New finds of rodents and insectivores from the Upper Miocene at Plakias (Crete, Greece)

Hans de Bruijn · Constantin S. Doukas · Lars W. van den Hoek Ostende · Willem Jan Zachariasse

Abstract This paper provides new information on the Late Miocene small mammal assemblage from Plakias, which includes a re-evaluation of the rodents described in De Bruijn and Meulenkamp (Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, Series B, 75(1), 54–60, 1972) and a description of the rodents and insectivores collected in 2011. Combined, they show a quite diverse fauna, dominated by the eomyid *Eomyops* cf. *catalaunicus*. The new collection yielded a hitherto unknown genus of murid (Cricetinae gen. et sp. indet), which brings, combined with *Eumyarion leemanni* and *Cricetulodon cretensis*, the number of murids on three. The previous identifications of the scuirids and glirids have been revised. Insectivores, not know from the original collection, are represented by Erinaceinae gen. et sp. indet, *Lantanotherium sanmigueli* and *Paenelimnoecus* sp. The assemblage is tentatively correlated to the lower part of MN 9, with an estimated age of ∼9.9 Ma.

Keywords Late Miocene · Rodentia · Insectivora · Crete

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Introduction

While attending a conference on Crete in 2009 Albert van der Meulen, Constantin Doukas and the first author (HdB) revisited the fossil locality of Plakias (Fig. 1) that yielded some small mammal remains in the 1970s. We then decided to enlarge the sample the next summer.

Although the old and the new collections both come from the same small outcrop (Fig. 2), the composition of the two samples is quite different. The old collection contains abundant fish teeth, but these are rare in the new collection. Among the mammalian remains in the old collection three out of the eight specimens are sciurids, while eomyids and insectivores are absent. In contrast, the dominating species in the new collection is an eomyid and insectivores are present, whereas sciurids and the murid that dominates the original sample are absent. Since the local situation has changed due to building activity during the 40 years that elapsed between our two visits to Plakias, it is conceivable that the two collections come from slightly different stratigraphic levels. However, the 25 cm thick grayish silty clay bed sampled in 2010 seems to be the only bed that contains vertebrate remains. Therefore, we shall treat the two samples as coming from the same site.

Methods

The collection of 2011 was recovered by wet-screening about 2 tons of fossiliferous marl on a set of sieves (finest mesh 0.5 mm.) using a water pump and four shower heads. Prior to the sieving process the marl was dried on the quay of the new fishing harbor that is situated about 2 km west of the village of Plakias. The residue obtained was treated
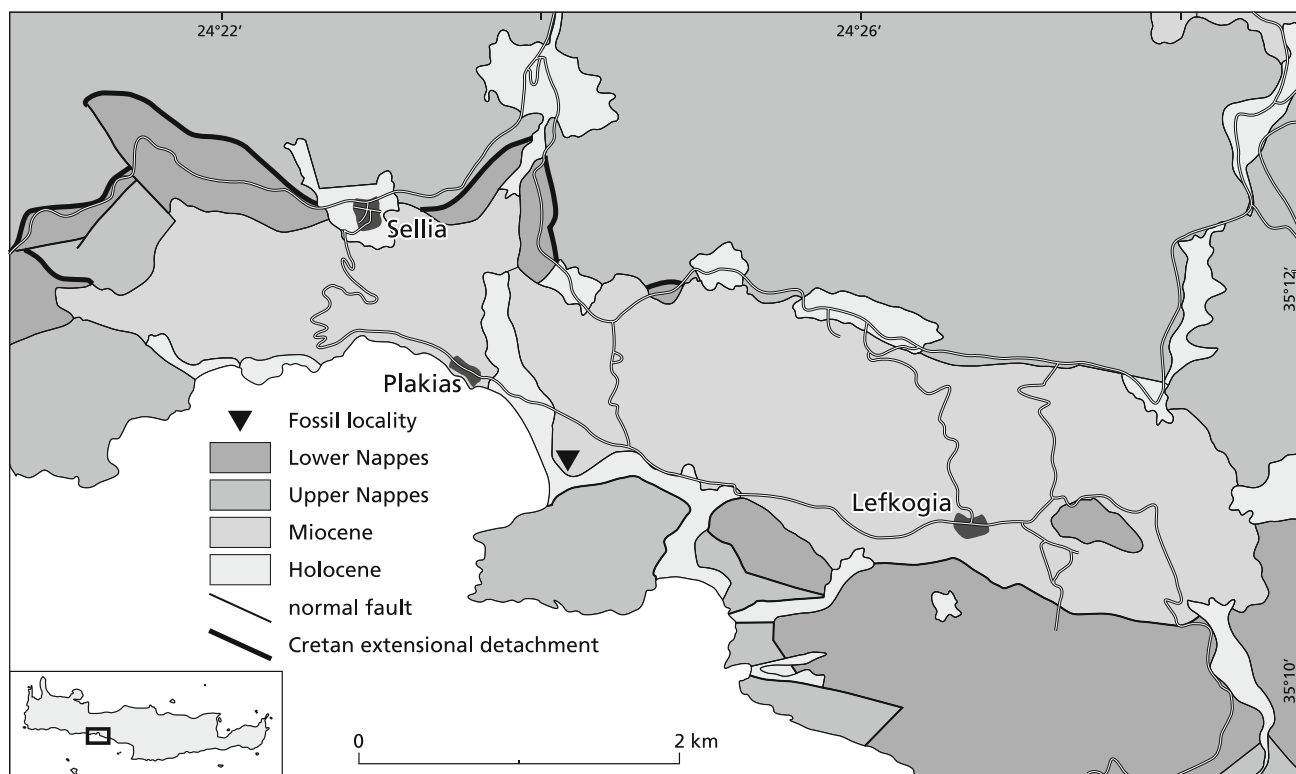
Fig. 1 Geologic map of the Plakias region (modified after IGME 1982); the location of the small mammal locality is indicated by a *triangle*

with diluted acetic acid in the laboratory in order to dissolve small limestone particles before it was sorted under the microscope.

The teeth on the plates are all figured as from the left side. If the original is from the right side its number on the plate has been underlined. The measurements of the cheek teeth were taken with a microscope with mechanical stage and measuring clocks. All measurements are given in 0.1 mm units. In order to obtain a measure for the relative abundance of the various species, we give the number of first and second upper, and lower molars (N) collected in the fauna list. If a species is represented by premolars or third molars only we have entered $N = !$. The material from Plakias is stored in the collection of the Department of Earth Sciences of the University of Utrecht, The Netherlands.

Setting and lithology

The Plakias Basin is floored by high-pressure, low-temperature metamorphic rocks of the Phyllite–Quartzite unit (IGME 1982). This unit is the highest tectonic unit of the Lower Nappes on Crete and is separated from the essentially non-metamorphic Upper Nappes by the Cretan extensional detachment (e.g., Fassoulas et al. 1994; Jolivet et al. 1996)

(Fig. 1). The Plakias Basin is filled with continental deposits characterized by alternations of silty clays, silts, (gravelly) sandstones, and conglomerates. Examples are to be found along the road to Plakias south of the junction with the road from Mariou to Mirthios, and along the road from Plakias to Sellia. Lignite levels and paleosols are rare, and the same holds true for fossils. The conglomerates are clast-supported and poorly sorted, and often show an erosive base. Occasionally, they show cross-bedding. Pebbles are (sub) rounded and derived from both the Lower and the Upper Nappes units. Contacts between basin fill and basement are mostly faulted (IGME 1982). A stratigraphic contact seems to be exposed in a small outcrop along the southern margin of the basin at 35°10.557′N–24°25.775′E. Here, unsorted boulder-conglomerates of local provenance are in faulted contact with and overlie metamorphic basement unless this basement represents a huge and partly exposed block. The thickness of the basin fill along the northern margin is ∼230 m as calculated from dip readings (012°–27°; $n = 5$) along the road from Plakias to Sellia at 200 m above sea level. The Plakias Basin is likely a half-graben with a basin-bounding normal fault in the north.

The small mammal remains are derived from grayish clays overlying beige to brown colored clays with calcretes in a shallow gully complex on a partly covered dipslope to the southeast of Plakias (35°11.073′N–24°24.181′E) (see

Fig. 2 The Plakias fossil mammal locality viewed from the west. *Stippled line* indicates top of paleosol. Samples were taken from the grayish clay directly overlying the paleosol

Figs. 1, 2). The dip of the strata is 10–20° to the NW (290°). The sampled clay interval is 25 cm thick and contains plant remains and scattered fragments and whole specimens of fresh-water molluscs. Identified molluscs belong to the fresh-water gastropods *Planorbis* and *Brotia*. The beige to brown-colored clays with calcretes represent a paleosol of ≥70 cm. Silty clays and silts with a thin lignite layer presumably older than the paleosol are exposed ~50 m to the NE on the same dipslope. These and other fine-grained continental deposits in the Plakias Basin are interpreted as floodplain deposits with the conglomerates and (gravelly) sandstones representing channel-belt sediments. The stratigraphic position of the sampled location is difficult to assess, but its proximity to the (faulted) southern margin renders it likely that the bed with small mammal remains belongs the basal part of the basin fill.

Systematic palaeontology

Erinaceomorpha Gregory, 1910
Erinaceidae Fischer, 1814

Erinaceinae Fischer, 1814

Erinaceinae indet.
Fig. 3, no 1–7

Material and measurements

One I1 sin. (PL.510.601), one, I2 sin. (?) (PL.510.602), one C sin. (PL.510.603; 15.3 × 8.1), one P1 sin. (?) (PL.510.604; 10.8 × 7.6), one i1sin. (?) (PL.510.605), one i2 dext. (?)(PL.510.606), m2 sin. (PL.510.607; 38.4 × 25.6).

Description

I1: The first incisor forms pointed hook. The crown is slightly curved, the curvature continuing into the strong root. The posterior flank bears a central rib. The root is distomedially flattened.

I2(?): The crown is triangular in distal view, with a sub-elliptical occlusal outline. There is a faint rib on the posteromedial side, and a patch of anteromedial cingulum.
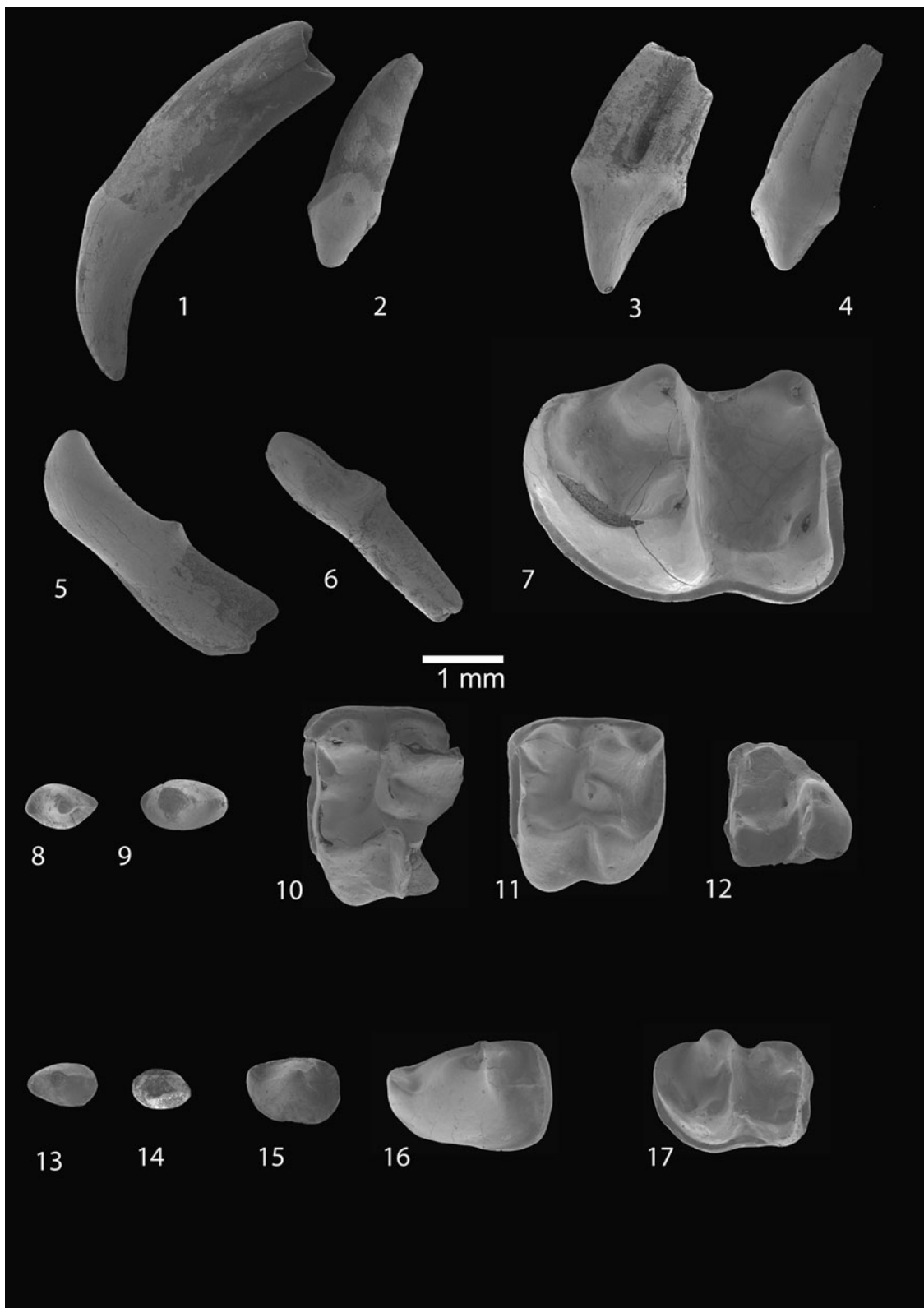
Fig. 3 Erinaceinae indet.: **1** PL.510.601 I1 sin.; **2** PL.510.602 I2 sin.(?); **3** PL.510.603C sin.; **4** PL.510.604 P1 sin.(?); **5** PL.510.605 i1 sin.(?); **6** PL.510.606 i2 dext.(?); **7** PL.510.607 m2 sin. *Lantanotherium sanmigueli*: **8** PL.510.611 P1 dext,; **9** PL.510.612 P2 dext.; **10** PL.510.613 M1 sin.; **11** PL.510.614 M2 sin.; **12** PL.510.615 M3 sin.; **13** PL.510.616 p1 sin.; **14** PL.510.617 p2 dext.; **15** PL.510.618 p3 sin.; **16** PL.510.621 p4 sin.; **17** PL.510.623 m2 sin

C: The crown is narrow and pointed, triangular in side view. The anterior face is rounded; there is a sharp posterocrista. The canine has two roots that are fused over their entire length.

P1 (?): The outline of the occlusal surface is elliptical. Like the canine, the side view of the premolar is triangular. The crown is, however, much lower and less pointed; the posterocrista is less sharp. The two roots are fused. A groove indicating the separate roots is visible over most of its length, but near the base of the root the fusion is complete.

i1 (?): The crown is large and pointed. The anterior face is convex. It bends backwards to form a long straight part, in line with the crown. The posterior flank is concave, and ends in a short talon. The strong root is elliptical in cross section.

i2 (?): The large crown is spatulate. The posterior face is concave. It presents a large talon which is triangular in occlusal view. At about one-third of our unworn specimen, there is a distal extension at the point where the talon starts bending backwards. The strong root is distomedially flattened.

m2: The occlusal outline is rectangular. Trigonid and talonid are of similar length and width. The paralophid is low, ending in a blade-like paraconid. A pronounced cingulum, starting at the anterior flank of the paraconid, runs continuously along the labial side, and becomes even wider at the posterior side. Here, it slopes up, ending against the hypolophid where it meets the posterior arm of the entoconid.

Remarks

The presence of Erinaceinae is indicated by an m2. Apart from that, elements of the anterior dentition have been found, which, based on the unworn state, seem to have belonged to a single individual. The molar morphology of the spiny hedgehogs is notoriously conservative. Furthermore, the taxonomy is largely unsolved (see Ziegler (2005) for a discussion). The Plakias species appears to have been relatively small, its measurements lying below those of *Mioechinus* sp. from several German Middle Miocene fissures (Ziegler 2005), and of "*Postpalerinaceus*" *intermedius* from Sansan (Engesser 2009) (which according to Ziegler (2005) is not referable to *Postpalerinaceus*).

Galericinae Pomel, 1848
Lantanotherium Filhol, 1888
Lantanotherium sanmigueli Villalta and Crusafont, 1944
Fig. 3, 8–17

Material and measurements

One P1 dext. (PL.510.611; 9.0 × 5.6), one P2 dext. (PL.510.612; 10.7 × 6.2), one M1 sin. (PL.510.613; 19.5 × 24.2), one M2 sin. (PL.510.614; 18.8 × 21.3), one M3 sin. (PL.510.615; 15.8 × 15.0), one p1 sin. (PL.510.616; 8.4 × 6.1), one p2 dext. (PL.510.617; 7.2 × 4.9), three p3 sin. (PL.510.618-20 11.3 × 6.9; 11.6 × 7.9; 11.1 × 8.3), one p4 sin. (PL.510.621; 20.6 × 14.0), one p4 dext. (PL.510.622; 18.7 × 13.5), one m2 sin. (PL.510.623; 1.97 × 12.7).

Description

P1: The outline of the occlusal surface is elliptical. The tip lies in the center of the premolar; there is a distinct posterocrista. The posterocrista ends at a tiny flattening. There is an equally small cusplet at the front of the P1. The only root is directed almost straight downwards.

P2: The outline of the occlusal surface is sub-elliptical. The tip of the cusp lies in the center of the unicuspid. The posterocrista is faint and ends in a tiny posterior cusplet. There is a small flattening c.q patch of cingulum on the anterolingual flank of the cusp. There were two roots, but these are broken off just below the crown.

M1: The only specimen is severely damaged on its posterior side, missing most of the hypocone and the posterior end of the metacone. The protocone is the largest cusp. On the labial side, the metacone is clearly larger than the paracone. The protoconule is well-defined. The metaconule is conical and lies near the center of the molar. Its narrow wear facet points toward the anterior flank of the metacone. The cingulum is well developed on the anterior and labial sides, with the parastyle as a cusp on the cingulum, directly anterior of the paracone.

M2: The occlusal outline is sub-square, the anterior part of the molar being only somewhat wider than the posterior part. The protocone is the largest cusp, with paracone, metacone, and hypocone being only mildly smaller. The protoconule is well defined, lying at the end of the anterior arm of the protocone, anterolingually of the paracone. The metaconule lies just behind the center of the molar. It is comma shaped; only having an anterior arm connecting to the anterolingual side of the metacone. The posterior arm of the metacone bends and extends to the posterolabial corner of the M2. A ridge, starting halfway down the posterior flank of the hypocone, ends low against the metastyle, bordering the back of the molar. There are well-developed cingulums on the anterior and labial sides. The parastyle appears as a small cusp on the anterior cingulum, directly in front of the paracone.

M3: The occlusal outline form a quarter of a circle, the anterior and lingual sides being straight and the posterolabial side rounded. The trigon is clearly recognizable, with a large protocone and paracone. The metacone itself is clearly smaller, but it is directly connected to a large, bulbous hypocone, which forms the posterior part of the

M3. There is a short cingulum between the base of the protocone and the hypocone. The anterior cingulum is well developed, ending in a low parastyle.

p1: This small element is interpreted as the p1 on the basis of its size and the oblique root. The outline of the occlusal surface is sub-oval, its largest width lying behind the middle of the premolar. The tip of the main cusp lies just in front of the center of the tooth. It forms the starting point of a faint rib, directly straight backwards. The only root is slightly directed backwards.

p2: The outline of the occlusal surface is elliptical. The tip of the only cusp lies in the front part of the premolar. It bears a sharp posterocristid. The only root is direct downwards.

p3: The front of the premolar is somewhat narrower than the back. The protoconid is the main cusp, and takes a central position. In the anterolingual corner, lies a very small paraconid which displays a paralophid in two of the three specimens. One of these also has a small bulge appearing on the posterolingual flank of the protoconid (incipient metaconid). Posteriorly, the premolar is bordered by a low ridge, separated from the protoconid by a narrow groove. The p3 has two roots.

p4: The p4 consists mainly of the high, large protoconid. The low paraconid lies anterolingually to the protoconid, and connects to its base by a short crest. The metaconid appears as a bulge on the posterolingual side of the protoconid. The premolars are bordered at the back by a short talonid, which in its turn is bordered posteriorly by a low ridge.

m2: The outline of the occlusal surface is sub-rectangular, the posterior part being narrower than the anterior part. The talonid is somewhat shorter and narrower than the trigonid. The paraconid is completely incorporated in the long, bladelike paralophid. There is a strong cingulum, which runs from the anterolingual corner to the base of the hypoconid. The posterior cingulum is also well developed. It is short, lying along the base of the hypolophid.

Remarks

Apart from the easily recognizable molars, a series of premolars have been found. The correct tooth position of these is more difficult to determine. Engesser (2009) described and illustrated the premolars of *Lantanotherium sansaniense*. However, this species has a reduced dental formula, missing the p1. Given the number of different types of premolars, we presume that the Plakias *Lantanotherium* had a more complete dentition. Ziegler (2006) did not have the anterior part of the premolar row of *L. sanmigueli*, but described several edentulous mandibles. From these it is clear that the p1 had a single oblique root, the p2 was also single-rooted, whereas the p3 had two

roots. Combining the two data, we came to our interpretation. This suggests that the P3 is missing in the assemblage. Indeed, none of the elements found even closely resembles the P3 figured by Engesser (2009, fig. 45f), which makes us confident that the *Lantanotherium* from Plakias had a complete dental formula. In this it agrees with the descriptions of *L. sanmigueli* from Austria (Ziegler 2006), a species with which it also agrees in size. *Lantanotherium sanmigueli* is a small-sized representative of the genus, which appears for the first time at the beginning of the Late Miocene.

Soricomorpha Gregory, 1910
Soricidae Fischer, 1814
Paenelimnoecus Baudelot, 1972
cf. *Paenelimnoecus*

Material and measurements

One m1 (PL.510.630; 11.9×7.4).

Description

m1: The trigonid is only somewhat narrower and longer than the talonid. The paraconid stands far to the front, leaving the trigonid basin very open. The oblique cristid ends rather lingually, at about two-thirds of the protolophid. The entoconid is strongly reduced, but due to slight damage, the degree of reduction cannot be assessed. The hypolophid is only slightly curved near its end and ends well short of the posterolingual corner of the m1. The anterior and posterior cingulum are strong, widest at the lingual and labial side, respectively. The development of the labial cingulum cannot be assessed due to damage.

Remarks

Usually shrews cannot be identified on the basis of a single molar. However, the reduced entoconid strongly suggests that the specimen can be attributed to the genus *Paenelimnoecus*. However, given the slight damage in the entoconid area, this identification must be treated with some caution.

Apart from the m1, the assemblage had yielded an m2, which, unfortunately, did not survive the preparations for the electron microscope. Also multiple fragments were found. It is well possible and even likely that more species of shrews were present in the Plakias fauna, but this can on the basis of the present material not be ascertained.

Rodentia Bowdich, 1821
Sciuridae Fischer, 1817
cf. *Hylopetes* Thomas, 1908

cf. *Hylopetes* sp.

(Fig. 1, no. 1 and 2 in De Bruijn and Meulenkamp (1972))

Synonyms: *Spermophilinus* cf. *bredai* and *Blackia*? sp. in De Bruijn and Meulenkamp (1972)

Material and measurements

One D4 sin. (PL.11; 15.2 × 17.0), one M3 sin. (PL.20; 19.7 × 18.7).

Remarks

The collection from Plakias described by De Bruijn and Meulenkamp (1972) contains three cheek teeth of sciurids: a D4, an M3 and an m2. The D4 (Fig. 1, no. 1) was assigned to the ground squirrel *Spermophilinus* cf. *bredai*, the M3 (Fig. 1, no. 2) and the m2 (Fig. 1, no. 3) with a question mark to the flying squirrels *Blackia* and *Forsythia*. We now consider the former two to belong to the same species, because the valley between the anteroloph and the protoloph of the D4 and M3 is unusually wide for a sciurid and much wider than in *Spermophilinus*. Moreover, the occlusal surface of both teeth is smooth, yet irregular, and the size difference between the D4 and the M3 is of the order of magnitude that one would expect it to be in one species. Comparison with extant and fossil sciurid material in the Utrecht collection revealed that the teeth from Plakias show a striking similarity in morphology to those of the extant red-cheeked flying squirrel *Hylopetes spadiceus* from Burma. We therefore tentatively reallocate these two teeth to the genus *Hylopetes*.

Blackia Mein, 1970
cf. *Blackia* sp.
(Fig. 1, no. 3 in De Bruijn and Meulenkamp, 1972)
Synonymy: *Forsythia*? sp. in De Bruijn and Meulenkamp (1972)

Material and measurements

One m2 sin. (PL.15; 13.1 × 14.2).

Remarks

This small rather worn m2 with extremely narrow trigonid basin, oblique ectolophid and labially situated hypoconid is now considered to belong to the genus *Blackia*. This small flying squirrel ranges throughout the Neogene of Europe showing very little change in its dentition through time.

Gliridae Muirhead, 1819
Glirulus (*Paraglirulus*) Engesser, 1972

Glirulus (*Paraglirulus*) *werenfelsi* Engesser, 1972
(Fig. 4, 17 and 18, De Bruijn and Meulenkamp (1972), fig. 1, no. 10)
Type locality: Anwil, MN7/8, Switzerland
Synonym: *Glirudinus* sp. In: De Bruijn and Meulenkamp (1972).

Material and measurements

One M2 dext. (PL.510.521; 14.0 × 14.6), One m2 dext. (PL.510.523; 14.0 × 13.6), one m3 sin. (PL.40; 13.1 × 12.4).

Description

M2: The dental pattern of the M2 consists of nine rather straight parallel ridges of different length. These are from the front to the back: the anteroloph, the anterior extra ridge, the protoloph, an extra ridge between the protoloph and the long anterior centroloph, the anterior centroloph, the posterior centroloph, the metaloph, the posterior extra ridge and the posteroloph. Although the endoloph is basically complete, there is a shallow notch between the lingual end of the anteroloph and the lingual end of the protoloph. The lingual side of the tooth is ornamented.

m2: The dental pattern of the m2 consists of ten ridges of different length. These are from the front to the back: the anterolophid, two anterior extra ridges, the metalophid, an extra ridge between the metalophid and the centrolophid, a long centrolophid, an extra ridge between the centrolophid and the hypolophid, the posterior extra ridge and the posterolophid.

m3: The dental pattern of the m3 consists of only nine ridges, because, in contrast to the m2, there is only one anterior extra ridge. Otherwise the pattern of the m3 is very similar to that of the m2.

Discussion

The old collection from Plakias contains one m3 of a glirid only (De Bruijn and Meulenkamp (1972), fig. 1, no. 10), which was at the time identified as *Glirudinus* sp. The new collection contains two more specimens of the same species, which is now recognized to be *Glirulus* (*Paraglirulus*) *werenfelsi* Engesser, 1972. The *Glirulus* (*Paraglirulus*) *werenfelsi* teeth from Plakias have a very similar morphology as the ones described from a number of localities in Central Europe (Engesser 1972; Daxner-Höck and Höck 2009), but are somewhat larger. Daxner-Höck and Höck (2009) maintain *Paraglirulus* as a genus separate from *Glirulus* on the basis of size difference only. We do not follow this usage. For reasons for this difference in appreciation see Van der Meulen and De Bruijn (1982).
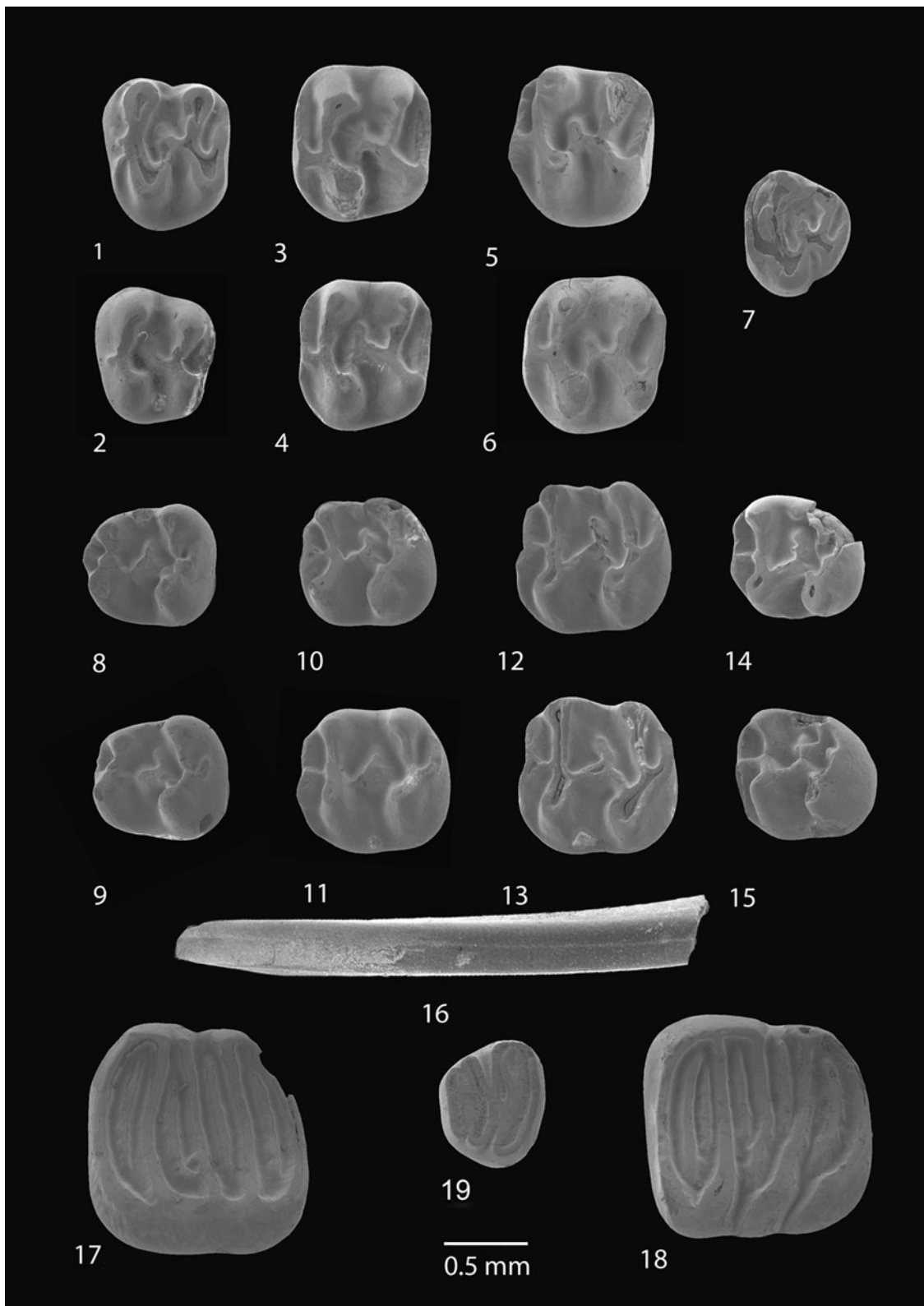
Fig. 4 *Eomyops* cf. *catalaunicus*: **1** PL.10.591 P4 sin.; **2** PL.10.592 P4 sin.; **3** PL.10.571 M1-2 sin.; **4** PL.10.572 M1-2 sin.; **5** PL.10.573 M1-2 dext.; **6** PL.10.574 M1-2 sin.; **7** PL.10.587 M3 sin.; **8** PL.10.531 p4 sin.; **9** PL.10.532 p4 sin.; **10** PL.10.541 m1-2 sin.; **11** PL.10.542 m1-2 sin.; **12** PL.10.543 m1-2 sin.; **13** PL.10.544 m1-2 sin.; **14** PL.10.561 m3 sin.; **15** PL.10.562 m3 sin.; **16** I inf. sin. *Glirulus* (*Paraglirulus*) *werenfelsi*: **17** PL.10.521 M2 dext.; **18** PL.10.523 m2 dext. Gliridae gen. et sp. indet.: **19** PL.10.5 28 p4 dext

Gliridae gen. et sp. indet.
(Fig. 4, 19)

Material and measurements

One p4 dext. (PL.10.528; 0.6 × 0.7).

Remarks

The dental pattern of this small worn tooth without inter-dental wear facets is difficult to interpret. We tentatively identify it as a p4 or d4, because it shows two notches on what seems to be the labial side. However, the homologies of the indistinct ridges are not clear and the roots are not preserved, so the identification remains uncertain. As the shape of the circumference of the occlusal surface differs from the p4 and d4 of *Glirulus* (*Paraglirulus*) *werenfelsi* in the literature, we list this specimen provisionally as Gliridae gen. et sp. indet.

Eomyidae Winge, 1887
Eomyops Engesser, 1979
Eomyops aff. *catalaunicus* (Hartenberger, 1966)
(Fig. 4)
Type locality: Can Llobateres, MN9, Spain

Material and measurements

Seven P4 (PL.510.591-597), twelve M1-2 (PL.510.571-583), one M3 (PL.510.587), eight p4 (PL.510.539), eighteen m1-2 (PL.510.541-558), four m3 (PL.510.561-564).

	Length		N	Width	
	R				
	Range	Mean		Mean	Range
P4	7.5–8.5	8.0	6	9.1	8.3–9.9
M1-2	8.0–9.2	8.8	12/11	10.2	9.8–10.8
M3	–	7.0	1	7.3	–
p4	7.6–8.7	8.0	8	7.6	7.1–7.9
m1-2	8.4–10.4	9.7	15/18	9.1	7.9–9.7
m3	8.4–9.1	8.6	4	8.1	7.7–8.5

Description

P4: The anteroloph of the P4 shows much variation. In some it is absent; in others, it has a weak lingual and labial branch. The protoloph, which connects the paracone to the protocone, basically forms the anterior margin of the occlusal surface. The short, thick mesoloph is directed towards the paracone. In one P4 the mesoloph bifurcates. The connection between the lingual end of the mesoloph and the protocone is much lower and weaker than its connection to the hypocone. The slightly forward-directed metaloph inserts on the anterior arm of the hypocone. The labial branch of the posteroloph varies in length. One P4 has a lingual branch of the posteroloph also.

M1-2: The anteroloph of the M1-2 usually has a straight labial branch and a weaker lingual branch that curves down to the base of the protocone. The protoloph inserts on the anterior arm of the protocone. The short mesoloph is directed towards the paracone. The connection between the lingual end of the mesoloph and the protocone is always much weaker than its connection to the hypocone. The slightly forward-directed metaloph inserts on the anterior arm of the hypocone. The rather long transverse posteroloph is separated from the metacone by a notch.

M3: The anterior part of the only M3 in the collection is, apart from the absence of the lingual branch of the anteroloph, very similar to the configuration of the homologous part of the M1 and M2. The hypocone is reduced to a mere cingulum that delimits the posteriorly situated sinus.

p4: The anterolophid of the p4 is reduced to a small anteroconid-like cusp that is situated on the central longitudinal axis of the occlusal surface. The short metalophid connects the metaconid to the protoconid. The mesolophid is thick, but short. Some p4 have a small mesostylid. The short hypolophid inserts on the posterior arm of the hypoconid.

m1-2: The lingual and labial branches of the antero-lophid have about the same length. The more or less transverse metalophid connects the metaconid to the pro-toconid. A mesolophid of variable length curves forwards toward the metaconid in many specimens, but in others it is transverse. Some of the M1-2 have a small mesostylid. The slightly posteriorly directed hypolophid inserts on the posterior arm of the hypoconid.

m3. The anterior part of the m3 is very similar to its homolog in the m1-2, but the posterior part shows a variable degree of reduction. The entoconid is incorporated into the posterolophid in some m3, but in one specimen identified as m3 it is prominent, while the posterolophid is isolated. The hypolophid is absent in one specimen, short and posteriorly directed in a second, and complete in a third.

Remarks

The new collection from Plakias is dominated by a small eomyid that is not present in the association from the same outcrop described by De Bruijn and Meulenkamp (1972). The small eomyids from the Miocene and Pliocene of Eurasia and North America, allocated to *Eomyops*

Engesser, 1979, *Leptodontomys* Shotwell, 1956, *Pentabuneomys* Engesser, 1990, *Plesieomys* Qiu, 2006 and *Heteroeomys* Qiu, 2006 all show the basic bunodont dental pattern that characterizes unspecialized members of the family. Whether or not the genera *Eomyops* from Europe and *Leptodontomys* from North America are synonymous has been discussed at length by Hugueney and Mein (1968), Engesser (1972, 1979), Fahlbusch (1973) and Qiu (1994), but the issue remains unresolved. The recent creation of the genera *Plesieomys* and *Heteroeomys* by Qiu (2006) has, unfortunately, added substantially to the complexity of the generic identification of the Neogene Holarctic eomyids. Ruiz-Sanchez et al. (2009), following Engesser (1979), suggested that the ornamentation of the enamel surface of the lower incisor, which has been reported as smooth in *Leptodontomys* and with two parallel longitudinal ridges in *Eomyops*, might provide a useful tool to distinguish these genera. The incisors of *Pentabuneomys* from France and Switzerland and of *Plesieomys* and *Heteroeomys* from China are not known. Engesser (1979) created some confusion by describing the enamel surface of the lower incisor of *Eomyops* as crenulated, but figuring a specimen (Engesser 1972, Fig. 8b) of *E.* aff. *catalaunicus* with two parallel longitudinal ridges. In our opinion it is not a good idea to use the ornamentation of the incisors to distinguish genera, because in most samples the cheek teeth and the incisors do not occur associated, so the identification of the latter remains uncertain. Moreover, it seems that the ornamentation of the lower incisor differs between samples of *Eomyops* from Europe, because the ones of *E.* aff. *catalaunicus* from Plakias, described below, show one longitudinal ridge only (Fig. 4, 16) and Kälin (1997) states that there is no incisor with two longitudinal ridges in his sample from the type locality of *Eomyops hebeiseni* (Chatzloch), which probably means that the surface of the lower incisor of this species is smooth as in *Leptodontomys oregonensis* Shotwell, 1956 and in *L. lii* (Qiu 1996).

To date 10 Eurasian species of "*Eomyops*" s.l. have been formally named: *E. catalaunicus* (Hartenberger 1966), MN9 and *E. noeliae* Ruiz-Sanchez et al. MN5 from Spain, *E. oppligeri* Engesser, 1990, MN 8, and *E. hebeiseni* Kälin, 1997, MN5 from Switzerland, *E. bodvanus* Janossy, 1972, MN14 from Hungary and *Leptodontomys gansus* (Zheng and Li 1982), MN14?, *L. lii* (Qiu, 1996), MN8?, *L.* pusillus MN12?, *Plesieomys mirabilis* Qiu, 2006, MN12? and *Heteroeomys yunnanensis* Qiu, 2006, MN12? from China. The size ranges of the cheek teeth of these species show in many instances overlap or are expected to show overlap if more material from the type localities will become available. The cheek teeth of *E. hebeiseni* are larger than the others and those of *E. oppligeri* and *Leptodontomys pusillus* are somewhat smaller than the rest. The morphologic characteristics used to distinguish the

various species are all subject to individual variation and can therefore be used only if large collections are compared. Since these are not available from a number of type localities and because all the species basically show the same primitive dental pattern, we consider the Neogene eomyids from Eurasia oversplit on the genus, as well as on the species level and in need of revision.

Although the ornamentation of the lower incisor of the eomyid from Plakias is clearly different from the one of *E. catalaunicus* we refer our material with reservation to that species on the basis of similarity in size and morphology of the cheek teeth. Some specimens are remarkably bunodont, have a rather large mesocone (id) and a weak connection between the mesocone and the protocone in the M1-2 and thus resemble *Pentabuneomys*. This suggests that *Eomyops* and *Pentabuneomys* are closely related genera.

Muridae Illiger, 1811

Introduction

Eumyarioninae Ünay-Bayraktar, 1989
Eumyarion Thaler, 1966
Eumyarion leemanni (Hartenberger 1966)
Synonym: *Cotimus* sp. De Bruijn and Meulenkamp (1972)
(Fig. 5, 1–3)
Type locality: Can Llobateres

Material and measurements

One M1 sin. (PL.510.501 19.7 × 15.0), one M2 dext. (PL.510.504 13.6 × 13.1), one m3 sin. (PL.510.510 14.2 × 11.5).

Description

M1: The anterocone of the M1 is broad and indistinctly divided into two cusps. The long labial spur of the anterolophule connects labially to the anterocone. The protoloph and metaloph are more or less transverse. A thin ridge connects the metaloph to the posteroloph. The sinus is deep and strongly forward-directed.

M2: The strong anteroloph lacks a lingual branch. The transverse protoloph inserts on the protocone. There is a small "cusp" in the lingual part of the valley between the anteroloph and the protoloph. The mesoloph is connected to the metacone and the metaloph is constricted before reaching the hypocone. The posteroloph descends from the hypocone towards the metacone and shows a thickening halfway its length.

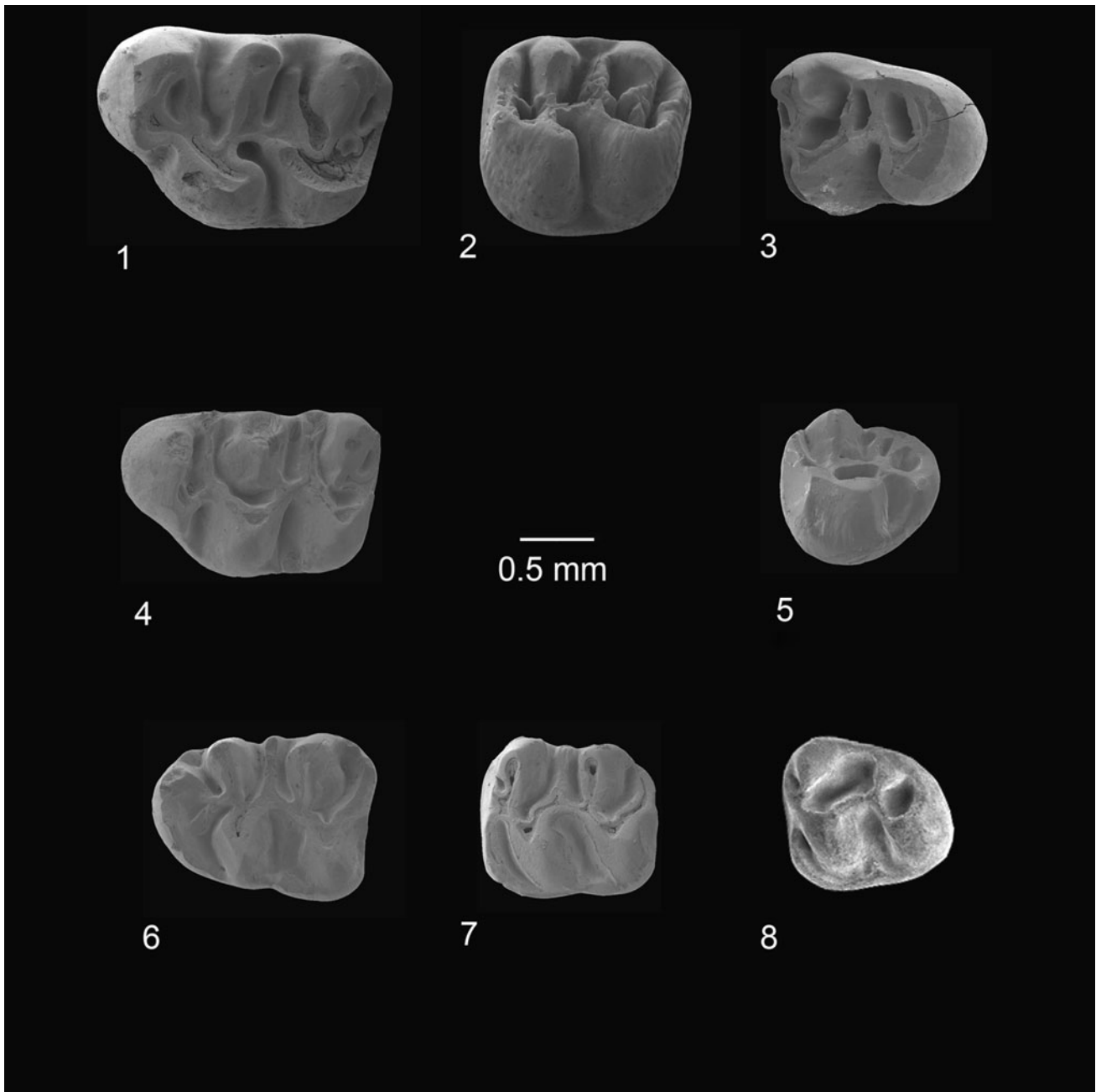*m3*: The anterior margin of the m3 is formed by the transverse metalophid. The labial branch of the

Fig. 5 *Eumyarion leemanni*: **1** PL.10.501 M1 sin.; **2** PL.10.504 M2 dext.; **3** PL.10. 510 m3 sin. Cricetinae gen. et sp. indet.: **4** PL.10.511 M1 dext.; **5** PL.10.516 M3 dext.; **6** PL.10.518 m1 sin.; **7** PL.10.520 m2 dext.; **8** PL.26 m3 sin

anterolophid is weak. The strong posterior arm of the protoconid reaches the complete entolophid. The transverse hypolophid and the strong posterolophid enclose a deep valley.

Remarks

The 1972 collection from Plakias contains two genera and species of Muridae. The fragmentary remains of the larger

of these (De Bruijn and Meulenkamp 1972, plate 1, figs. 8 and 9) were at the time identified as *Cotimus* sp., close to *C. leemanni* (Hartenberger 1966). Engesser (1979), however, showed that the North American genera *Cotimus* Black, 1961 and *Leidymys* Wood, 1936 are synonymous and differ from the European species previously allocated to *Cotimus*. for these Thaler (1966) introduced the genus *Eumyarion* (based on *Cricetodon medius* Lartet, 1851). Hence the correct name for these specimens from Plakias is

now *Eumyarion* sp. This species is represented in the new collection by material that allows identification to the species level. The few *Eumyarion* cheek teeth from Plakias match the specimens of *E. leemanni* from the type locality Can Llobateres in size, crown height and overall morphology. The minor irregularities observed in the upper teeth from Crete are not present in our comparative material, but are expected to be within the individual variation of the species.

Cricetinae Fischer, 1817

Introduction

Cricetulodon cretensis (De Bruijn and Meulenkamp 1972)
    Synonym: *Democricetodon affinis cretensis* De Bruijn and Meulenkamp, 1972 (Figured in De Bruijn and Meulenkamp, 1972, fig. 1 nr. 4–6).

Material and measurements

One M1 sin. (PL.23; 16.2 × 11.3; holotype), one M1 dext. (PL.24; 17.3 × 12.3), two fragmentary M1 (PL. 21, 22), one M2 sin. (PL.26; 13.3 × 12.4).
    For description see De Bruijn and Meulenkamp (1972).

Remarks

The few Cricetinae cheek teeth from Plakias clearly represent two different genera and species. Each of these shows characteristics that are reminiscent of their hypothetical ancestor *Democricetodon* as well as of the true Cricetinae. The smaller cricetid in the old Plakias collection was described as a subspecies of *Democricetodon affinis* (Schaub 1925), *D. affinis cretensis*. I (HdB) now see this action as a youthful sin, because the material, enigmatic though it may be, is inadequate to properly define an unspecialized hamster species. The m3 (op. cit. plate 1, fig. 7) originally allocated to this species is now referred to a third cricetine. The generic allocation of the "*Democricetodon*" material was, and still is, problematic. Unfortunately this species is not represented in the collection made in 2010. The problems in the generic allocation lie in: (1) the anterocone of the M1 is narrow, basically undivided and situated labially, (2) the protolophule 2 of the M1 and M2 is stronger than the protolophule 1 and connects the paracone to the anterior arm of the hypocone instead of to the posterior side of the protocone as in most cricetines. These unusual features occur in some cheek teeth of *Cricetulodon* also, but neither in *Democricetodon* nor in later cricetines. Although the material available is insufficient, we provisionally reallocate these specimens to *Cricetulodon*. Comparison with the smallest species of this

genus, *C. hartenbergeri* Freudenthal, 1967 shows that the teeth from Crete are somewhat smaller, have a narrower anterocone of the M1 and a stronger paracone-hypocone connection in the M1 and M2. Since this material was formally named in 1972, we suggest to maintain the subspecies name and to refer to this species as *Cricetulodon cretensis* (De Bruijn and Meulenkamp, 1972).

Cricetinae gen. et sp. indet.
(Fig. 5, 4–8)

Material and measurements

One M1 dext. (PL.10.511; 17.4 × 11.7), one M3 dext. (PL.10.516; 10.5 × 10.5), one m1 sin. (PL.10.518; 15.2 × 11.1), one m2 dext. (PL.10.520; 12.3 × 10.9), one m3 sin. (PL.26; 12.3 × 10.2).

Description

M1: The relatively wide M1 has a broad crescent-shaped anterocone. The anterolophule connects the protocone to the lingual side of the anterocone. The strong labial spur of the anterolophule is long and reaches the labial border of the occlusal surface. The large paracone and metacone leave little space for the parallel posteriorly directed protolophule 2 and metalophule 2. The strong mesoloph is long and reaches the labial border of the tooth. The thin posteroloph, the metacone and the metalophule 2 enclose a very small posterosinus.

M3: The protocone and the "new longitudinal ridge" enclose a deep pit. The short protolophule is transverse. The hypocone and metacone are incorporated into the posteroloph. The metalophule and mesoloph are thin ridges.

m1: The broad crescent-shaped anteroconid of the m1 is situated close to the protoconid/metaconid. The anterolophulid bifurcates halfway the metalophid and anteroconid. The strong transverse mesolophid is long and reaches the lingual border of the occlusal surface. The short metalopid and hypolophid are approximately transverse and insert labially on the anterior arm of the protoconid and hypoconid. The roots of the m1 are not preserved.

m2: The labial branch of the anterolophid is very strong, but the lingual branch is absent. The short metalophid and hypolophid are approximately transverse and insert on the anterior arm of the protoconid and hypoconid. The strong mesolophid reaches the lingual border of the occlusal surface. The roots of the m2 are not preserved.

m3: The m3 in the old collection (Fig. 1, nr. 7) now attributed to this species is unusual in having a weak lingual branch of the anterolophid preserved as well as a very

long labial branch of the anterolophid that extends as a labial cingulum all the way to the base of the hypoconid.

Remarks

The larger cricetine is represented by one m3 in the old collection (which was erroneously allocated to the smaller species in 1972) and one M1, one M3, one m1 and one m2 in the new collection. The anterocone and anteroconid of the wide first molars of this species are not divided, the labial spur of the anterolophule and the mesoloph of the M1 are very well developed and so is the mesolophid of the m1 and m2. Since the morphology of neither one of these teeth fits the diagnoses of any European genus, we briefly reviewed the literature on the Miocene to Recent Cricetinae from the Old World. To our astonishment the teeth from Plakias do not match the morphology of any of the twenty genera of small to medium-sized hamsters that are listed below in the order of their publication date.

Cricetulus Milne Edwards, 1867, *Phodopus* Miller, 1910, *Tcherskia* Ognev, 1914, *Paracricetulus* Young, 1927, *Cansumys* Allen, 1928, *Cricetinus* Zdanski, 1928, *Sinocricetus* Schaub, 1930, *Allocricetus* Schaub, 1930, *Allocricetulus* Archyropulo, 1932, *Neocricetodon* Schaub, 1934, *Nannocricetus* Schaub, 1934, *Cricetulodon* Hartenberger, 1966, *Kowalskia* Fahlbusch, 1969, *Pseudocricetus* Topachevski and Skorik, 1992, *Stylocricetus* Topachevski and Skorik, 1992, *Odessamys* Topachevski and Skorik, 1992, *Hypsocricetus* Daxner- Höck, 1992, *Chuanocricetus* Zheng, 1993, *Amblycricetus* Zheng, 1993 and *Apocricetus* Freudenthal et al. 1998.

In contrast to the specimens from Plakias, most if not all these genera have slender first molars that bear a double anterocone (id). The appalling number of generic names for what, judging by the figures, often seem to be animals with a similar dental morphology, suggests that a number of them may be synonymous. This has been established for *Karstocricetus* Kordos, (a synonym of *Kowalskia* according to Daxner-Höck et al. 1996), but the synonymy of *Kowalskia* and *Neocricetodon* suggested by Freudenthal et al. 1998 is not generally accepted. Flynn and Wu (pers. comm. 2011) were so kind to send me (HdB) pictures of unpublished new material from the type locality of the type species of *Neocricetodon*: *N. grangeri* Schaub, 1934. Comparison of these with the figures of *Kowalskia polonica*, the type species of *Kowalskia*, suggests that Freudenthal et al. (1998) are right in considering *Kowalskia* a junior synonym of *Neocricetodon*. A revision of the Late Neogene to Recent small and medium-sized hamsters based on dental morphology is badly needed, but far beyond the scope of this paper. However, our brief review shows that Plakias documents a stage of evolution of the Cricetinae that is not known from elsewhere.

The five cheek teeth described under the heading Cricetinae gen. et sp. indet. show a combination of characteristics that does not occur in any of the genera listed in the introduction. The single anterocone (id) of the relatively wide first molars, the single posteriorly directed protolophule and metalophule of the M1 and the short, almost transverse, metalophid and hypolophid of the m1, the exceptionally strong and long labial spur of the anterolophule and the mesoloph of the M1 are a unique combination of derived and primitive features. The reason not to name this hamster formally is that we consider it too poorly documented. Chances that more collecting will take place in the near future seem slim, because nothing has been undertaken during the 40 years that have elapsed after the discovery of the site.

The age of the Plakias fauna

The small mammal assemblage from Plakias consists of 48 first and second upper and lower molars. Forty-three of these are rodents, five are insectivores and lagomorphs are absent. Considering this limited number of specimens the assemblage is, with eight species of rodents and three species of insectivores, quite diverse. In spite of this diversity its correlation to the MN scale cannot be precise, because the taxa recognized have either long stratigraphic ranges or are not known from elsewhere. However, the co-occurrence of *Glirulus* (*Paraglirulus*) *werenfelsi*, *Eumyarion leemanni* and two true cricetinae with single anterocones in the M1 suggests a correlation with the lower part of MN9. The arrival of the true cricetinae seems to have taken place earlier in the eastern Mediterranean than in Spain, because the first record of *Cricetulodon* predates the *Hipparion*-event in Turkey (Ünay and de Bruijn 1984), while it postdates that event in Spain, so these immigrations are diachronous. Moreover, the morphology of the cricetine teeth from Plakias is more primitive than it is in the oldest ones from southwestern Europe.

The absence of Murinae in the extended collection firmly establishes Plakias as older than the *Progonomys*-event which, in analogy with the cricetine immigration, is expected to have taken place earlier in Greece than in Spain. Relevant in this context is that the first record of the genus *Progonomys* in locality 8A in the Sinaptepe composite section (Anatolia) has been dated between 10.00 and 9.75 Ma (Sen 2003). Unfortunately, there are no cricetines known from that section. Since there is no record of large mammals from the Plakias Basin we do not know whether or not the strata with small mammals antedates the arrival of *Hipparion*, which is dated in the Sinaptepe composite section between 10.75 and 10.0 Ma. The analysis of the extended collection thus corroborates the conclusion of De

Bruijn and Meulenkamp (1972) that the assemblage from Plakias is younger that the one from La Grive M (reference of MN7 + 8) and older than the one from Can Llobateres (reference of MN9). We now tentatively correlate the assemblage from Plakias with the lower part of MN9, which following Kappelman et al. (2003) implies an age of ~9.9 Ma.

An age of ~9.9 Ma is on the safe side of the maximum age of 10.4–10.3 Ma for the Plakias fauna, which is inferred from the tectonic setting of the basin: the oldest sediments on Crete with debris from the high-pressure, low-temperature metamorphic rocks of the Lower Nappes (Fig. 1) have an age of 10.4–10.3 Ma (Zachariasse et al. 2011). The Plakias Basin is floored by these metamorphic rocks, and thus postdates the exhumation of the footwall of the Cretan detachment (van Hinsbergen and Meulenkamp 2006; Zachariasse et al. 2011).

The age for the Plakias fauna can also be approached along a different line of reasoning. Firstly, the Plakias fauna is older than the Kastellios Hill fauna from central Crete because the latter fauna correlates to MN 10 (De Bruijn et al. 1992). Secondly, the sequence of Kastellios Hill accumulated in the South Heraklion Basin the formation of which is dated at ~9.6 Ma and related to a change from dominant N–S extension to E–W and N–S extension on Crete (Zachariasse et al. 2011). The formation of the Plakias Basin reflects the same change in the regional stress field and, therefore, may have formed at the same time as the South Heraklion Basin, i.e. at ~9.6 Ma. The reversed polarities in the lower part of the Kastellios Hill section (Duermeijer et al. 1998) then either correlates to Chron C4Ar.1r or C4Ar.2r by which C4Ar.1r is the most likely option because it allows the Plakias fauna to be older than 9.311 Ma (age for top of Chron C4Ar.1n in Hüsing et al. 2007) but younger than 9.6 Ma.

The implication of these age brackets is that the Murinae, which are absent in the Plakias fauna but present in the Kastellios Hill fauna (De Bruijn et al. 1971, 1992), invaded Crete not before 9.3 Ma, but if the true age of Plakias fauna is close to 9.6 Ma then they may have reached Crete earlier, at some time between 9.6 and 9.3 Ma. The first evidence for deep marine basins to the north of Crete dates back to 8.8 Ma (Zachariasse et al. 2011) and from that time Crete was probably inaccessible for many mammals.

The Murinae possibly originated in S.E Asia and arrived in Anatolia at about 9.9 Ma based on their first occurrence in strata that seem to correlate to a level just below Chron C5n.1n (Kappelman et al. 2003) (age for base is 9.937 Ma ± 0.008 in Hüsing et al. 2007). Their arrival in Spain seems therefore not much later than on Crete (Wessels 2009).

Fauna list

Erinaceomorpha

Erinaceidae

Erinaceinae gen. et sp. indet. ($N = 1$)
Lantanotherium sanmigueli ($N = 3$)

Soricomorpha

Soricidae

Paenelimnoecus sp. ($N = 1$)

Rodentia

Sciuridae

cf. *Hylopetes* sp. ($N = 1$)
cf. *Blackia* sp. ($N = 1$)

Gliridae

Glirulus (*Paraglirulus*) *werenfelsi* ($N = 2$)
Gliridae gen. et sp. indet. ($N = 1$)

Eomyidae

Eomyops aff. *Catalaunicus* ($N = 29$)

Muridae

Eumyarion leemanni ($N = 2$)
Cricetulodon cretensis ($N = 4$)
Cricetinae gen. et sp. indet. ($N = 3$)

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