

# Insectivores (Erinaceomorpha, Soricomorpha; Mammalia) from Karydia and Komotini (Thrace, Greece; MN 4/5)

by

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## Abstract

The insectivores from the Thrace locality of Karydia (MN 4) are described, as well as an erinaceid molar from the nearby locality of Komotini (MN 5). The Karydia assemblage contains the same genera of the Greek MN 4 locality Aliveri, with the addition of a shrew and of *Plesiosorex*. An M2 of the latter is the southernmost occurrence of this genus, and the first record from the Mediterranean area. At the species level there are differences between Karydia and Aliveri. As *Galerix kostakii* n.sp. from Karydia is interpreted as a descendant of *G. symeonidisi* from Aliveri, a younger age for the Thrace locality, as was already assumed on the basis of the rodents, is confirmed. A model is proposed in which the *symeonidisi-kostakii* lineage gives rise to *Parasorex*, of which *Parasorex pristinus* (ZIEGLER, 2003) from Mühlbach (Austria, MN 5) is here considered the oldest representative. Thus the original classification of the Austrian galericine as *Schizogalerix* is challenged. The relative abundance of the different insectivores differs greatly between Aliveri and Karydia, mainly because of the dominance of erinaceids in the latter locality.

**Keywords:** insectivores, new species, evolution, Miocene, Greece

## Kurzfassung

Es werden die thrakischen Fundstelle Karydia (MN 4) beschrieben sowie der Molar eines Erinaceiden aus der nahegelegenen Fundstelle Komotini (MN 5). Die Karydia-Fauna umfaßt die selben Genera wie die griechische MN

4-Fundstelle Aliveri und zusätzlich noch eine Spitzmaus sowie *Plesiosorex*. Ein M2 der letzteren ist der südlichste Nachweis dieser Gattung und zugleich auch der erste im mediterranen Raum. Auf Artniveau gibt es Unterschiede zwischen den Fundstellen Karydia und Aliveri. Da *Galerix kostakii* n. sp. aus Karydia als Nachfahre von *G. symeonidisi* aus Aliveri interpretiert wird, bestätigt sich die aufgrund der Nagetier-Fauna gemachten Annahme eines jüngeren Alters dieser thrakischen Fundstelle. Es wird ein Modell vorgeschlagen, bei dem aus der *symeonidisi-kostakii*-Linie *Parasorex* hervorgeht. *Parasorex pristinus* (ZIEGLER, 2003) aus Mühlbach (Österreich, MN 5) wird als ältester Vertreter dieses Genus betrachtet. Dadurch ändert sich die ursprüngliche Klassifizierung der österreichischen Galericine als *Schizogalerix*. Die relative Häufigkeit der verschiedenen Insectivoren unterscheidet sich deutlich zwischen Aliveri und Karydia, vor allem durch die Dominanz der Erinaceidae in der letzteren Fundstelle.

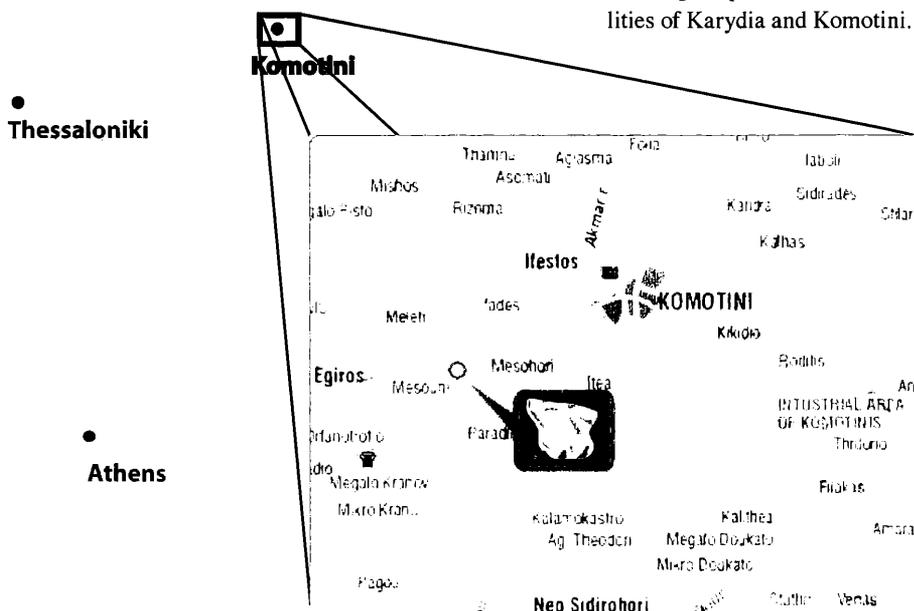
## 1. Introduction

The fossil record for micromammals in Greece for the early part of the Neogene can be called scanty at best. In fact, for a long time the only known locality was the lignite mine of Aliveri on the island of Evia (DE BRUIJN et al., 1980; DOUKAS, 1986). In 1976 Hans de Bruijn (Utrecht University) had already discovered fossil micromammals at Komotini in Thrace, but this fauna is very poor. On the basis of *Cricetodon meini* it could be assigned to MN 5 (DE BRUIJN et al., 1993). In 1989, again by Hans de Bruijn with Dimitri Foussekis, the nearby locality of Karydia was discovered (Fig. 1), which proved to be far more fossiliferous than Komotini. The cricetids of the two localities were described in the PhD thesis of the late Constantin (Kostaki) THEOCHAROPOULOS (2000). The second largest group of micromammals, however, remained undescribed, although faunal lists were given by DOUKAS (2003, 2005). Recently, rodents and insectivores were also described from the locality of Antonios on the Chalkidiki, which is probably of similar age as the finds from Karydia and Komotini (VASSILIADOU & KOUFOS, 2005).

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**Figure 1:** Topographical map showing the position of the localities of Karydia and Komotini.



## 2. Material and methods

Both Komotini and Karydia are in the area of the town of Komotini (277 km East of Thessaloniki). The material from Karydia was collected from a clay quarry used by the company Oxymachon to make bricks. Three fossiliferous levels KRD 1, KRD 2, and KRD 3 were sampled in consecutive years. Of these KRD 1 is situated at one side of a hill and KRD 2 and 3 at the other. All levels are considered synchronous although the lithology would point to a slightly older KRD 3. By and large the numbers rather denote the year of sampling, and the Karydia material is treated in this paper as a single assemblage.

The number in brackets given in the descriptions denotes the number of available specimens. The teeth were measured on a Leitz microscope with a mechanical stage and measuring clocks. All specimens have been illustrated as left ones. If a picture of a right element has been reversed, this is indicated by underlining the number of that figure. All measurements are in mm.

## 3. Systematic palaeontology

Ordo Erinaceomorpha GREGORY, 1910

Familia Erinaceidae FISCHER VON WALDHEIM, 1817

Subfamilia Galericinae POMEL, 1848

Genus *Galerix* POMEL, 1848

### *Galerix kostakii* n.sp.

(Plate 1, figs. 1-10; Plate 2, figs. 1-8)

**Derivatio nominis:** The species is named in memory of Constantin 'Kostaki' Theocharopoulos, who described the cricetids from Karydia.

**Holotype:** M1 sin. KRD 3/04 (2.47 x 3.02), (Pl. 1, Fig. 5).

**Type locality:** Karydia

**Type level:** Early Miocene (MN 4)

**Diagnosis:** Medium-sized species of *Galerix* ( $m2 = 2.54$ ). P3 with hypocone. Protocone-metaconule connection absent in M1, rare in M2. The metaconule of the first two upper molars connects with the buccal part of the posterior cingulum. The metaconid on the p4 usually well developed, the paralophid is rarely connected to the tip of the protoconid.

**Differential diagnosis:** The invariable presence of a hypocone on the P3 distinguishes *Galerix kostakii* n.sp. from *G. exilis* DE BLAINVILLE, 1839, *G. stehlini* (GAILLARD, 1929), *G. africana* BUTLER, 1956, *G. rutlandae* MUNTHE & WEST, 1980, *G. aurelianensis* ZIEGLER, 1990, *G. saratji* VAN DEN HOEK OSTENDE, 1992, *G. uenayae* VAN DEN HOEK OSTENDE, 1992, and *G. remmerti* VAN DEN HOEK OSTENDE, 2003. This feature is shared with *G. symeonidisi* DOUKAS, 1986, "*Schizogalerix*" *iliensis* KORDIKOVA, 2000, and "*Schizogalerix*" *pristina* ZIEGLER, 2003. *Galerix kostakii* is larger than *G. symeonidisi*, and smaller than "*S.*" *iliensis*. "*Schizogalerix*" *pristina* is similar in size to *G. kostakii*, but the molars are relatively shorter, and the p4 is smaller.

	Length		N	Width	
	range	mean		mean	range
C		1.78	1	0.87	
P3	1.65-2.04	1.91	8	1.88	1.74-2.26
P4		2.21	1	2.79	
M1	2.34-2.61	2.46	5	2.94	2.78-3.03
M2	2.01-2.15	2.09	7	2.79	2.70-2.98
M3	1.24-1.62	1.44	7	1.73	1.61-1.85
d3		1.41	1	0.70	
p4	1.94-2.17	2.04	3	1.43	1.27-1.67
m1	2.97-3.32	3.10	5	2.15	1.99-2.45
m2	2.41-2.85	2.54	6	1.92	1.84-2.05
m3		2.07	1	1.42	

**Table 1:** Measurements for *Galerix kostakii* n. sp. from Karydia.

In contrast to the Austrian species, the anterior arm of the metacone of the M2 is straight. Species of *Parasorex* also have a P3 bearing a hypocone. *Galerix kostakii* differs from these species in rarely having a protocone-metaconule connection in the M2 as opposed to the invariable absence in *Parasorex*.

**Measurements:** The measurements are listed in Table 1.

#### Description:

**C** (1). The canine is a simple unicuspid. The tip of the high cusp lies just in front of the centre of the tooth. It is slightly inclined to the lingual side. There are no cingula.

**P3** (10). The premolar is about as long as it is wide. The paracone occupies the labial side of the premolar. Its anterior side is rounded; at the back there is a posterocrista, which curves to the posterolabial corner. In front of the paracone there may be a short flattening. This flattening may be anteriorly bordered by a low ridge, which connects to the base of the protocone.

On the lingual side, there is both a protocone and a hypocone. Usually, the protocone is somewhat larger, but in some specimens the lingual cusps are equal in size. There is an indistinct posterior cingulum following the curved posterior outline of the tooth.

**P4** (2). The outline of the occlusal surface is irregularly quadrangular. The lingual part of the premolar is occupied by the very large and high paracone. The anterior flank of this cusp is rounded. There is a sharp posterocrista, quickly sloping down to about halfway its length. At that point it bends at an angle of 45° and, retaining the same height throughout and extends to the posterolabial corner of the premolar. In front of the paracone lies a tiny parastyle on a hardly protruding parastylar flange.

The protocone lies in the anterolingual corner of the P4. It is connected by a labial arm to the base of the paracone. The hypocone is conical. It is somewhat over half the height of the protocone, and stands directly behind that cusp, without, however, touching it. The only cingulum is on the posterior side. It starts at the base of the hypocone

and, following the curved posterior outline of the premolar, ends in the posterolabial corner.

**M1** (10). The outline of the occlusal surface is sub-rectangular; the back of the molar is somewhat wider than the front. The anterior arm of the protocone ends against the anterolingual side of the paracone. The protoconule is well developed and is formed by a posterior thickening in this arm, halfway between the protocone and the paracone. The posterior arm of the protocone is invariably connected to the hypocone; there is no protocone-metaconule connection. The hypocone is conical. It has a rounded posterior flank. The crescent-shaped metaconule is large. Its anterior arm ends against the anterolingual flank of the metacone. The posterior arm of the metaconule extends along the posterior flank of the metacone to the posterolabial corner of the M1.

The arm of the paracone runs straight backwards while sloping down. It connects to the slightly curved anterior arm of the metacone. The posterior arm of the metacone is strongly curved and extends to the posterolabial side. In front of the paracone lies a low, ridge-shaped parastyle on the anterior cingulum. It is connected to the base of the paracone by a short transverse ridge. The anterior cingulum is well developed and runs from the parastyle, where it is thickest, to halfway the anterior flank of the protocone. There is a labial cingulum, which also is thickest near the parastyle. There is a posterior cingulum starting halfway the posterior flank of the hypocone and ending against the side of the posterior arm of the metaconule. A tiny patch of lingual cingulum may be present in the emargination between the protocone and the hypocone.

**M2** (17). The outline of the occlusal surface is sub-rectangular. The M2 is somewhat wider at its front than at its back. The basic arrangement of the cusps is the same as in the M1. The protoconule is less developed than in the first upper molar. The posterior flank of the hypocone is generally rounded, but in some specimens there is a faint ridge that connects to the posterior cingulum. The protocone-hypocone connection is curved and passes close by the base of the metaconule. There is no connection between the protocone and the metaconule in nine of the thirteen specimens in which this character could be observed. Such a connection is present in three specimens. In one specimen (KRD3 6) the protocone-metaconule connection is stronger than the protocone-hypocone ridge.

As in the M1, the posterior cingulum is bi-partitioned, consisting partly of the posterior arm of the metaconule, partly of a cingulum between the hypocone and the posterior flank of this arm. In contrast to the first upper molar, the anterior arm of the metacone is nearly straight. The posterior arm of the metacone is still curved, but is not as long as on the M1. The cingular development is similar as in the M1.

**M3** (10). The outline of the occlusal surface is sub-triangular. The anterior arm of the protocone usually ends against the base of the paracone. In two specimens from Karydia 3 this arm ends in front of the paracone. There is a small posterior thickening in the anterior arm of the protocone, indicating the presence of a protoconule. The

paracone is somewhat larger than the metacone. Their arms meet halfway between the two cusps. The protocone and metacone are connected by a posterior ridge. A small parastyle lies in front of, or anterolabially to, the paracone and may be connected to that cusp by a short ridge. There is a well-developed anterior cingulum; a weak posterior cingulum may be indicated in some specimens. Remarkably, all of the M3 from Karydia 3 are larger than those from Karydia 1. This is mainly due to a somewhat different position of the parastyle.

**d3** (1). The outline of the occlusal surface is sub-elliptical. The front of the milk molar is somewhat narrower than the back. The protoconid is tri-faced. Its tip lies in the centre of the tooth. In the front of the d3 lies a small cusp with a circular circumference. Behind the straight posterior flank of the protoconid there is a wide flattening. The enamel-dentine boundary slopes up between the two roots on both sides, but more so on the labial than on the lingual one.

**d4** (1). The only available specimen is damaged. The outline of the occlusal surface is lozenge-shaped. The milk molar consists of a trigonid bordered at its back by a large flattening. The protoconid is only somewhat higher than the metaconid. The low paraconid lies at the end of a long, curved paralophid. The posterior flattening is widest in its middle. It is bordered by a low posterior ridge.

**p4** (6). The premolar consists of a trigonid, bordered at its back by a very short talonid, consisting of a posterior ridge that is separated from the protoconid-metaconid complex by a narrow groove. The protoconid is the highest cusp. The metacone is butted against its lingual flank. The development of the metaconid varies. In one specimen (KRD3 7) it is missing, on the others it ranges from small to well-developed. The paralophid is a low, elongate cusp. It ends low against the rounded anterior flank of the protoconid. Only in one specimen (KRD3 9), the anterior flank of the protoconid bears a ridge connecting to the paraconid, thus forming a kind of paralophid. There is a thickening in the posterior ridge behind the notch separating protoconid and metaconid. Labially of this point the ridge slopes down. On the lingual side there is either a second thickening, or the ridge slightly slopes down. There are no cingula.

**m1** (8). The outline of the occlusal surface is sub-rectangular. The trigonid and talonid are of the same length; the trigonid is slightly narrower than the talonid. The protoconid and metaconid are high and are separated by a deep notch. The paraconid is somewhat lower and lies at the end of a long, straight paralophid. The trigonid basin is quite wide. There is a tiny metacristid at the base of the metaconid.

The entoconid is clearly larger and higher than the hypoconid. The entocristid is completely merged with the entoconid. This complex closes the wide talonid basin at the lingual side for about two-thirds its length. The hypolophid is slightly S-curved. The oblique cristid is low and ends near the base of the protoconid. The anterior cingulum varies from narrow to well-developed. There is a short labial cingulum along the flank of the oblique cristid. The thick

posterior cingulum lies behind the hypoconid. It slopes up lingually, but does not connect to the entoconid.

**m2** (5). The outline of the occlusal surface is sub-rectangular. Trigonid and talonid are of the same width, but the trigonid is clearly shorter than the talonid. The trigonid differs markedly from that of the m1. The paraconid is completely incorporated in the low, curved paralophid. The trigonid basin is narrow; in specimens with a large metaconid it is little more than a groove separating this cusp from the paralophid. The small metacristid at the base of the metaconid is a bit larger than in the m1. The entoconid is clearly larger and higher than the hypoconid. The entocristid is merged with the entoconid and partly closes the wide talonid basin. The oblique cristid is low and ends near the base of the protoconid.

There is a narrow anterior cingulum. Labially, there is only a short cingulum along the base of the oblique cristid. A short, thick cingulum lies directly behind the hypoconid, sloping up in the direction of the entoconid. In one moderately worn specimen, this cingulum almost connects to the hypolophid.

**m3** (1). The talonid is somewhat wider and shorter than the talonid. The protoconid and metaconid are of the same height; the ridge connecting them has a clear notch. The paraconid is much lower. It is incorporated in the blade-like paralophid. The trigonid basin is relatively open. There is a very low metacristid at the base of the metaconid. The entoconid is conical. There is a clear entocristid that connects to the metacristid. The hypoconid is much lower than the entoconid, and lies anterolabially of that cusp. The oblique cristid is very short, sloping down from the side of the hypoconid to the base of the protoconid. There is a well-developed anterior cingulum.

### *Galerix* sp.

(Plate 2, fig. 9)

**Measurements:** Komotini: M1 (2.69 x 3.39).

**M1** (1). The single M1 from Komotini differs, apart from its larger dimensions, from those from Karydia in a more robust appearance. The anterior arm of the metacone curves back towards the mesostyle, forming a loop (= 'Schlaufenbildung' in German literature). The posterior side of the hypocone bears a distinct crest.

**Discussion:** Before discussing the taxonomical and phylogenetical position of the Karydia and Komotini galericines, we give a short overview of the taxonomy of the Galericipini. A generic revision has been published by VAN DEN HOEK OSTENDE (2001). Since then, several new finds have shown that the evolution of the tribe is rather complex, and open to different interpretations, especially around the Early/Middle Miocene transition. Such an alternative view was presented by ZIEGLER (2005), who gave a phylogenetic analysis of the Galericipini, transferring various species included in *Parasorex* by Van den Hoek Ostende to the genus *Schizogalerix*.

Until 1980, the genus *Galerix* was more or less a waist basket. It held very different forms, such as *Galerix exilis* on the one hand, and *G. zapfei* on the other. ENGESSER

(1980) made a first division, placing the - mostly Greek and Austrian - species with a divided mesostyle apart in the genus *Schizogalerix*. At the same time he described several new species from Anatolia, the area in which the genus appeared to be most abundant, and in which the oldest and most primitive representative at the time, *S. pasalarensis* was found. Particularly in the upper dentition, the genus is highly characteristic. The molars are transversely elongated. The P3 bears a hypocone, there is no connection between the protocone and the metaconule, and the p4 has a well-developed trigonid. These latter characters were, however, also found in *Galerix socialis*. BUTLER (1980) had therefore suggested that all species with a hypocone on the P3 (i.e. *G. socialis* and the Greek and Austrian species that were included in *Schizogalerix*) should be grouped, for which the genus name *Parasorex* VON MEYER, 1865 was available. This suggestion was, however, not followed by other authors.

Whereas separating the *Schizogalerix* species separately was a major improvement, the taxonomy of the genus *Galerix* remained unsatisfactorily. This is, e.g., clear from the description of *G. symeonidisi* by DOUKAS (1986). He recognised within *Galerix* and 'exilis-group' and a 'socialis-group'. The Greek species, however, seems to possess characters from both. The P3 had a hypocone, resembling *Galerix socialis*, but unlike that species the p4 of *G. symeonidisi* does not have a paralophid, and a protocone-metaconule connection in the M1/M2 is regularly found. *Galerix symeonidisi* proved to be a wide-spread species in MN 4, with finds from Spain, Germany, Austria and Greece (VAN DEN HOEK OSTENDE & DOUKAS, 2003).

VAN DEN HOEK OSTENDE (2001a) separated the 'socialis-group' of *Galerix*, re-instating the genus *Parasorex*. The similarities between *Parasorex* and *Schizogalerix* (P3 with hypocone, p4 with well-developed trigonid, invariable absence protocone-metaconule connection, and metaconules of which the posterior arm fuses with the buccal part of the posterior cingulum) were interpreted as the result of parallel evolution. The divided mesostyle on the M1 and M2 and the transversely elongate shape of these molars in the latter genus, clearly separates *Schizogalerix* and *Parasorex*, and the set of characters that they share sets each of them apart from *Galerix*. However, *Galerix* itself is not as easily defined. All of the characters found in *Parasorex* can be found as part of the variation in species of *Galerix*. And sometimes, one of these characters may even be invariably present, such as the P3 with a hypocone in *G. symeonidisi*.

VAN DEN HOEK OSTENDE (2001a) did not discuss "*Schizogalerix*" *iliensis*, a species that was described a year earlier from the Early/Middle Miocene of Kazakhstan (KORDIKOVA, 2000). This species does not have the bipartitioned cingulum found in all species of *Schizogalerix* and *Parasorex*. The tentative classification as *Schizogalerix* was based on a superficially divided mesostyle, which is mentioned in the diagnosis. The description of the molars, however, clearly states that the mesostyle is undivided. Even more *Schizogalerix*-like is a small galericine from the Austrian MN 5 locality Mühlbach am Manhartsberg,

which ZIEGLER (2003) described as *Schizogalerix pristinus* [= *pristina*]. The find was interpreted as the most primitive *Schizogalerix*, suggesting a scenario in which the most primitive members of the genus were wide-spread (the Kazakhstan species was also included in the genus by ZIEGLER (2003)), gave rise to *Schizogalerix* lineage in Anatolia, which in the Late Miocene spread out once more. The ascription to *Schizogalerix* of the galericine from the Greek MN 5 locality Antonios (VASSILIADOU & KOUFOS, 2005) fits well with this model.

In his generic revision VAN DEN HOEK OSTENDE (2001a) sought to explain the distribution in time and space. As the genus *Parasorex* appeared later than *Schizogalerix*, but was more primitive in the absence of a divided mesostyle, the similarities between the two were explained by parallel evolution. ZIEGLER (2005) took a somewhat different approach, purely basing his phylogenetic analysis on morphological characters. This automatically leads to the grouping of *Schizogalerix* and *Parasorex*. A conspicuous difference with the classification of VAN DEN HOEK OSTENDE (2001) is the transfer of *P. ibericus* and *P. depereti* to *Schizogalerix*. Ziegler based this reclassification on the 'at least superficially divided mesostyle'. The illustrations of these species (CROCHET, 1986: pl. 1, fig. 1; MEIN & MARTIN-SUÁREZ, 1993: fig. 5 b, c), however, show a configuration of the mesostyle which is similar to that of *P. socialis*, and certainly not to the contemporaneous species of *Schizogalerix*. Furthermore, *P. ibericus* and *P. depereti* do not have the typical transversely elongated upper molars, but resemble also in the W/L ratio of M2 *Parasorex socialis* rather than *Schizogalerix* (VAN DEN HOEK OSTENDE, 2001a: fig. 2). Dr. R. Ziegler graciously informed us that W/L ratios of *Parasorex socialis* from Steinheim, the type locality of the species, range from 1.35 to 1.44, and actually show some overlap with *Schizogalerix*. We therefore prefer to maintain the Spanish and French species in *Parasorex*. This also provides a more parsimonious solution if we consider the distribution in time. As species of the genus *Schizogalerix*, *iberica* and *depereti* would be by far the most primitive representatives, even though they are among the youngest Galericipini. At the time of its description, *Schizogalerix pristina* made a more convincing ancestral form within its genus. However, the discovery in Anatolia of a species of *Schizogalerix* that is both older and more advanced than *S. pristina*, makes this scenario unlikely (DE BRUIJN et al., 2007).

Where does the Karydia erinaceid fit into all this? Two out of the four characters typical for *Schizogalerix* and *Parasorex* are invariably present. All of the P3 have a hypocone, and the posterior cingulum of the M1 and M2 is always bipartitioned. The species also scores well when it comes down to the protocone-metaconule connection. Such a connection is absent in c. 80 % of the M1 and M2. The p4, however, is certainly not *Schizogalerix/Parasorex* like. There is no continuous paralophid connecting the tip of the protoconid to the paraconid, and the metaconid may be small or even absent.

*Galerix kostakii* can easily be envisioned as a descendant

of *G. symeonidisi*. The main difference between the two lies in the larger size of the Karydia species. Other than that, the protocone-metaconule connection is even more rare than it is in *G. symeonidisi*, and the posterior arm of the metaconule of the M1 and M2 invariably reaches the posterolabial corner of these molars. At the same time, the new species can also be seen as an ancestor to "*Schizogalerix*" *pristina*. In this species the protocone-metaconule is invariably absent, and the p4 has a paralophid joining to the tip of the protoconid. The upper molars are somewhat wider (W/L ratio = 1.40 vs 1.33 in *Galerix kostakii*).

The characters involved in a lineage *symeonidisi* - *kostakii* - *pristina* are exactly those that are shared by *Parasorex* and *Schizogalerix*. VAN DEN HOEK OSTENDE (2001a) assumed that the similarity between these two genera was due to parallel evolution. He considered the similar characteristics to be adaptations to a more herbivorous diet. The distribution of the species provided an additional argument for the presumed similar ecological adaptation in *Parasorex* and *Schizogalerix*. Species of both genera co-occur occasionally with *Galerix*, but never with one another. Because whenever more than one species of *Galerix* are found together, one of the two is *G. symeonidisi*, VAN DEN HOEK OSTENDE (2001a) already assumed that this species may have had a niche similar to *Parasorex* and *Schizogalerix*. Indeed, it becomes apparent now that within *Galerix* there were various species that already show a tendency towards the adaptation found in *Parasorex* and *Schizogalerix*, namely *Galerix symeonidisi*, *G. kostakii* and *G. iliensis*.

The classification of "*Schizogalerix*" *pristina* is somewhat problematic. The three species mentioned above retain some primitive characters as found in *Galerix*. None of the specimens from the type series from Mühlbach am Manhartsberg shows any such features, but on the other hand, the assemblage from this Austrian locality is relatively small (e.g., only one p4 was found). The original designation to *Schizogalerix*, though not illogical at the time, can no longer be maintained, but the species has all the characteristics of *Parasorex*. The W/L-ratio of the M2 fits very well with that of other species assigned to that genus (cf. VAN DEN HOEK OSTENDE, 2001a: fig. 2). In time and place (Austria, MN 5) the species would be well placed as the most primitive *Parasorex*, given that the oldest occurrence now is in Central Europe in MN 7/8 (La Grive, Anwil, Steinheim).

Familia Plesiosoricidae WINGE, 1917

Genus *Plesiosorex* POMEL, 1848

*Plesiosorex* sp.  
(Plate 2, fig. 10)

**Measurements:** Ka 3: M2 (2.09 x 3.24)

**Description:**

**M2** (1). The molar is much wider than long. The molar is wider at its front than at its back. The anterior side is

straight; the labial, lingual and posterior sides are concave. The protocone is by far the largest and highest cusp, with sharp anterior and posterior arms encircling a deep trigon basin. The anterior arm splits just before reaching the paracone into two arms of equal width, but much narrower than before the split. The posterior of the two arms is short and ends against the base of the paracone at the lingual side of that cusp. The anterior one connects to the parastyle, but is shortly interrupted at the anterolingual flank of the paracone. The posterior arm of the protocone also splits into two thinner arms, at about two-thirds its length. One part connects to the base of the metacone, the other forms a short transverse connection to the arm of the hypocone. The latter is a conical and rather bulbous cusp. The hypocone is separated from the protocone by a deep valley. The single arm of the hypocone is directed slightly anterolabially, but changes direction to posterolabially after the transverse connection with the posterior arm of the protocone. At the same time, it slopes down. After changing direction once more to directly labially, it remains of the same height and tapers out against the posterior flank of the metacone.

The labial cusps are semicircular in cross-section, with a flat labial side. The metacone is slightly larger than the paracone. The posterior arm of the paracone and the anterior arm of the metacone are straight and directed straight towards each other. They slope down towards the middle and touch low at their ends. The anterior arm of the paracone and the posterior arm of the metacone bend sharply to the labial side, the former being longer than the latter. Between these arms and the labial flank of the labial cusps there is a large, rather flat area.

**Discussion:** This is the first find of a plesiosoricid in Greece, and the most southern find of the family ever. Plesiosoricidae are mostly found in Central Europe, with several occurrences in France and Germany (ZIEGLER, 1999), but the family is, for instance, entirely lacking in Spain (VAN DEN HOEK OSTENDE & FURIO, 2005). Their distribution, however, is not limited to Europe, as is clear from the description of a *Plesiosorex* from the late Early Miocene of Kazakhstan (KORDIKOVA, 2000), and even from the Early Miocene of Colorado (WILSON, 1960).

As *Plesiosorex* is a rare element in Miocene faunas, and not all of the assemblages contain an M2, there are only a few specimens with which the molar from Karydia can be compared. An M2 from the German MN 2- locality of Ulm-Westtangente classified as *Plesiosorex* cf. *soricinoides* (c. 2.1 x 3.62) is about the same length as the Greek specimen, but is considerably wider (ZIEGLER, 1990). The second upper molar of *Plesiosorex germanicus* from the MN 5 localities of Hambach 6C (2.34 x 3.45; ZIEGLER & MÖRS, 2000) and of Maßendorf (2.40 x 3.44 / 2.41 x 3.59; SCHÖTZ, 1989) are larger than the M2 from Karydia. Unfortunately, no direct comparison can be made with the Kazakhstan *P. aydarlensis* (KORDIKOVA, 2000), since the M2 of that species is a yet unknown. Notably, the M1 of that species is somewhat smaller than those of *P. germanicus*, which suggests that *P. aydarlensis* is of similar size as the Greek species.

Familia Dimylidae SCHLOSSER, 1887

Genus *Plesiodimylus* GAILLARD, 1897

*Plesiodimylus* aff. *crassidens* ENGESSER, 1980

(Plate 3, figs. 1-5)

**Measurements:** The measurements are listed in Table 2.

**Description:**

**P4** (2). The labial side of the premolar is occupied by the large, bulbous paracone, which bears a faint posterocrista. The posterolingual side of this cusp is slightly concave, the other sides are rounded. The equally bulbous protocone is about half the length and half the height of the paracone. Its tip lies directly lingually of the tip of the paracone. There is a small posterior flattening bordered in front by the protocone and the concave flank of the paracone. A well-developed cingulum surrounds the premolar, only being interrupted at the anterior flank of the protocone.

**M2** (2). The outline of the occlusal surface is sub-triangular. The anterior and lingual sides are lightly curved, and stand nearly at a right angle. The postero-labial side is S-curved. The very large protocone is conical. It occupies the antero-lingual part of the molar. It bears a very faint lingual-labially directed, curved crest over its tip. This crest ends at the anterior side of the molar at both its ends. The paracone lies lingually of the protocone and is separated from it by a narrow valley. Its anterior arm runs directly to the labial side, bending near its end to form the parastyle. The posterior arm runs straight back and connects to the undivided mesostyle.

The metacone is large and lies behind the protocone. It is ridge-shaped. This ridge starts low just behind the protocone. It slopes up, remaining near the lingual side till it nearly reaches the posterior side. It then curves to the labial side. Retaining the same height, it runs close to the posterior side until it connects to the mesostyle. In front of this ridge, the flank of the metacone slopes down into the narrow valley between protocone and metacone. The narrow flank behind the ridge is rounded. There is a cingulum along the anterior flank of the paracone. Along the posterior flank of the anterior arm of the paracone a faint cingulum is indicated.

**p4** (1). The premolar is much longer than wide. The outline of the occlusal surface is sub-elliptical, with a straight posterior side. The tip of the only cusp lies to the front, at about one-third the length of the premolar. There is a faint centerocristid, and a low but wide, blunt ridge, running from the tip to the lingual side. Lingually of the centerocristid the surface of the cusp is convex; labially it is rather flat. The premolar is surrounded by a well-developed cingulum, which is thicker at the back than at the front.

**m1** (1). The cusps are robust and bulbous, but the molar is not exaenodont. The trigonid and talonid are of similar length and width, and in our moderately worn specimen the height difference between the two is very small. The protoconid and metaconid are worn down to form a sin-

	Length		N	Width	
	range	mean		mean	range
P4	1.83-1.89	1.86	2	1.76	1.69-1.83
M2	1.96-2.03	2.00	2/1	2.73	
p4		1.73	1	1.14	
m1		2.63	1	1.64	
m2	2.67-2.69	2.68	2	1.42	1.41-1.42

**Table 2:** Measurements for *Plesiodimylus* aff. *crassidens* from Karydia.

gle wear facet. Remarkably, this facet is highest between the two cusps, indicating that the cusps themselves wore down more quickly than the interconnecting ridge. From this and the other wear facets it is clear, that the enamel is very thick. The paraconid is very low. It is a small, comma-shaped cusp. The tail of the comma ends against the flank of the protoconid, at about half its height.

The oblique cristid is mainly indicated by its wear facet, which is completely merged with the wear facet of the hypoconid. It runs straight forward, connecting the hypoconid to the base of the protoconid. The entoconid is rather conical. It closes the shallow talonid basin on the lingual side. There is a narrow opening between the entoconid and the metaconid.

A well-developed cingulum encircles most of the m1. Running forward from the metaconid it rounds the paraconid. It is somewhat wider on the anterior side than on the labial side. After rounding the hypoconid it becomes a thick posterior cingulum, which slopes up and ends just short of the point where the hypolophid meets the base of the entoconid.

**m2** (2). The outline of the occlusal surface is elliptical. The trigonid is clearly longer and somewhat wider than the talonid. The protoconid has two sharp arms. The anterior one –the paralophid- is curved and gently slopes down. The paraconid is totally incorporated in this ridge. The posterior arm of the protoconid is straight and ends high against the conical metaconid.

The talonid is slanted against the back of the trigonid. The talonid basin is very shallow. The entoconid is rather bulbous and low. An indistinct entocristid ends just short of the metaconid. The oblique cristid, hypoconid and hypolophid form a continuous ridge, ending high against the entoconid on one side, close to the base of the protoconid on the other side. The cingulum is widest on the anterior side. It rounds the paraconid, forming a very narrow lingual cingulum that ends at the trigonid basin. Labially the cingulum is well developed, and it continues along the posterior side, ending against the base of the entoconid.

**Discussion:** Most finds of *Plesiodimylus* are described as *P. chantrei*, giving the species an incredibly large stratigraphical and geographical range. The oldest finds are placed in MN 4, the youngest are from MN 11 (ZIEGLER, 1999). MÜLLER (1967) had separated the finds from Wintershof-West (Germany, MN 3) as *P. huerzeleri*. ENGESSER (1976) synonymized *huerzeleri* with *chantrei*, but SCHÖTZ

(1985) reinstated the species. ZIEGLER & FAHLBUSCH (1986) argued that the differences with *P. chantrei* were insufficient to warrant distinction at the species level, and classified the early *Plesiodimylus* finds as *P. aff. chantrei*. In recent publications, however, we find *P. huerzeleri* again as a separate species (ZIEGLER, 1999; 2007). Apart from these names, three other species were proposed from Central Europe. SCHÖTZ (1989) described *P. bavaricus* from the German locality of Maßendorf (Germany, MN 5). According to VAN DEN HOEK OSTENDE (1995), the differences with both *P. chantrei* and *P. huerzeleri* are small. ZIEGLER (1999, 2007) and KÄLIN & ENGESSER (2001), however, maintain that the Maßendorf species can be distinguished as a separate lineage within the genus. *Plesiodimylus helveticus* was described from the Swiss MN 4 locality of Jona-Täger-naustraße (BOLLINGER, 1992). The fourth European species, *P. johanni*, was also described from Switzerland, from the MN 9 locality of Nebelbergweg (KÄLIN & ENGESSER, 2001). Apart from these named species, ZIEGLER & MÖRS (2000) considered two very large specimens from their *Plesiodimylus* assemblage as possibly a new species, and RZEBIK-KOWALSKA (1996) also recognised a second form of *Plesiodimylus* next to *P. chantrei* in her material from Belchatów A.

The only *Plesiodimylus* outside of Europe so far was published by ENGESSER (1980), who described *P. crassidens* from the Anatolian MN 7/8 locality of Sari Çay. This species was also listed for the Czech MN 10 locality Suchomasty by FEJFAR & SABOL (2005).

The Karydia *Plesiodimylus* stands out for being large. It falls outside the range of the various forms described as *P. (aff.) chantrei* (including *P. huerzeleri*) as given by ZIEGLER & FAHLBUSCH (1986: fig. 7). The lower m2 agree well with those from *P. chantrei* from Aliveri, but the P4 are about 20 % larger than the one from that locality. On the other hand, the molars from Karydia are somewhat smaller than those of *P. crassidens* (unfortunately, no measurements were given for the premolars of that species), thus having an intermediate size between the two species. In some characters, the Greek dimylid resembles the Anatolian species. From the wear facets on the m1 it is clear that the enamel is very thick. The arm of the paraconid does not reach the tip of the protoconid, as it does in *P. chantrei*, but remains low. However, both the p4 and m2 of *P. crassidens* are clearly wider at their fronts than at their backs, whereas in Karydia these elements are of the same width throughout.

Based on literature, *Plesiodimylus* has a somewhat peculiar if interesting record. The main stem appears to be a relatively constant species, with an incredibly long life span, from which occasionally short side stems evolve. With the description of a series of new species over the last fifteen years, however, it becomes more and more important to assess the record as a whole. After all, *P. chantrei* may in the past have served partly as a wastebasket taxon, or temporal and/or geographical variations may have gone unnoticed in older literature. We found it no easy task to find a proper classification for the *Plesiodimylus* from Karydia. Although we think *P. aff. crassidens* is the most

suitable classification, this identification should be considered with some caution. A revision of all the *Plesiodimylus* material is needed to evaluate the taxonomical value of the various characters used to distinguish between species in this genus.

Familia Talpidae FISCHER VON WALDHEIM, 1817

Genus *Desmanodon* ENGESSER, 1980

*Desmanodon antiquus* ZIEGLER, 1985  
(Plate 3, figs. 6-11)

**Measurements:** Ka 1: M2 (1.73 x 2.05); m2 (1.77 x 1.17). Ka 3: 3 M2 (1.78 x 2.11, 1.85 x 2.13, 1.82 x 2.01); p4 (1.34 x 0.76).

**Description:**

**Dentary (1).** Only one fragment of the dentary has been preserved, with a p4. Halfway the height of the mandible, below the p4, there is a large sulcus, in which a small foramen below the anterior root of the p4, and a large foramen between the posterior root of the p4 and the anterior root of the m1 are found.

**M2 (4).** The outline of the occlusal surface is slightly asymmetrical, due to the anterior position of the protocone. The paracone is somewhat smaller than the metacone. In both lingual cusps the anterior and posterior arms are of the same length, and run parallel to one another, leaving a narrow basin. The parastyle has developed as a separate cuspule at the end of the anterior arm of the paracone, and protrudes slightly. In similar fashion the anterior part of the mesostyle lies as a separate cuspule at the end of the posterior arm of the paracone. The posterior cuspule of the mesostyle and the metastyle are, however, incorporated in the anterior and posterior arms of the metacone, respectively. The metastyle protrudes slightly. The mesostyle is deeply divided.

The protocone occupies the lingual part of the M2. In one unworn specimen, the protoconule is clearly discernable, directly adjacent to the tip of the protocone on the anterolabial side of that cusp. In the other specimens the protoconule cannot be discerned. The hypocone is a small and low cusplet, lingually of the tip of the metacone. The posterior arm of the protocone ends against the base of the hypocone. There are no cingulums, except for two very short stretches near the parastyle and metastyle.

**p4 (1).** The outline of the occlusal surface is sub-rectangular, with a straight lingual side. The last lower premolar consists mainly of the very high paraconid, which is bordered at the back by a short talonid. The lingual face of the paraconid is flat; the labial face is rounded, making the cross-section of the cusp semi-circular. The talonid, which slopes down towards the labial side, is bordered at its back by a well-developed ridge. There is a continuous cingulum on the anterolabial side of the paraconid; some patches of cingulum are visible on the lingual side.

**m2 (2).** The trigonid is clearly shorter than the talonid. Trigonid and talonid are of similar width. The cusps are very high. The trigonid basin is narrow. The oblique cristid ends against the middle of the protoconid-metaconid crest.

The talonid basin slopes down toward the front, having its deepest point just behind the trigonid. The hypoconid is very large; the entoconid is somewhat smaller. There is an entocristid, but no metacristid. The anterior cingulum is well developed, and is at its lingual end somewhat wider than near the base of the protoconid. The posterior cingulum is somewhat less developed. At its lingual end it gives rise to a small entostylid. The re-entrant valley is bordered by a labial cingulum.

**Remarks:** Five species of *Desmanodon* have been described from the Early Miocene: *D. zieglerei* VAN DEN HOEK OSTENDE, 1997, *D. burkarti* VAN DEN HOEK OSTENDE, 1997, *D. daamsi* VAN DEN HOEK OSTENDE, 1997, *D. meuleni* DOUKAS, 1986, and *D. antiquus* ZIEGLER, 1985. *Desmanodon zieglerei* and *D. burkarti* were described from Anatolia. In these species the protoconule is still clearly present on M1 and M2 (*D. zieglerei*) or only on the M2 (*D. burkarti*). Although a protoconule could be observed in one unworn specimen, it is clear that it is more reduced in the Karydia assemblage than in the Anatolian species. Other than that, the cingular development of the p4 is less in the Greek locality. *Desmanodon daamsi* from Spain has a rather weak hypocone and an incompletely divided mesostyle. This leaves *D. meuleni* and *D. antiquus* as possible candidates for the Karydia *Desmanodon*. These two species were described separately from one another at about the same time, which makes their history somewhat confusing. When ZIEGLER (1985) described *D. antiquus*, he knew of the unpublished Ph.D. thesis of Doukas, in which *D. meuleni* from the Greek locality of Aliveri was coined for the first time. At that time, Doukas still recognised two morphotypes in the upper molars from Aliveri. Although Ziegler pointed out differences with either morphotype in his differential diagnosis, he gave no distinction between *D. antiquus* and *D. meuleni* as a whole. When the species *D. meuleni* was officially published, DOUKAS (1986) considered the assemblage to be homogeneous, the transition between the two morphotypes being gradual. He noted that *D. meuleni* might well be conspecific to *D. antiquus*. However, assessing conspecificity was hampered by the small type series of both species, which allowed little insight in the variation. Furthermore, the two assemblages only had a few elements in common, making the comparison even more difficult. The study of a large series of *Desmanodon* molars from Central Spain (VAN DEN HOEK OSTENDE, 1997, 2003) showed that the morphological variation in this genus can be quite large. The minor differences between *D. antiquus* and *D. meuleni* certainly seem too small for specific distinction. This is confirmed by the Karydia assemblage, which, based on the diagnoses of the two species, would be referable to either. As the description of *D. meuleni* in the Greek Ph.D thesis of Doukas does not constitute an official publication, ZIEGLER'S (1985) description of *D. antiquus*, predates that of *D. meuleni*. The latter is therefore considered a junior synonym.

Genus *Myxomygale* FILHOL, 1890

*Myxomygale cf. hutchisoni* (ZIEGLER, 1985)

(Plate 3, figs. 12, 13)

**Measurements:** Ka 3: 1 M2 (1.66 x 1.78), 2 M3 (1.08 x 1.48; 1.06 x 1.52)

**Description:**

**M2** (1). The outline of the occlusal surface is slightly asymmetrical due to the anterior position of the protocone. The only available specimen is moderately worn. The presence of a protoconule is indicated by small constrictions in the wear facet of the lingual complex, directly in front of the protocone. Judging from the wear facet, the protoconule was only slightly smaller than the protocone. The hypocone is a small elevation posterolabially to the protocone, directly lingual to the base of the metacone. The anterior arm of the protoconule and the posterior arm of the hypocone end against the anterior flank of the paracone and the posterior flank of the metacone, respectively, near the bases of these cusps.

The labial cusps are of similar size and shape, creating a large W-shaped complex that occupies about three-quarters of the molar. The anterior arm of the paracone and the posterior arm of the metacone bend at their respective ends to form the parastyle and metastyle. The mesostyle is undivided. There are no cingula.

**M3** (2). The outline of the occlusal surface is sub-triangular. The lingual side is completely occupied by the protocone. Its anterior arm ends against the anterior flank of the paracone near the base of that cusp in one specimen. In the other, it continues as an anterior cingulum up to the parastyle. A protoconule is not discernable. The hypocone is only indicated as an elevation in the posterior arm of the protocone, directly lingual of the base of the metacone. The posterior arm of the paracone is only somewhat shorter than the anterior arm. The anterior, and only, arm of the metacone is somewhat shorter still. The anterior arm of the paracone bends at its end to form the parastyle. The mesostyle is undivided. The specimen with an anterior cingulum also has a short labial cingulum along the flank of the metacone. The other specimen has no cingula whatsoever.

**Discussion:** Apart from the type species *Myxomygale antiqua* from Middle Oligocene of France, the genus *Myxomygale* is known from three Early Miocene species: *M. hutchisoni* (ZIEGLER, 1985), *M. engesseri* DOUKAS, 1986, and *M. minor* ZIEGLER, 1990. The latter was described from the German MN 2 locality of Ulm-Westtangente, and is the smallest of the three species. VAN DEN HOEK OSTENDE & FEJFAR (2007) noted the presence of this species in the Czech MN 3 locality of Merkur-Nord. The three specimens from Karydia are clearly larger than those of *M. minor*. They are also larger than those from the nearby Greek locality of Aliveri, the type locality of *M. engesseri*. Furthermore, in contrast to *M. engesseri* the M3 are considerably larger, and do not possess a clear protoconule, as the Aliveri species does. In size, the Karydia M2 show the best fit with *M. hutchisoni*. ZIEGLER (1985) did not include measurements for the M3 in his diagrams, but kindly provided us with data. These show that particularly the M3 from Erkertshofen 1 are comparable in size to the M3 of Karydia, whereas the Greek material is even larger than that from the type locality Petersbuch 2. Furthermore,

the M3 of *M. hutchisoni* also lack the protoconule. In the description Ziegler (o.c.: 150) also mentions the absence of a paraconule, which we take is a lapsis lapili for the metaconule [= hypocone]. However, his illustration shows a similar elevation in the posterior crest of the protocone near the base of the metacone as was described above as the hypocone. In view of these similarities, and taking into account the scarcity of the material, the Karydia talpid is classified as *Myxomygale* cf. *hutchisoni*.

*Myxomygale* seems to be a typical European faunal element. Apart from the German and Czech finds mentioned above, it was also shown to be present in MN 3 of Spain (VAN DEN HOEK OSTENDE, 2003).

Its possible presence in Anatolia was indicated by VAN DEN HOEK OSTENDE (1989), who suggested that the small-sized *Desmanodon* sp. from Sari Çay in ENGESSER (1980) could in fact be a *Myxomygale*. However, that same author later suggested that it was more likely that these molars were attributable to *Theratiskos* (VAN DEN HOEK OSTENDE, 2001b). Following that suggestion, the presence of *Myxomygale* in Karydia would be the easternmost occurrence of the genus.

Heterosoricidae VIRET & ZAPFE, 1951

#### Genus *Heterosorex* VIRET & ZAPFE, 1951

##### *Heterosorex* sp.

(Plate 4, figs. 1-7)

**Measurements:** The measurements are listed in Table 3.

##### **Description:**

**I1** (1). The upper incisor is large with a moderate hook, which bears a fissident tip. The talon reaches to about two-third of the length of the tooth, and bears a small cusplet. The labial side of the talon is marked by a distinct groove, inside which the enamel is wrinkled. The cingulum is very pronounced at the back of this groove, but far less distinct on the upper side of the incisor. The tooth has one, very stout root.

**A1** (2). The outline of the occlusal surface is sub-rectangular. The posterior side is emarginated and there is a slight anterolingual flange. The antemolar is somewhat longer than wide. The tip of the main cusp lies just in front of the centre of the antemolar and is slightly inclined to the lingual side. A sharp centrocrista runs over the tip of the main cusp, and there is a faint lingually directed ridge between the tip and a minute cusplet on the lingual flange. The latter ridge divides the labial side of the main cusp into two concave surfaces; the labial side of that cusp is convex. The posterior cingulum is very pronounced. The lingual cingulum is weak. A cingulum is lacking on the anterolabial part of the A1. The labial cingulum starts labially of the tip of the main cusp, and then quickly thickens, connecting to the posterior cingulum. The roots of the A1 have not been preserved in our material.

**Ax** (1) The antemolar is somewhat longer than wide. The labial side is curved; the posterior side is slightly emarginated. The anterior and lingual sides are rather straight. The

	Length		N	Width	
	range	mean		mean	range
I1		4.91	1		
Ax		1.00	1	0.86	
A1		1.93	1	1.36	
P4		1.73	1	1.57	
M1	1.62-1.72	1.67	3	1.73	1.69-1.78
M2		1.46	1/0		
i1		6.19	1		
ax		1.06	1	0.93	

**Table 3:** Measurements for *Heterosorex* sp. from Karydia.

tip of the only cusp lies just in front of the centre of the tooth. The centrocrista starts on the anterior side in the anterolabial corner. At the back, it connects to a posterior ridge in the middle of the posterior emargination. Apart from the centrocrista there is a second ridge, connecting the tip of the main cusp to the anterolingual corner. The anterolingual and posterolingual faces of the main cusp are concave; the labial side is rounded. There is a marked ridge along the back of the antemolar. Labially, it connects to a cingulum, which tapers out towards the front of the tooth.

**P4** (2). The outline of the occlusal surface is subtriangular. The paracone is the largest cusp and occupies the labial part of the premolar. Its tip lies in front of the middle of the tooth. The anterior face of the paracone is rounded; posteriorly it bears a sharp postero-crista, which bends shortly behind the tip of the cusp. In front of the paracone lies a large parastylar flange, which slopes to the labial side. In one of the two specimens a short transverse ridge connects the base of the paracone to the anterior side. The protocone is a low, conical cusp, which lies lingually of the tip of the paracone. A faint ridge runs from the base of the paracone to the labial side, partly bordering the parastylar flange. A far more pronounced ridge runs posterolingually from the base of the protocone to the lingual side, and then continues as the posterior ridge to the posterolabial corner of the P4. This ridge borders a rather deep trigon basin. The P4 has three roots; two on the labial side and the third positioned lingually.

**M1** (4). The outline of the occlusal surface is square. The labial cusps form a pronounced W, the paracone being somewhat smaller and lower than the metacone. The posterior arms of the labial cusps are somewhat longer than their respective anterior arms. The mesostyle is undivided.

The lingual cusps are poorly developed, and form a continuous ridge. The tip of the protocone lies close to the anterior border of the molar, with a short anterior arm connected to the base of the paracone. Its posterior arm forms the beginning of the lingual ridge, which bends slightly to the lingual side halfway the molar. The hypocone appears as a slight elevation in this ridge. In two specimens there is a faint transverse ridge connecting the hypocone to the base of the metacone. The lingual ridge continues as a well-developed posterior ridge, which is

most pronounced in its lingual part, and connects to the posterior arm of the metacone in the posterolabial corner of the M1. The M1 has four roots, positioned under the corners of the molar.

**M2** (2). The outline of the occlusal surface is quadrangular, the anterior side being wider than the posterior side. The labial cusps occupy c. 75 % of the occlusal surface. The posterior arms of the paracone and metacone are somewhat shorter than their respective anterior arms. The mesostyle is undivided. The lingual cusps are poorly developed and form a single lingual ridge. The protocone is smaller than that of the m1; the hypocone is hardly discernable as a separate cusp. The posterior ridge is clearly less developed than in the m1. It is slightly curved and ends against the posterior arm of the metacone just short of the posterolabial corner of the molar. The posterior basin it envelops is rather shallow. The M2 has four roots, one under each of the main cusps.

**i1** (2). The incisor is long, tricuspluate with an upward curved apex. The symphyseal side is strongly emarginated. The upper surface is convex and forms a sharp edge with the symphyseal side. There is a ridge on the edge with the labial side, carrying blunt cuspules. The enamel on the labial side is slightly wrinkled. The i1 has one, very stout root.

**ax** (1). As this element was found isolated, its position in the jaw cannot be ascertained. It seems to be too small to be the last antemolar (= p4). The outline of the occlusal surface is heart-shaped, with a pointed anterior side and an emarginated posterior side. The tip of the only cusp lies just labially of the centre of the antemolar. There are three faint ridges, running from the tip to the anterior, posterolabial and posteriolingual side. The antemolar has one root, which is directed backwards.

**Remarks:** The heterosoricid from Karydia was earlier identified as a *Dinosorex* (DOUKAS, 2003, 2005). However, the weak development of the lingual cusps on the upper molars, in combination with a triangular outline of the P4 is typical for *Heterosorex* (ENGESSER, 1975). ZIEGLER (1998) added to these characters the cuspluate lower incisor; the i1 of *Dinosorex* is acuspulate. Since the lower incisors from Karydia are clearly cuspluate, this confirms that the heterosoricid from the locality is in fact a *Heterosorex*.

DOUKAS (1986) described *Heterosorex ruemkae* from Aliveri. The material, like in Karydia, consisted of isolated molars. As heterosoricid taxonomy is largely based on mandibular characters, including the number of antemolars, this is not a very ideal situation. Nevertheless, the description of a new species in Aliveri was warranted, since the material was considerably smaller than that of *H. delphinensis* from La Grive and *H. neumayrianus* from various German localities, the other two species in the genus.

The German record provides by far the best series of *Heterosorex* sites. On the basis of the reduction of the antemolars, DOBIN-FLOREN (1964) recognised two subspecies of *H. neumayrianus*. An even further reduced dentition was found in the MN 4 assemblages from Petersbuch 2 and Erkertshofen 1 and 2, which were classified as *H. neumayrianus* aff. *subsequens* (ZIEGLER & FAHLBUSCH, 1986).

The German record was further enlarged when ZIEGLER (1989) described additional material from Early Miocene localities such as Stubersheim and Ulm-Westtangente. This new material showed that there was no clear trend in size, accompanying the observed reduction. The heterosoricid from Ulm-Westtangente (MN 2) was relatively small, the one from Wintershof-West (MN 3) considerably larger, whereas *H. n.* aff. *subsequens* from various MN 4 localities was small again. ZIEGLER (1989) explained these differences by assuming that the size reflected the local environmental conditions.

Although the M1 from Karydia are similarly sized as those from Aliveri, the I1, A1 and P4 are considerably larger than in that locality. Compared to the German localities, the Karydia *Heterosorex* is comparable in size with the one from Ulm-Westtangente, the smallest sized German assemblage. Thus, the assemblage could be identified either as *H. ruemkae* or as *H. neumayrianus*. Without additional material this cannot be solved, and therefore the material is classified as *Heterosorex* sp.

VAN DEN HOEK OSTENDE (1995) listed *Dinosorex* for Komotini, which was in line with his assumption that this genus migrated into Europe during MN 5. Unfortunately, we were unable to recover the material seen at that time.

Familia Soricidae GRAY, 1821

Subfamilia Crocidosoricinae REUMER, 1987

Genus *Lartetium* ZIEGLER, 1989

*Lartetium* cf. *dehmi* (VIRET & ZAPFE, 1951)

(Plate 4, figs. 8-11)

**Measurements:** KRD 1: 1 M1 (1.31 x 1.73), 1 m2 (1.32 x 0.85); KRD 2: 1 P4 (1.51 x 1.26); 2 M1 (1.29 x 1.73; 1.44 x 1.87).

**Description:**

**P4** (2). The angle between the lingual and labial sides is small. The posterior side is concave. The lingual flange reaches just beyond the middle of the premolar. The tip of the paracone lies in the middle of the tooth, far to the labial side. The postero-crista is only slightly curved. A tiny parastyle lies far to the front, and is separated from the paracone by a wide valley. An indistinct ridge borders this valley at the labial side. The protocone lies anterolingually of the paracone. There is an indistinct ridge connecting the protocone to the parastyle. The hypocone is ridge-shaped. It lies posterolingually of the protocone and borders largely the lingual side of the premolar. The only cingulum runs along the posterior border of the P4. At its labial end it is considerably wider than at the lingual side.

**M1** (4). The molar is somewhat wider than long. The posterior side is moderately emarginated (PE-ratio = 0.23 to 0.25). The protocone is a large and robust cusp. Its anterior arm ends against the base of the paracone, bordering the trigon basin at the front. The posterior arm of the protocone ends freely between the base of the metacone and the hypocone. The latter is well developed and

ridge-shaped. It is separated from the protocone by a wide valley, which is bordered by a short lingual cingulum. The posterior arms of the paracone and metacone are clearly longer than their respective anterior arms. The mesostyle is undivided. There is a well-defined posterior cingulum, which starts at the base of the hypocone. Along the base of the posterior arm of the metacone this cingulum becomes increasingly wider.

**m1** (1). The trigonid is somewhat longer and narrower than the talonid. The paraconid stands far to the front at the end of a notched paralophid, leaving the trigonid basin very wide and open. The entoconid is low and forms the starting point of a long entocristid. There is a tiny metacristid at the base of the metaconid. The hypoconid is large. The oblique cristid connects to the back of the trigonid close to the base of the protoconid. The hypolophid ends behind the entoconid. The anterior cingulum is strong, the posterior cingulum weak. Due to damage on the labial side, the cingular development on that side cannot be assessed.

**m2** (1). The m2 is only little different from the m1. The trigonid is wider, and the oblique cristid end slightly more lingually. The labial cingulum is continuous, and slopes slightly up under the protoconid.

**Remarks:** The shrews from Karydia are represented by isolated molars only, which hampers the identification. The larger species stands out by its large size, the relatively wide upper molars and the presence of a well-developed hypocone. The upper molars closely resemble the fossils from Forsthart illustrated by ZIEGLER & FAHLBUSCH (1986, pl. 2, figs. 32-35) under the name "*Sorex*" *dehmi*, and indeed, the lower molars share with the illustrated specimens (o.c., pl. 2, figs. 29-31) the weak entocristids, the labial termination of the oblique cristid, and the relatively wide talonid. Although ZIEGLER (1989:48) included the absence of entocristids is part of the diagnosis of *Lartetium*, it is clear from his inclusion of "*Sorex*" *dehmi* in the genus that in fact weak entocristids may occur within the genus.

#### Genus *Paenelimnoecus* BAUDELLOT, 1972

##### *Paenelimnoecus* sp.

(Plate 4, fig. 12)

**Measurements:** Ka 2: 1 m2 (1.19 x 0.78).

##### **Description:**

**m2** (1). The outline of the occlusal surface is rectangular. The trigonid and talonid are of the same length and width. The combined wear face of the three cusps of the trigonid forms a V. The oblique cristid ends against the middle of the back wall of the trigonid. The entoconid is strongly reduced, but the talonid basin is bordered by a distinct, low entocristid. The hypolophid and entocristid are separated by a wide valley. The molar has equally strong cingula on the anterior, labial and posterior sides. The lingual cingulum is weak and patchy.

**Remarks:** *Paenelimnoecus* is represented by a single m2 only, clearly showing the typical reduction of the

entoconid. In comparison to the known Early and Middle Miocene species, *P. micromorphus* (DOBIN-FLORIN, 1964) and *P. crouzeli* BAUDELLOT, 1972 the Karydia specimen is remarkably large (cf. ZIEGLER, 1989: fig. 7).

## 4. Discussion

THEOCHAROPOULOS (2000) assumed a younger age for Karydia than for Aliveri, based on the Muroidea from the localities. As *Galerix kostakii* from Karydia is interpreted as a descendant from *G. symeonidisi* from Aliveri, the insectivores confirm the age assessment of Theocharopoulos.

DOUKAS (2003) noted: "the insectivores assemblage of Karydia contains, except for the Dimylidae, all the genera present in the Aliveri fauna." The tables in that article, however, indicate the absence of *Myxomygale*, whereas the heterosoricid appears as *Dinosorex*, as it does in the listing by DOUKAS (2005). The latter list, however, does indicate the presence of a dimylid. Now that the Karydia assemblage is described in full detail, it is clear that the initial remark is correct. All of insectivore genera found in Aliveri are also known from Karydia, with two additions: *Plesiosorex* is present and there are two species of shrew versus only one in Aliveri. Even the dimylid is referable to the same genus as found in Aliveri.

At the species level, the two assemblages show considerable differences. In Aliveri, *Galerix symeonidisi* was found, whereas in Karydia the genus is represented by the new species *G. kostakii*, and there is a different species of *Myxomygale* (*M. engesseri* vs. *M. cf. hutchisoni*). The classification of both the dimylid *Plesiodimylus* and the heterosoricid *Heterosorex* is somewhat problematic, but in both genera it is at least clear that the representative from Karydia is somewhat larger than that in Aliveri. The *Desmanodon* of both localities is referred to *D. antiquus*.

Whereas the composition of the insectivore assemblage of Aliveri and Karydia is similar, the relative abundance of the various faunal elements is markedly different (Fig. 2). The main difference is the much higher percentage of *Galerix* (60 % in Karydia vs. 25 % in Aliveri). If we were to exclude the erinaceid, the percentage of the remaining faunal elements is similar in both assemblages, with the exception of *Plesiodimylus*, which is much better represented in Karydia (19 % vs. 4 % of the assemblage excluding *Galerix*). We have no obvious explanation for either the dominance of *Galerix* in Karydia, or the higher abundance of dimylids. The ecological factors responsible for the differences between the assemblages can only be determined on the basis of the micromammal fauna as a whole, not just on the insectivores.

DOUKAS (2003) noted that the similarity between the rodents of the two localities was larger than that within the insectivores. This certainly holds true if we count the number of species in common. However, the most common rodent in Aliveri, *Pseudotheridomys parvulus*, does not appear on the Karydia faunal list, in which the eomyids are represented by *Ligerimys* instead. Given these differences,

**Figure 2:** Relative abundances of the various insectivores from Aliveri and Karydia.

Karydia and Aliveri seem to represent different time slices. Although both localities are referred to MN 4, we suspect a considerable difference in time within these limits. But before definite conclusions about the stratigraphy and palaeoecology can be drawn, the non-muroid rodents from Karydia need to be evaluated.

## 5. Acknowledgements

We dedicate this paper to Dr. Gudrun Höck-Daxner for her invaluable contribution to science and in fond memories of our time together in the Maramena expeditions.

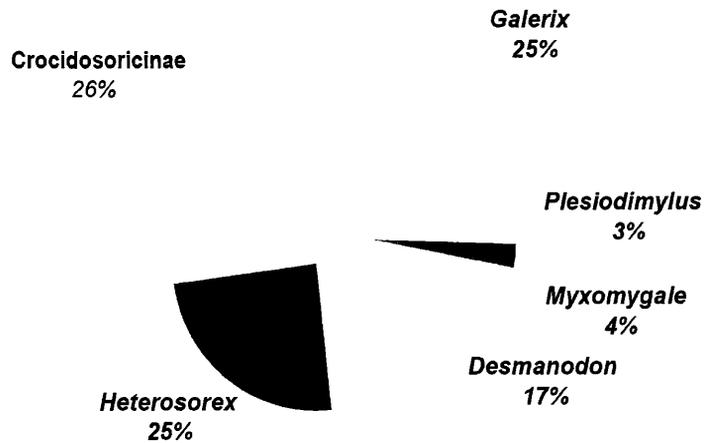
We thank Hans de Bruijn, Dimitri Foussekis and Giannis Dimitriou for helping the first author collecting the material. Our thoughts are with Kostaki Theocharopoulos, who also participated in the field work.

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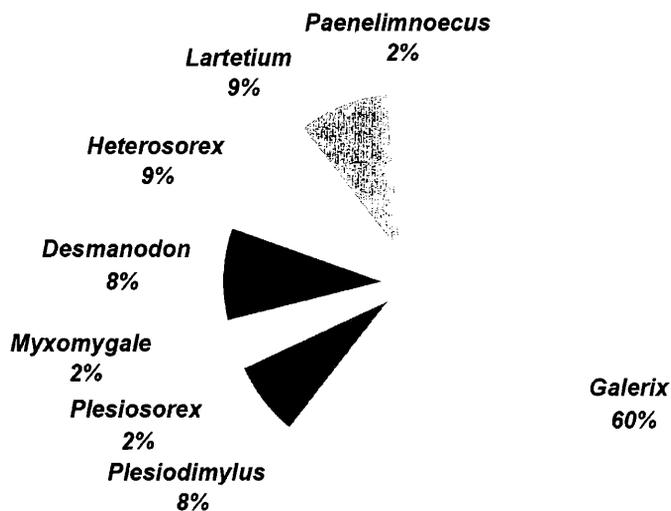
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## Aliveri



N = 114

## Karydia



N = 66

and *Cricetodon* with a discussion of the evolutionary history of the *Cricetodontini*. — *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, **96** (2):151–216, Amsterdam.

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## PLATE 1

### *Galerix kostakii* n. sp.

Fig. 1 Maxillary with C sin. (KRD 3/06)

Fig. 2 P3 sin. (KRD 1/46)

Fig. 3 P3 sin. (KRD 1/47)

Fig. 4 P4 sin. (KRD 3/02)

Fig. 5 M1 sin. (KRD 3/04, holotype)

Fig. 6 M1 sin. (KRD 1/03)

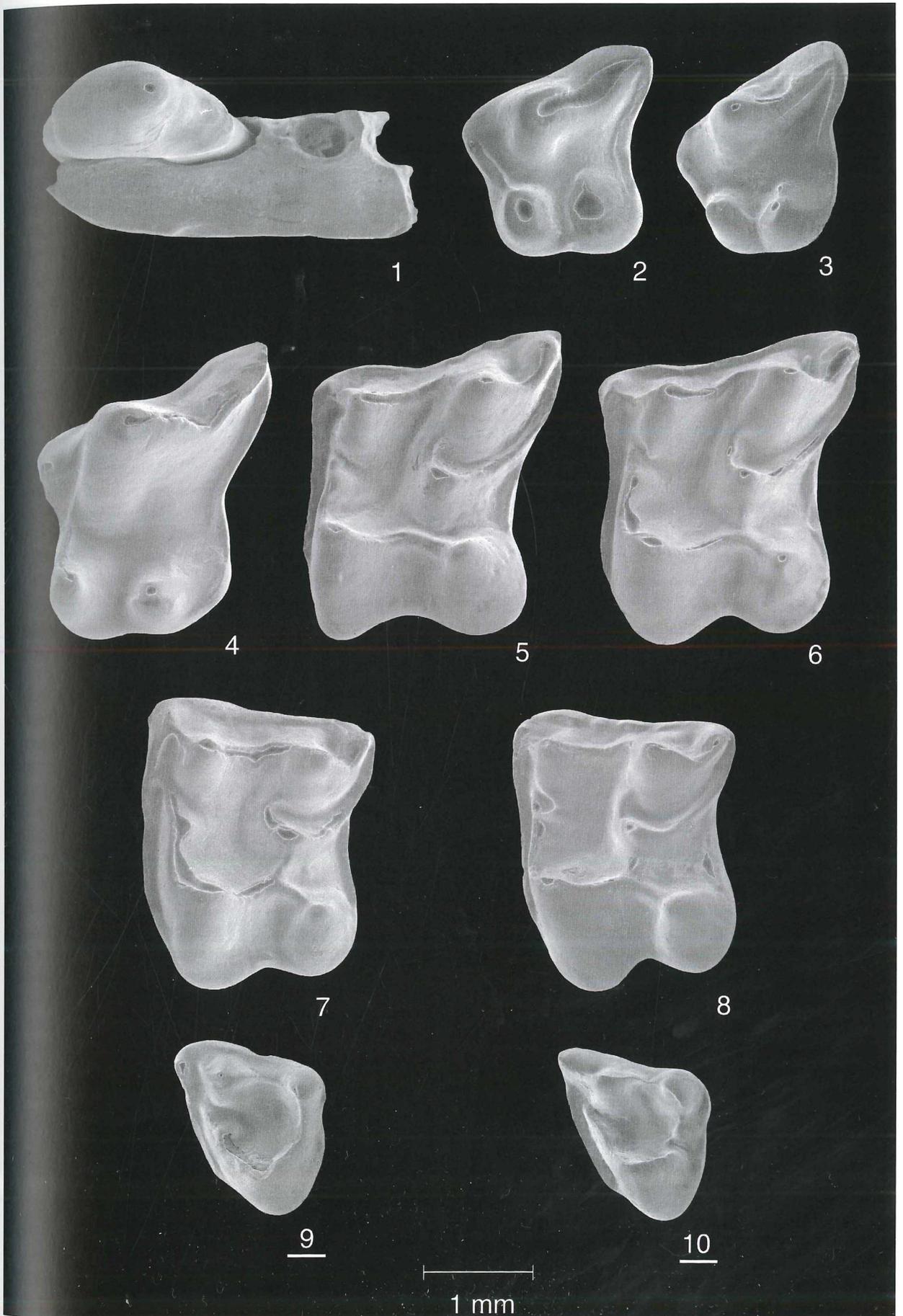
Fig. 7 M2 sin. (KRD 1/12)

Fig. 8 M2. sin. (KRD 1/20)

Fig. 9 M3 dext. (KRD 1/29)

Fig. 10 M3 dext. (KRD 3/12)

PLATE 1



## PLATE 2

### *Galerix kostakii* n. sp.

- Fig. 1 d3 sin. (KRD 1/36)  
Fig. 2 d4 dext. (KRD 3/21)  
Fig. 3 p4 dext. (KRD 1/39)  
Fig. 4 m1 sin. (KRD 3/32)  
Fig. 5 m1 sin. (KRD 1/51)  
Fig. 6 m2 dext. (KRD 1/58)  
Fig. 7 m2 dext. (KRD 3/37)  
Fig. 8 m3 dext. (KRD 3/39)

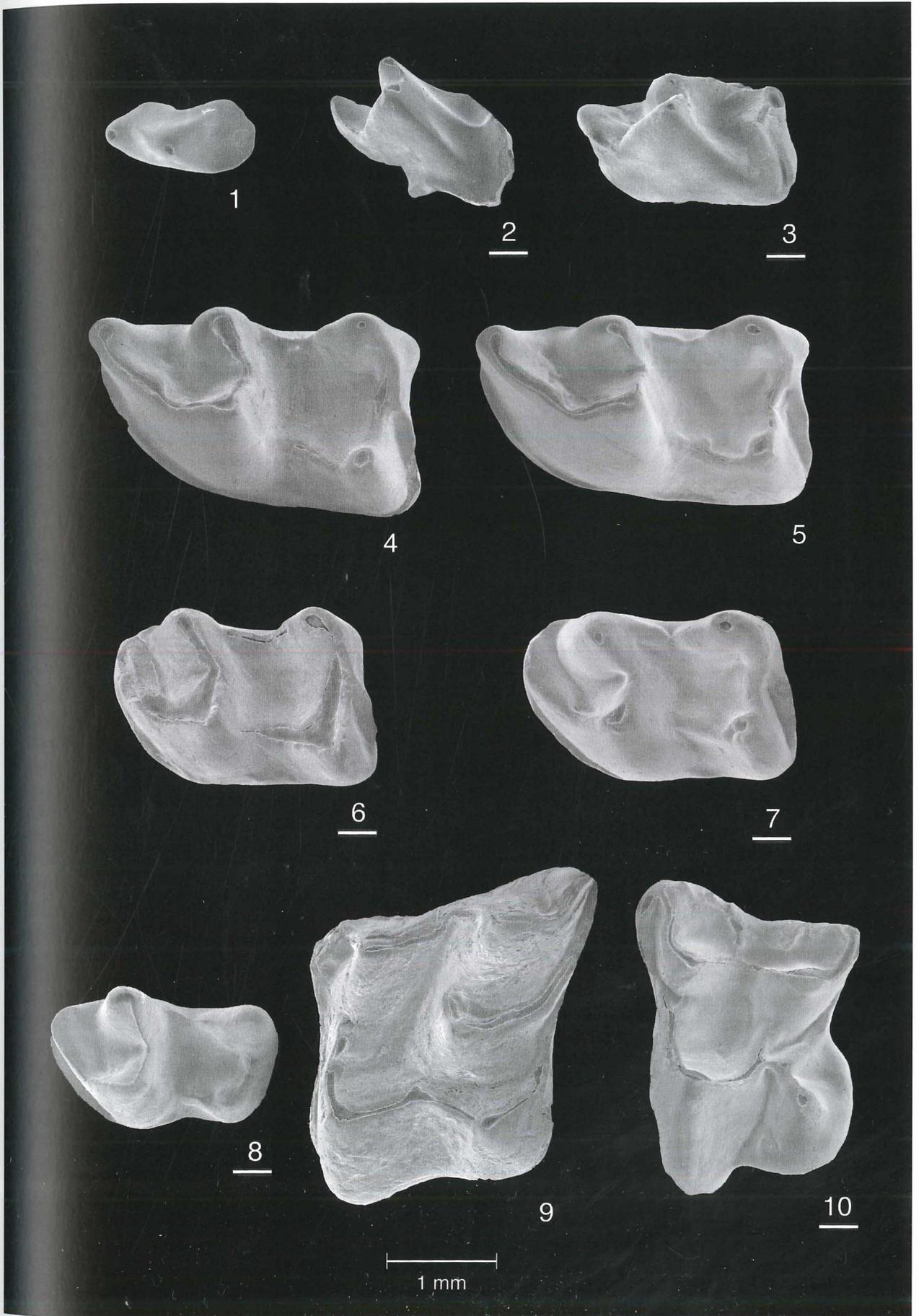
### *Galerix* sp.

- Fig. 9 M1 sin. (KOM/01)

### *Plesiosorex* sp.

- Fig. 10 M2 dext. (KRD 3/81)

PLATE 2



## PLATE 3

### *Plesiodimylus aff. crassidens*

- Fig. 1 P4 sin. (KRD 3/69)
- Fig. 2 M2 dext. (KRD 3/67)
- Fig. 3 p4 dext. (KRD 3/68)
- Fig. 4 m1 dext. (KRD 1/70)
- Fig. 5 m2 sin. (KRD 3/70)

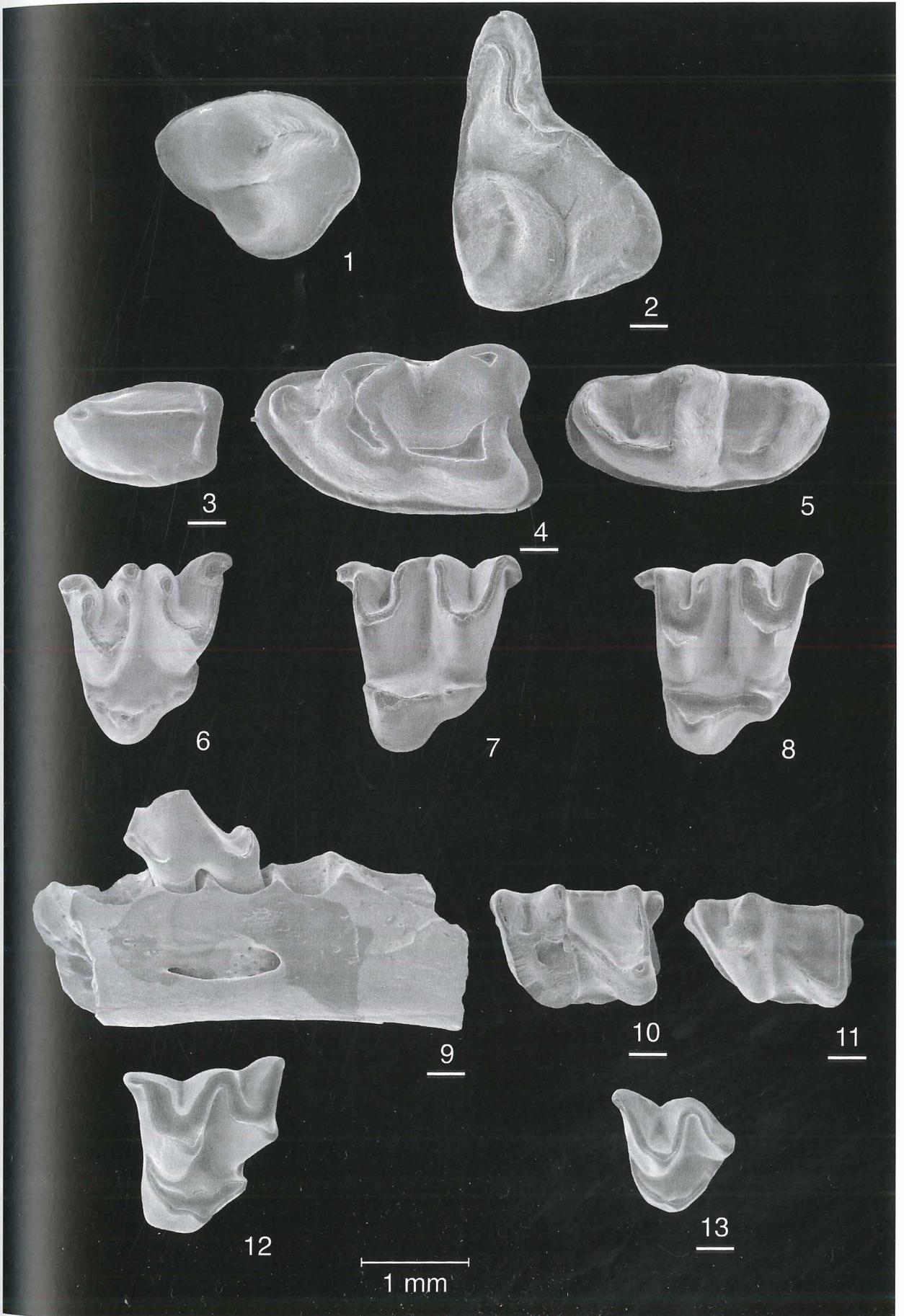
### *Desmanodon antiquus*

- Fig. 6 M2 sin. (KRD 1/61)
- Fig. 7 M2 sin. (KRD 3/71)
- Fig. 8 M2 sin. (KRD 3/72)
- Fig. 9 Mandible with p4 dext. (KRD 3/65, labial view)
- Fig. 10 m2 dext. (KRD 3/74)
- Fig. 11 m3 dext. (KRD 1/62)

### *Myxomygale cf. hutchisoni*

- Fig. 12 M2 sin. (KRD 3/78)
- Fig. 13 M3 dext. (KRD 3/62)

PLATE 3



## PLATE 4

### *Heterosorex* sp.

Fig. 1 I1 dext. (KRD 2/11)

Fig. 2 A1 dext. (KRD 2/1)

Fig. 3 Ax sin. (KRD 1/71)

Fig. 4 ax sin. (KRD 2/19)

Fig. 5 P4 dext. (KRD 2/4)

Fig. 6 M1 dext. (KRD 2/5)

Fig. 7 i1 sin. (KRD 2/13)

### *Lartetium* cf. *dehmi*

Fig. 8 P4 sin. (KRD 2/16)

Fig. 9 M1 sin. (KRD 1/72)

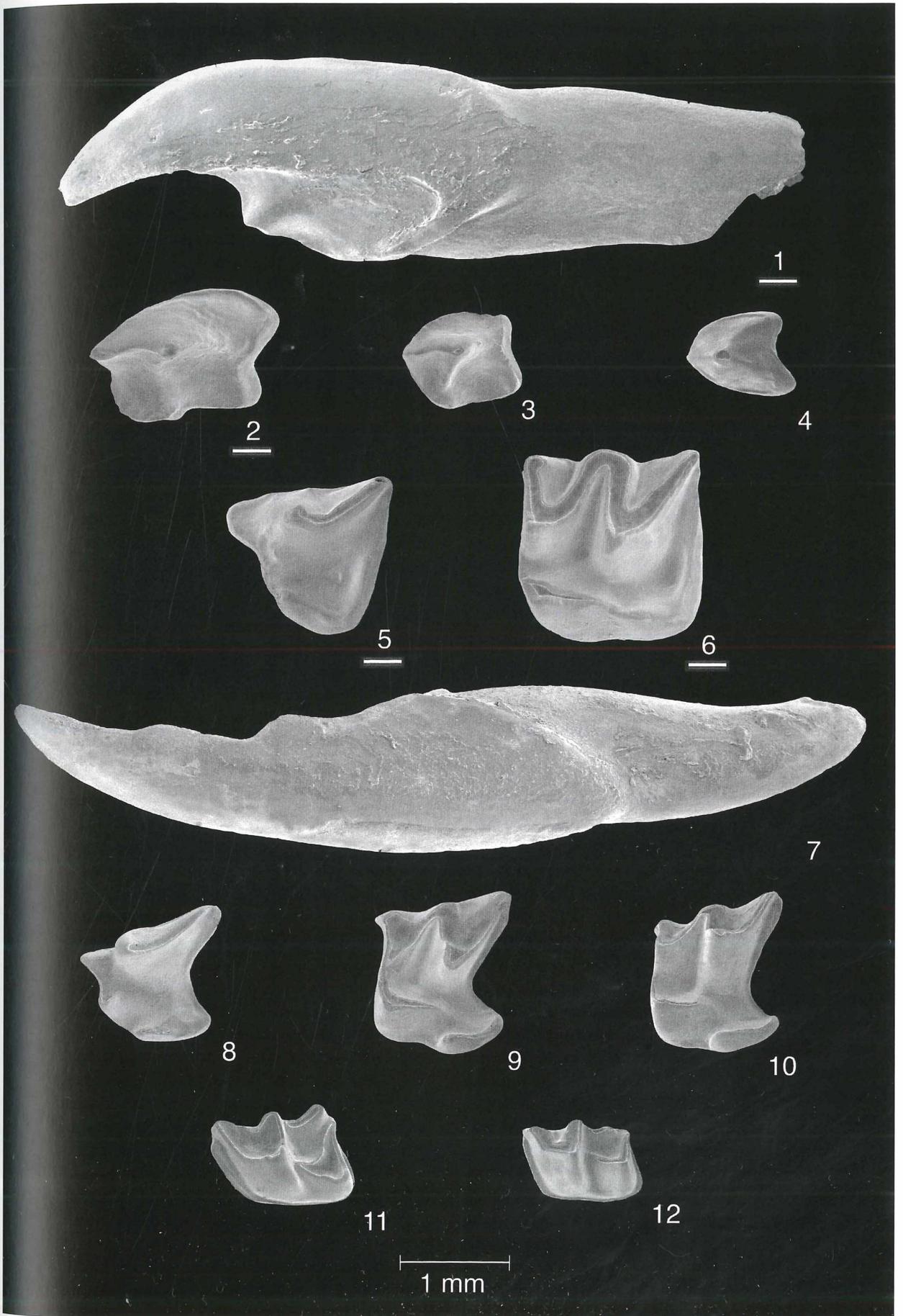
Fig. 10 M1 sin. (KRD 2/17)

Fig. 11 m2 sin. (KRD 1/74)

### *Paenelimnoecus* sp.

Fig. 12 m2 sin. (KRD 2/20)

PLATE 4



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