1
KR-53	Fresh	1	1
KR-55	Worn	1	1
KR-57	Very worn	1	1
KR-58	Worn	1	1
KR-59	Worn	1	1
KR-60	Worn	1	1

M <sup>2</sup>						
Reference	Wear level	Development of the posterior spur of the paracone		Length of the mesoloph	Configuration of the protoloph	Connection between the metacone and the mesoloph
		Absent	Connected to the mesoloph			
KR-11	Fresh	1	1	1	1	1
KR-12	Worn	1	1	1	1	1
KR-13	Fresh	1	1	1	1	1
KR-16	Fresh	1	1	1	1	1
KR-17	Very worn	1	1	1	1	1
KR-18	Damaged, very worn	1	1	1	1	1
KR-19	Very worn	1	1	1	1	1
KR-20	Worn	1	1	1	1	1

m <sub>2</sub>						
Reference	Wear level	Development of the posterior arm of the hypoconid		Length of the mesoloph	Configuration of the protoloph	Connection between the metacone and the mesoloph
		Absent	Present			
KR-41	Very worn	1	1	1	1	1
KR-42	Fresh	1	1	1	1	1
KR-45	Worn	1	1	1	1	1
KR-46	Fresh	1	1	1	1	1
KR-47	Fresh	1	1	1	1	1
KR-48	Worn	1	1	1	1	1
KR-49	Worn	1	1	1	1	1
KR-50	Damaged, worn	1	1	1	1	1

PLATES

**1A-1D: *Pseudotherydomys* (aff) *parvulus* (pre)molars from Karydiá**

**2A-2D: *Eumyarion* (aff) *latior* molars from Karydiá**

PLATE 1A:

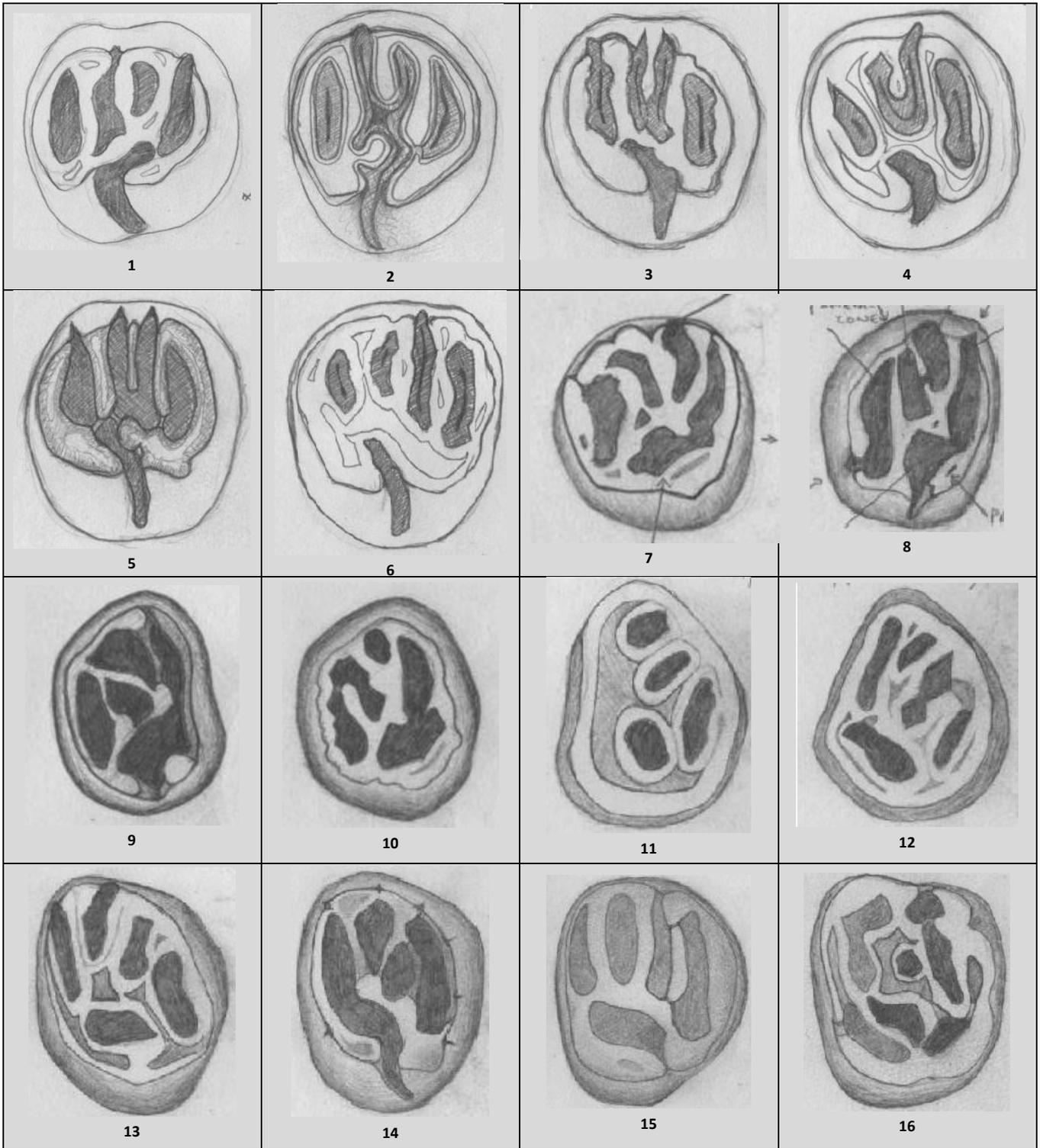


Fig. 1-2: P<sup>4</sup> dex.

Fig. 3-6: P<sup>4</sup> sin.

Fig. 7-10: M<sup>3</sup> dex.

Fig. 10-16: M<sup>3</sup> sin.

PLATE 1B:

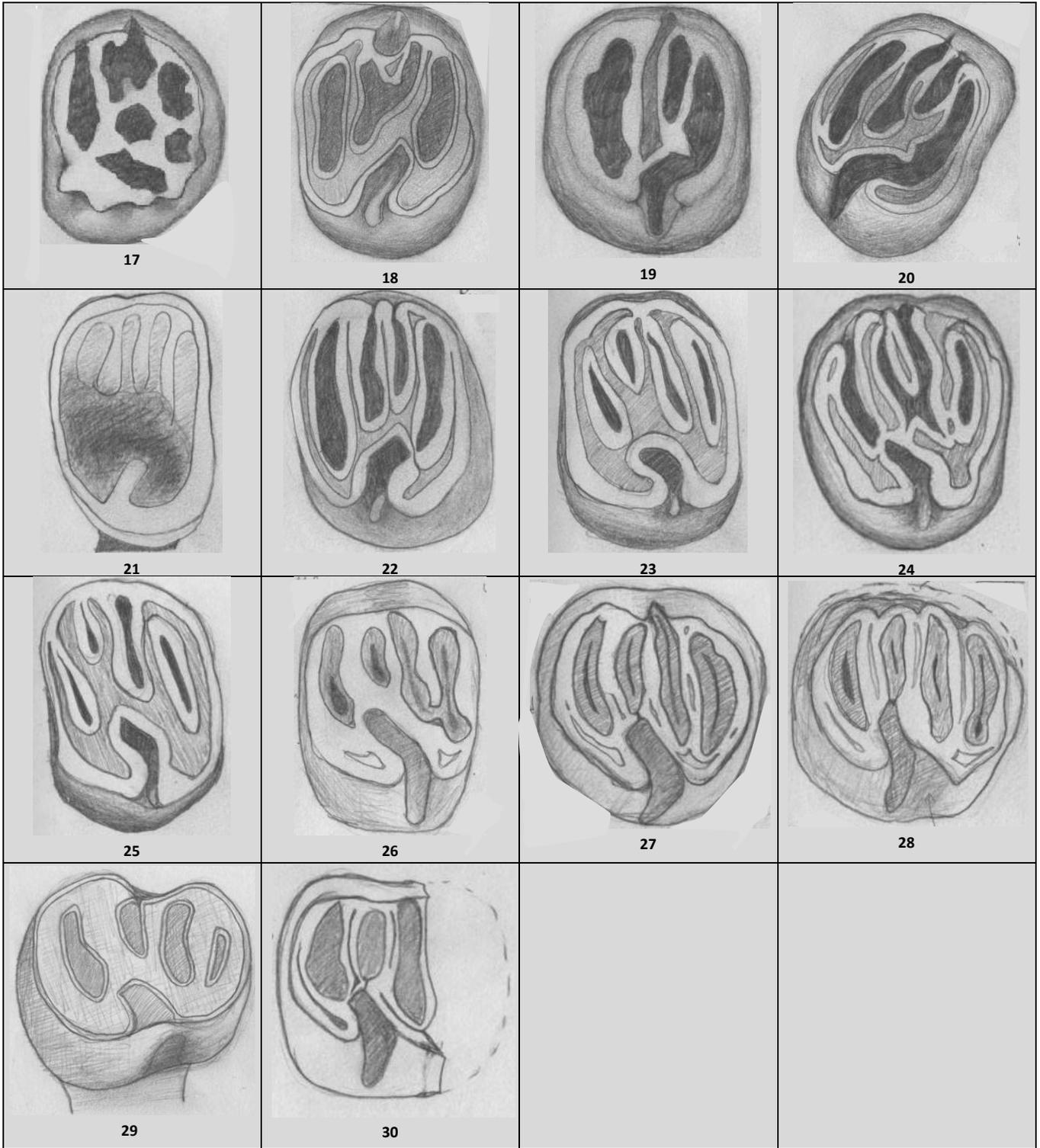


Fig. 17:  $M^3$  sin.

Fig. 18-22:  $M^{1-2}$  dex.

Fig. 23-30:  $M^{1-2}$  sin.

PLATE 1C:

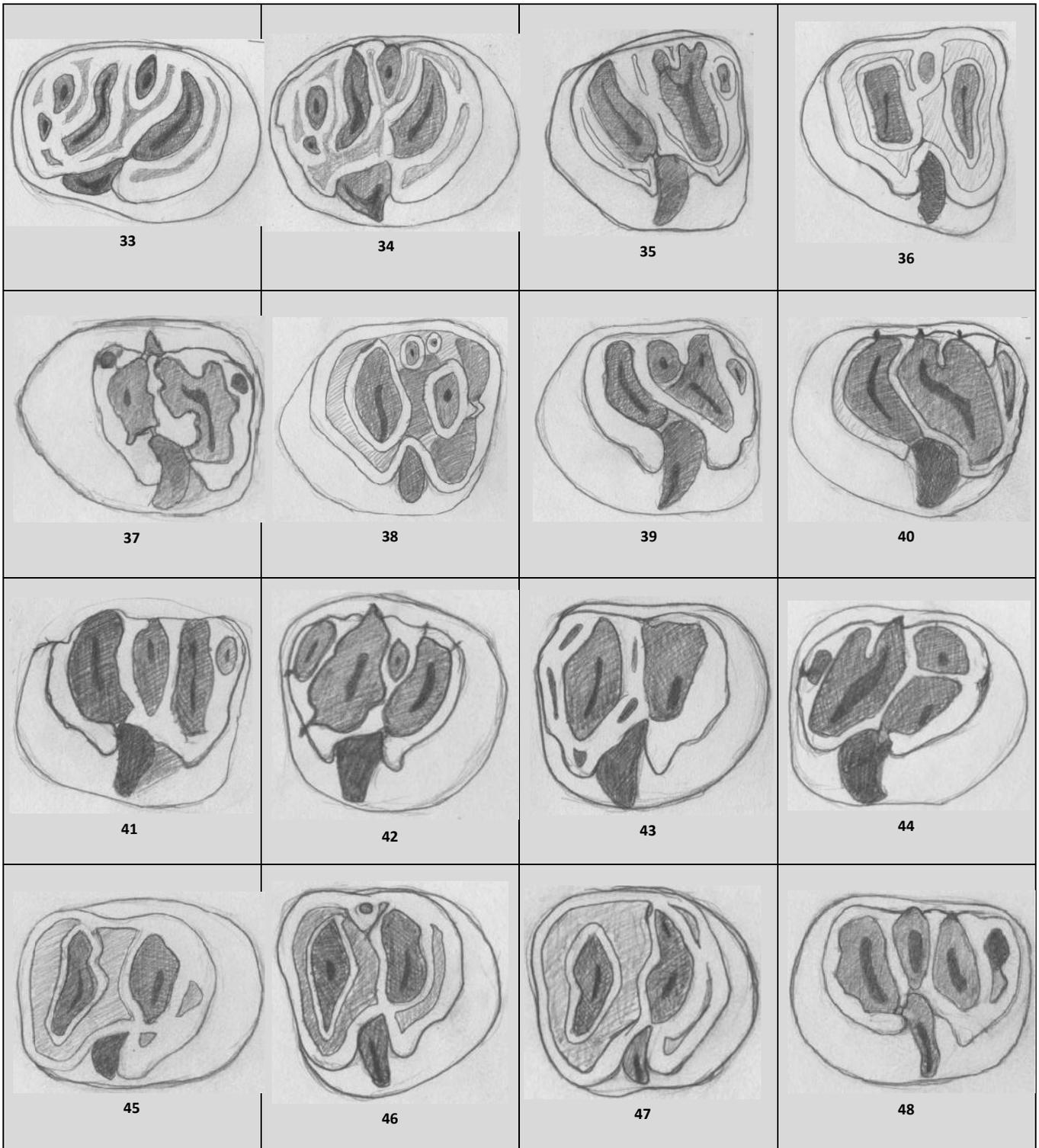


Fig. 33-34:  $p_4$  sin.

Fig. 42-47:  $m_3$  sin.

Fig. 35-41:  $m_3$  dex.

Fig. 48:  $m_{1-2}$  dex.

PLATE 1D:

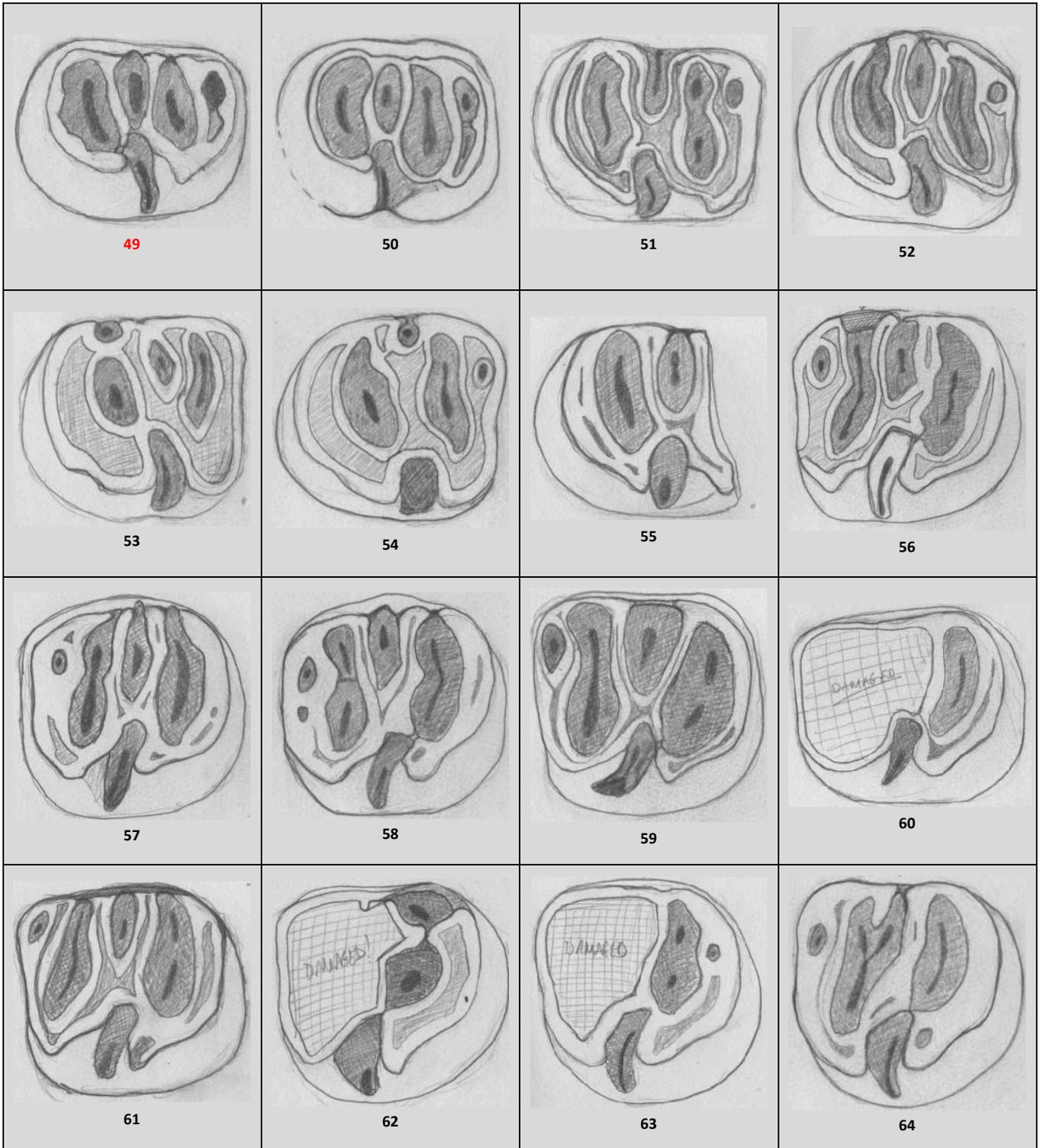


Fig. 49-55: m<sub>1-2</sub> dex.

Fig. 56-64: m<sub>1-2</sub> sin.

PLATE 1E:

 <p>65</p>			

Fig. 65: m<sub>1-2</sub> sin.

PLATE 2A:

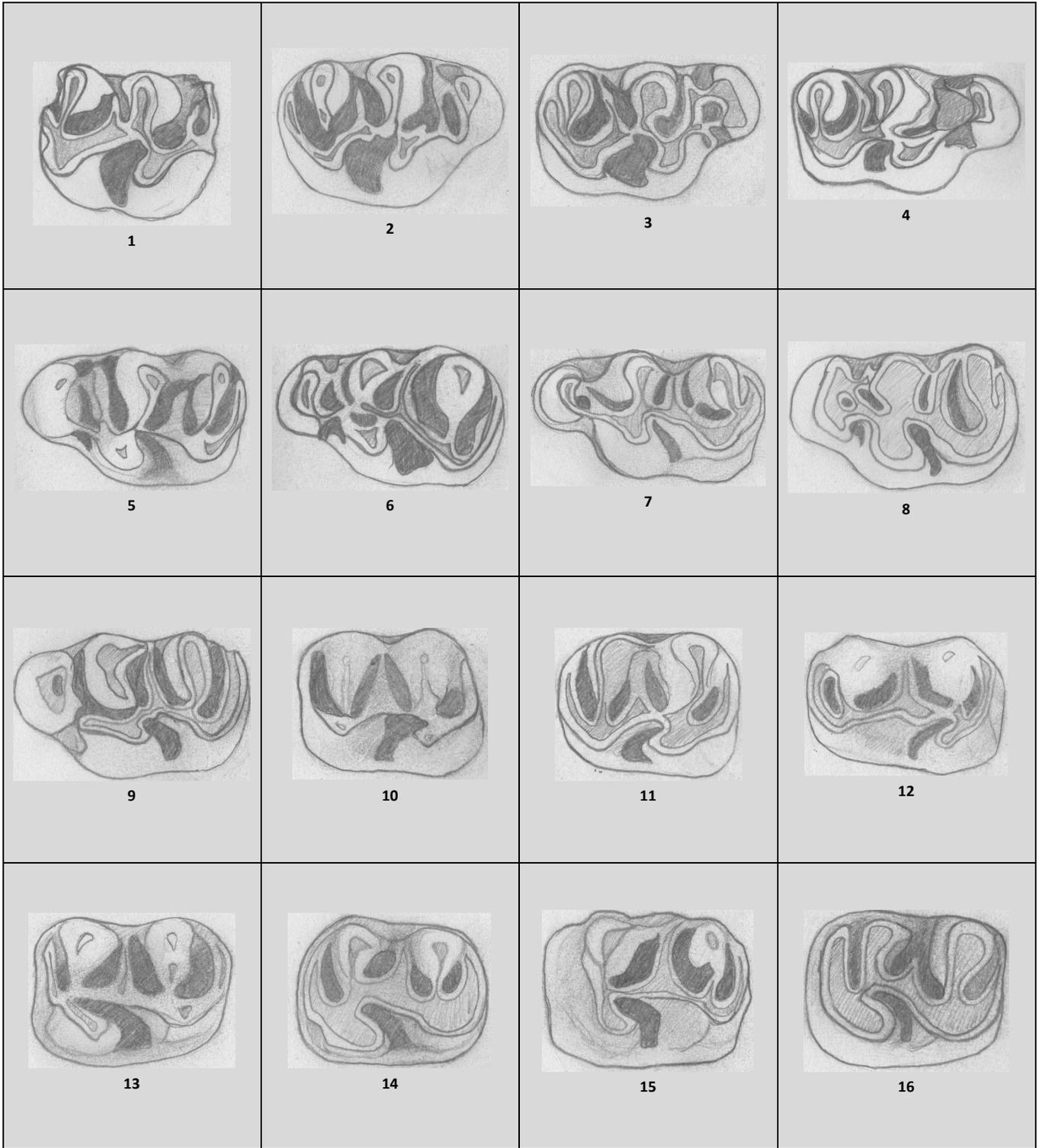


Fig. 1-4: M<sup>1</sup> dex.

Fig. 5-9: M<sup>1</sup> sin.

Fig. 10-12: M<sup>2</sup> dex.

Fig. 13-16: M<sup>2</sup> sin.

PLATE 2B:

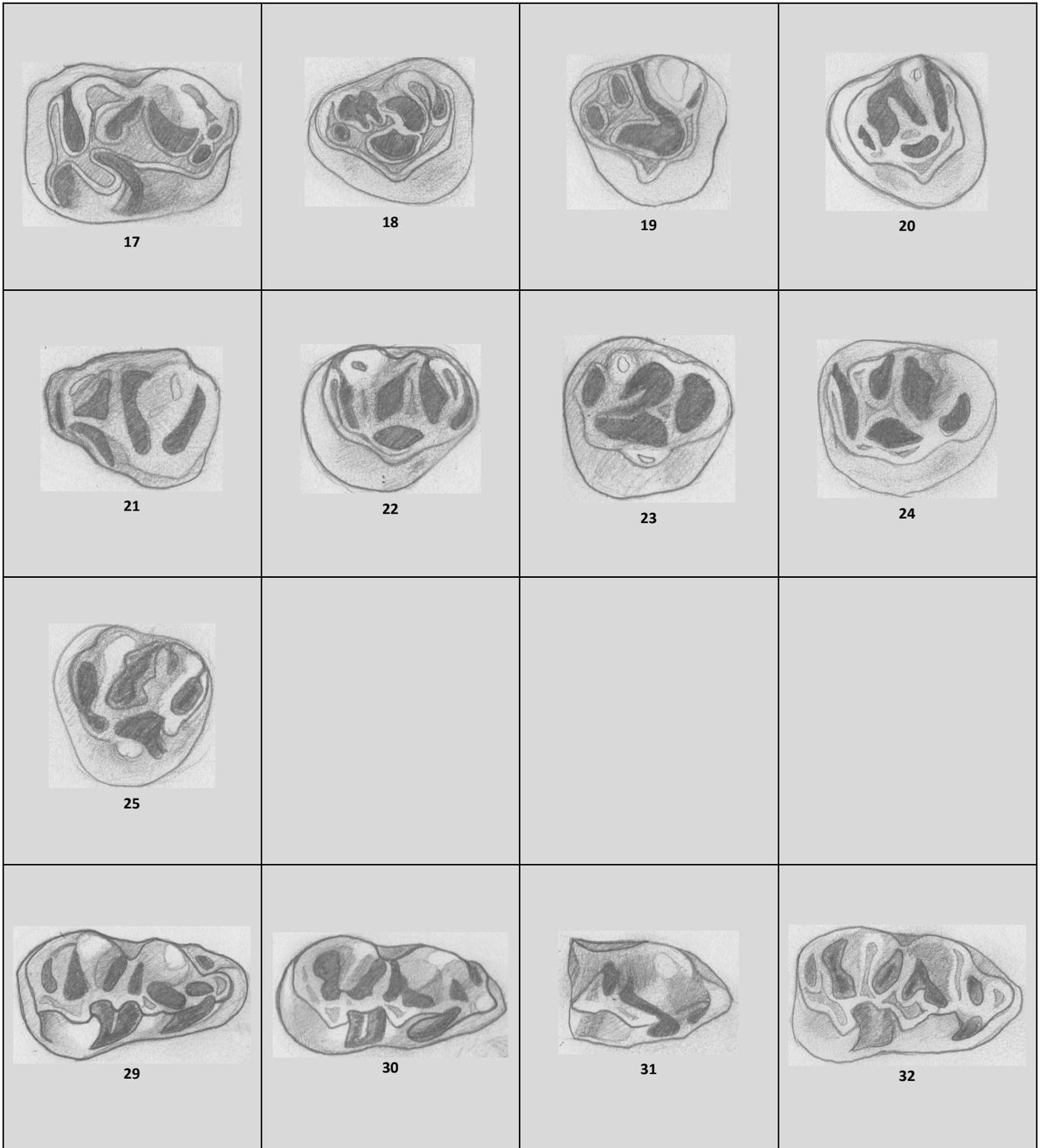


Fig. 17:  $M^2$  sin.

Fig. 18-21:  $M^3$  dex.

Fig. 22-25:  $M^3$  sin.

Fig. 29-32:  $m_1$  dex.

PLATE 2C:

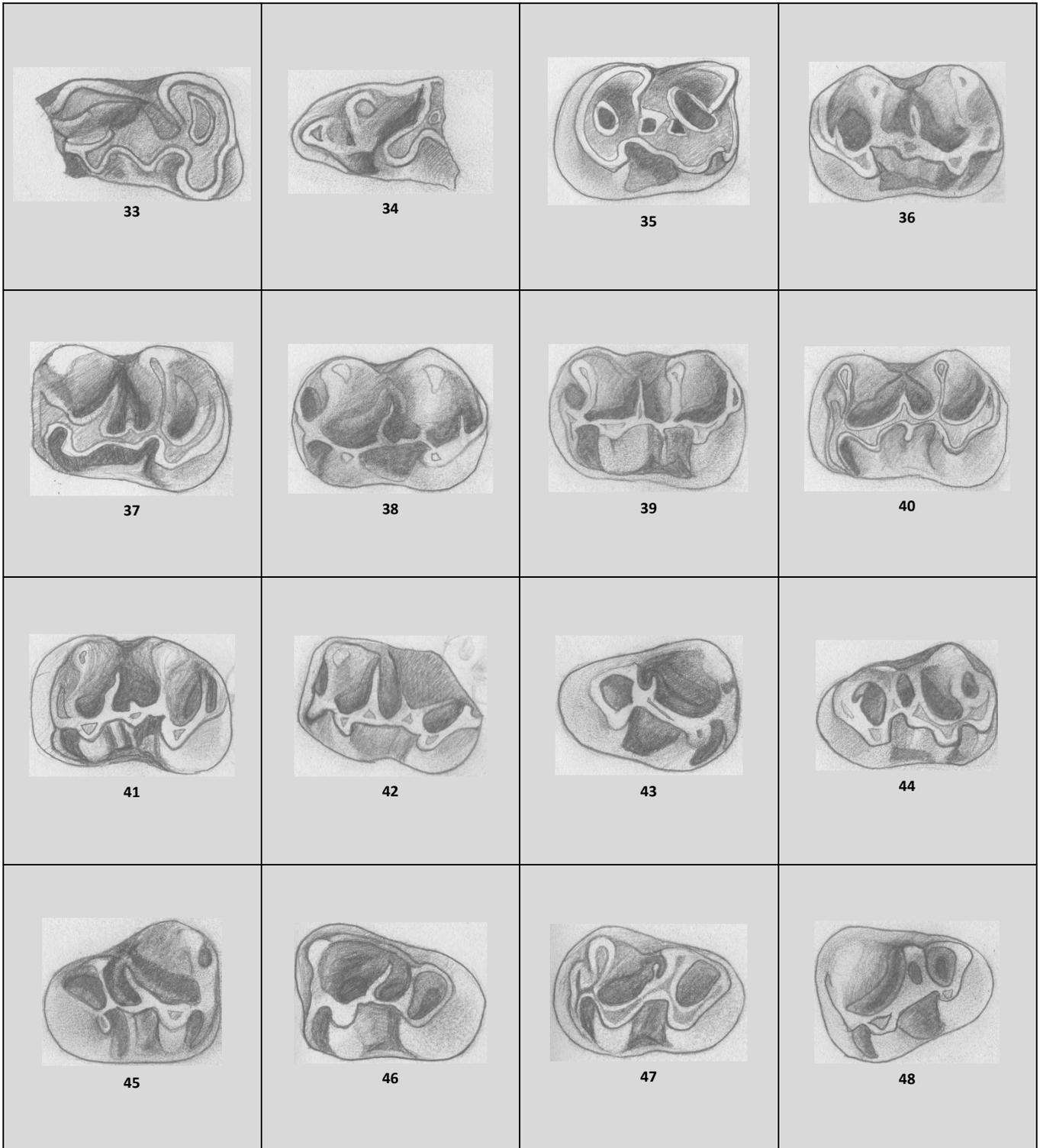
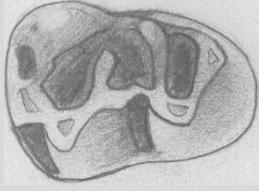


Fig. 33-34:  $m_1$  sin.  
Fig. 35-36:  $m_2$  dex.

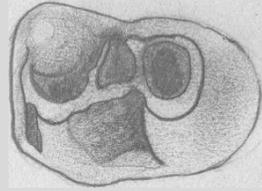
Fig. 37-42:  $m_2$  sin.  
Fig. 43-45:  $m_3$  dex.

Fig. 46-48:  $m_3$  sin.

PLATE 2D:



49



50

Fig. 49-50: m<sub>3</sub> sin.