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**NEW SPECIES OF KARYDOMYS (RODENTIA) FROM THE
MIOCENE OF CHIOS ISLAND (GREECE) AND PHYLOGENETIC
RELATIONSHIPS OF THIS RARE DEMOCRICETODONTINE
GENUS**

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7 **NEW SPECIES OF *KARYDOMYS* (RODENTIA) FROM THE MIOCENE**
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9 **OF CHIOS ISLAND (GREECE) AND PHYLOGENETIC**
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11 **RELATIONSHIPS OF THIS RARE DEMOCRICETODONTINE GENUS**
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14 **Abstract:** *Karydomys* is a rare and little diversified democricetodontine, of which only six
15 species are currently recognised. This group of rodents is ~~first recorded known since~~ in the
16 Early Miocene (MN3) in China and spread quickly after to Kazakhstan and Greece (MN 4).
17 *Karydomys* reached south-western and central Europe by early Middle Miocene times
18 (MN5), where it became extinct shortly thereafter (MN6). New findings from the Miocene of
19 Chios Island (north-eastern Aegean Sea) reveal the presence of a new species of *Karydomys*
20 in the Keramia Formation. ~~*Karydomys*~~ *K. strati* sp. nov. is characterized by the presence of a
21 labial spur on the anterolophule, the lack of anterior protolophule on the M1 and by the
22 presence of a double metalophule on the M2. A cladistics analysis involving all the species of
23 *Karydomys* and some closely related species of *Democricetodon* and *Cricetodon* ~~has been~~
24 ~~carried out. The results~~ show that *Karydomys* split early into two different lineages, an
25 “eastern stock”, ~~which that~~ includes the central Asian (~~*Karydomys*~~ *debruijni* and
26 ~~*Karydomys*~~ *dzerzhinskii*) and Greek (~~*Karydomys*~~ *symeonidisi*, ~~*Karydomys*~~ *boskosi* and
27 ~~*Karydomys*~~ *strati* sp. nov.) species, and a “western lineage”, which is constituted by the
28 western and central European species (~~*Karydomys*~~ *wigharti* and ~~*Karydomys*~~ *zapfei*). The
29 evolutionary stage of *Karydomys strati* sp. nov. suggests that the lowermost part of the
30 Keramia Formation, usually attributed to the Middle Miocene, is older than previously
31 thought.
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50 **Key words:** Mammalia, Cricetidae, *Karydomys*, ~~phylogeny~~ ~~cladistics~~, taxonomy, Miocene,
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INTRODUCTION

Asia Minor has been an important area for the exchange of faunas between Europe, Asia and Africa, especially during the ~~early-Early~~ Miocene (~~Rogl~~Rögl, 1999; Koufos et al, 2005). At that time, important dispersals from the East occurred through that area, deeply transforming the mammalian composition of Europe (Van der Made 1999; Agustí et al 2001). The faunal changes were particularly important for rodents, since the entrance of “modern” cricetids in Europe at the end of the Early Miocene disrupted the structure of communities ~~at the end of the Early Miocene~~, which, ~~had been till then, were~~ dominated by eomyids and glirids until then (Daams & Van der Meulen, 1984; Van der Meulen & Daams, 1992; Agustí et al 2001). The ~~entrance-appearance~~ of cricetids in Europe was, ~~nevertheless,~~ not the result of an isolated single dispersal event migration but instead occurred in a succession of events several successive waves, as shown by the timing of arrival of the three main groups of cricetids, the Democricetodontinae, Megacricetodontinae and Cricetodontinae (De Bruijn et al 1992; Theocharopoulos 2000; Van den Hoek Ostende et al 2015; Oliver & Peláez-Campomanes 2016). In order to fully understand ~~all these~~such faunal ~~migrations~~interchanges, it is important to improve our knowledge of the fossil record from key areas and develop phylogenetic hypotheses ~~of~~about the taxa involved in a robust chronological framework. In this way, the fossil record of small mammals from the ~~early-Early~~ and ~~middle-Middle~~ Miocene of the north-eastern Aegean island of Chios, at the crossroad between Anatolia and south-eastern Europe, is of key-critical importance for the establishment of a more precise biogeographic framework.

In the summer of 2010, two of us (RLA and FK) prospected in Chios Island. After sampling various levels in the Michalos’ pit and its surroundings, they were able to locate two layers with Miocene vertebrates (López-Antoñanzas & Knoll, 2011). The higher fossiliferous horizon was an arenaceous stratum that yielded only a cranial fragment of a

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6 large indeterminate mammal. ~~Nevertheless~~However, ~~the a~~ lower in the Keramia Formation
7 ~~one was a a~~ thin argillaceous lens ~~in the Keramia Formation that~~ produced a diverse
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10 vertebrate fauna after screen-washing and sorting, which motivated a return to the site in the
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12 summer of 2012 and the exploitation of the lens to near ~~its~~ exhaustion. Altogether, over two
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14 metric tons of rock were processed, obtaining as a result nearly 200 teeth of small mammals.
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16 In fact, even though remains of large mammals (comprising a phalange of an indeterminate
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18 ruminant, a possible tooth fragment of *Cainotherium* and another of *Sanitherium*) and
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20 reptilian jaw and osteoderm fragments were retrieved from this new spot, rodents and, to a
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22 lesser extent, lagomorphs and insectivores are best represented by far. Preliminary
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24 identification of the lagomorphs suggests the presence of *Albertona*. The insectivore record
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26 consists of galericines. Rodents include a wide range of taxa belonging to cricetids, glirids,
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28 sciurids and ctenodactylids. Among them, cricetids are the most abundant, in particular
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30 species belonging to genera usually present in the eastern Mediterranean region during the
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32 early Miocene, such as *Cricetodon*, *Megacricetodon* and *Democricetodon*, but remains of the
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34 ~~rare unusual~~ democricetodontine genus *Karydomys* were also found.

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36 *Karydomys* is a rare and little diversified democricetodontine, which shows a
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38 discontinuous record, geographically as well as chronologically. Its oldest record (*Karydomys*
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40 *debruijni*) comes from the early Miocene (MN3) of northern Xinjian (China) (Maridet et al.,
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42 2011). ~~This taxon~~The genus may have rapidly expanded its range westward, as its presence is
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44 attested shortly later in the early Miocene (MN4) of eastern Kazakhstan (*Karydomys*
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46 *dzerzhinskii*) (Kordikova and De Bruijn, 2001) and Greece (*Karydomys boskosi* and
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48 *Karydomys symeonidisi*) (Theocharopoulos, 2000). Some undescribed findings of *Karydomys*
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50 from the early Miocene (MN 4) of western Anatolia (Ünay & Goktas, 1999; Kaya et al.,
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52 2007) indicate that this area may well have been on a route between central Asia and Greece.
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54 *Karydomys* may have reached south-western (*Karydomys zapfei*) (Mein & Freudentahl 1981)
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and central Europe (*Karydomys wigharti*) (Mörs and Kalthoff, 2004, Prieto, 2012, 2013) by Middle Miocene times, where it became most probably extinct at about 13.8 Ma (Aa single M2 from the fissure filling Petersbuch 6; Prieto, 2012).

Because of its geographic position between Asia and Europe as well as its age, somewhat older than the first European occurrences known so far, the presence of *Karydomys* in the Keramia Formation ("Keramaria" in Besenecker, 1973) of Chios is not a trivial record. The aim of the present work is to provide a description of the teeth of the new species of *Karydomys* discovered from the Keramia Formation of Chios Island and seize the opportunity to ~~try and~~ shed light on the evolutionary history of this group of rodents by deciphering their phylogenetic relationships with other Democricetodontinae and representative Cricetodontinae, ~~and~~ touching upon the possible dispersal routes of this hamster.

GEOLOGICAL SETTING

Stratigraphical context

Chios Island is situated in the north-eastern part of the Aegean Sea. The continental Tertiary-Cenozoic sediments of Chios are located mainly in the southeastern part of the island, unconformably overlying Mesozoic strata (Fig. 1). The Neogene deposits have been subdivided by Besenecker (1973) into four lithostratigraphical units, which are from bottom to top: the Thymiana Formation (Early Miocene), Zyfia Formation (Early-Middle Miocene), Keramia Formation (Middle Miocene) and Nenita Formation (Middle Miocene-Pliocene).

The Keramia Formation is about 120 m thick (Kondopolous et al., 2011). It consists mainly of layers of green-reddish clay and silt with less important layers of green sandstones intercalated (Besenecker, 1973). The green and reddish colours are characteristic of this formation and make it easily recognizable in the field (Besenecker, 1973). Besides, the

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sediments of the Keramia Formation are clearly delimited by a light "Tuff-horizon" ~~below, on the base~~ and by the overlying white limestones of the Nenita Formation ~~on the top~~ (Besenecker, 1973).

Kondopoulou *et al.* (1993) conducted a magnetostratigraphical study in a 46 m-thick section of the Keramia Formation in the Michalos' pit area that included the three fossiliferous localities THA, THB and THC. The long reversal dominating the section was tentatively correlated ~~to~~ either with chron C5Br or chron C5Cr based on the biochronological age ~~given then suggested~~ by ~~the~~ mammals ~~found~~. Later on, Kondopoulou *et al.* (2011) provided some supplementary magnetostratigraphical data resulting from the sampling of the almost complete Keramia Formation in the Michalos section (about 120 m thickness), also including approximately 10 m of the Zayfa Formation at the bottom ~~of the section~~. Thus, they include presented information about the lower and uppermost parts of the section that was not considered in Kondopoulou *et al.* (1993). Even if the detailed magnetostratigraphical results study are is still pending publication (Kondopoulou *et al.* 2011), their preliminary interpretation of their results could be seem to be in agreement correlating with a correlation of the section ~~to with~~ the interval ~~including chron~~ C5Dr to ~~C5bn~~C5Bn (Hilgen *et al.*, 2012, fig. 29.9).

Palaeontological background and biochronology

All of the vertebrate specimens yielded so far by the Miocene layers of Chios (at least in modern history) come from the exposure of the Keramia Formation in or close to the brickyard quarry known as "Michalos", which is situated SSE of the village of Thymiana, about 8 km from Chios city. The first finding of vertebrate remains from Michalos' pit was made in 1924 by the geologist GeorgalasGeorgaleas, but Paraskevaidis (1940, 1955) was the first to publish on the Miocene vertebrate fauna from Chios (macromammals, *Sanitherium* and others, but also evidence of tortoises). Additional, but more cursory, observations on

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6 similar vertebrate remains (macromammal —particularly sanitheriid and bovid— but also
7 chelonian fragments) from the Neogene of the vicinity of Thymiana were published by
8 Kreatsas (1963). Palaeontological field-works in the Michalos area that were conducted in
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10 1967 and 1968 in the framework of a Germano-Hellenic project ~~led-contributed~~ to ~~improves~~
11 significantly ~~improvement improved of our the~~ understanding of the mammalian fauna from
12 the Keramia Formation (see Melentis & Tobien, 1967, 1968, Tobien, 1968, 1969, 1977,
13 1980, Rothausen, 1977, Lehmann & Tobien, 1995). In total, nine fossiliferous layers were
14 recognized at the end of 60's, Thy 1-9, ~~which were and~~ described by Rothausen (1977). Most
15 of the material collected then was fragmentary remains of bovids and giraffids, but a nearly
16 complete skull of *Gomphotherium angustidens* was also discovered (and is still remembered
17 locally!). Micromammals were also found, but were never described in detail and their
18 present whereabouts ~~are-is~~ unknown. The same holds true for the lizards, tortoises and fish
19 remains ~~also foundretrieved-along~~. Complementary studies on the vertebrate faunas from
20 Chios arose from Helleno-French field campaigns in 1991 and 1993 (Kondopoulou et al.,
21 1993; Koufos et al., 1995; Bonis et al., 1997a, 1997b, 1998; López-Antoñanzas et al., 2005).
22 In addition to the nine fossiliferous levels described by Rothausen (1973), three new levels
23 were found ~~in the 90's by the Hellenic French team on this occasion~~, "Thymiana A" (THA),
24 "Thymiana B" (THB) and "Thymiana C" (THC) (Kondopoulou *et al.*, 1993). Besides a few
25 interesting macromammalian remains (mostly of sanitheriid and bovid affinities), some of
26 them well preserved, these fieldworks resulted in the ~~collection-building up~~ of a rich
27 micromammal ~~fauna~~ collection, which is yet to be studied in its entirety.

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40 Our main fossiliferous layer is situated on the coast, about 340 ~~meters~~ SSW from the
41 main brick building. It does not correspond to any of the localities previously sampled. The
42 stratigraphical position of the new layer suggests it may be coeval with the most basal
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fossiliferous layers (Thy 1 and Thy 5), ~~but~~ older than the other ones. We name it informally Thy 0.

The mammalian fauna of the Keramia Formation is considered as from the biozone MN 5 (Mein, 1989; Steininger et al., 1989; Bruijn *et al.*, 1992; Bonis *et al.*, 1997a, 1997b; 1998; Bonis & Koufos, 1999; Made, 1999; Koufos, 2006). This ~~dating-age~~ is based both on the macromammals and the evolutionary stage and composition of the micromammal fauna, notably the cricetids. However, the macromammal remains from this area are fragmentary and the micromammals have never been properly described. In fact, only Tobien (1968) and Bonis *et al.* (1997a) listed the micromammals that they recognized and ~~only a~~ single group of rodents, the ctenodactylines, has been the object of a detailed study (López-Antoñanzas et al., 2005). Kondoupoulou *et al.* (1993) showed that the fossiliferous levels THA, THB and THC were included in a long reverse episode that, considering the MN5 age provided by the mammalian fauna, could be correlated with the Chron C5Br, which in turn provided an age of about 15.5 Ma (Koufos, 2006). For instance, the micromammals from THA and THC were supposed to be younger than ~~that those~~ of Aliveri (MN 4) but quite similar to the to that of Komotini (MN 5) assemblage (Bonis *et al.*, 1997a; Bonis and Koufos, 1999). Considering that our fossiliferous level Thymiana 0 is at the base of the Keramia Formation, it may be correlated with the Chron C5Cr, which would correspond to an Early Miocene age of 16.7-17.23 Ma.

MATERIAL AND METHODS

Remains of micromammals were obtained by screen washing almost 2 tons of sediment with a mesh ~~light~~ of 0.5 mm. First, second and third lower molars are designated as m1, m2 and m3, and first, second and third upper molars as M1, M2 and M3, respectively. The

terminology used in the tooth descriptions follows those of Freudenthal et al. (1994) and López-Antoñanzas et al. (2010). Measurements of the occlusal surface of the teeth (maximum length [L] and maximum width [W]) were obtained with a Nikon digital counter CM-6S measuring device, following the method of van de Weerd (1976) (Table 1). All measurements are given in millimetres. The teeth of the species of *Karydomys* described in this work were compared with [all](#) the ~~all~~ known species belonging to this genus. Scans and SEMs of the teeth of the specimens have been taken with a [CT-SCAN Nikon XT H-160](#) and a Scanning Electron Microscope FEI QUANTA 200.

All the species of *Karydomys* known to date were included in the ingroup. These are:

~~*Karydomys* *K. debruijni*, *Karydomys* *K. dzerzhinskii*, *Karydomys* *K. symeonidisi*, *Karydomys* *K. boskosi*, *Karydomys* *K. wigharti*, *Karydomys* *K. zapfei* and *Karydomys* *K. strati*, ~~sp. nov.~~~~

~~from Chios~~. In addition, a selection of closely related non-congeneric species were added to

the ingroup so as to test the monophyly of the genus *Karydomys* and to clear up its phylogenetic relationships with species currently attributed to *Democricetodon*, from which

Karydomys may have evolved, and *Cricetodon*. These are *Democricetodon anatolicus*,

~~*Democricetodon* *D. doukasi*, *Democricetodon* *D. gracilis*, *Democricetodon* *D. franconicus*,~~

~~*Democricetodon* *D. mutilus*, *Cricetodon versteegi*, *Cricetodon* *C. tobieni*, *Cricetodon* *C.*~~

~~*kasapligili*, *Cricetodon* *C. aliveriensis*, *Cricetodon* *C. trallesensis*, *Cricetodon* *C. orientalis*,~~

~~*Cricetodon* *C. meini*, *Cricetodon* *C. engesseri*, *Cricetodon* *C. hungaricus*, *Cricetodon* *C.*~~

~~*bolligeri*. *Eucricetodon wangae*, a primitive *Cricetidae* ~~*cricetid* rodent~~~~, was selected as

outgroup. A total of 32 phylogenetically informative characters (mainly of dental

morphology) have been coded (see appendix [S1-S4](#)). 19 characters are binary, whereas 13 are

multistate. The data matrix ([archived in the Dryad Digital Data Repository: López-](#)

[Antoñanzas et al. 2018](#)) ~~see appendix S2~~ was built using Mesquite [23.6-04](#) (Maddison and

Maddison 2009) and the analysis was run in TNT (Goloboff et al. 2008) with the “traditional

search” option (using TBR). Owing to the lack of a priori information, all characters were unordered and equally weighted (Fitch optimality criterion). As some species are known so far from only a few specimens, the influence of intraspecific variation in the scoring of the characters could not be assessed. Branch support was estimated through two complementary indices: Bremer Support (Bremer 1994) and Relative Bremer Support (Goloboff and Farris 2001).

All the specimens are provisionally stored at the University of Montpellier, Montpellier (France)

SYSTEMATIC PALAEOLOGY

Order RODENTIA Bowdich, 1821

Family CRICETIDAE Fischer von Waldheim, 1817

Subfamily DEMOCRICETODONTINAE Lindsay, 1987

Genus *KARYDOMYS* Theocharopoulos, 2000

Type species. *Karydomys symeonidisi* Theocharopoulos, 2000

Karydomys strati sp. nov.

[LSID:urn:lsid:zoobank.org:act:0958B82F-9788-4DE3-94EF-6287172E1103](https://zoobank.org/act:0958B82F-9788-4DE3-94EF-6287172E1103)

Figs 2-3

Derivatio nominis. From Stratus, ~~latinized~~ latinised form of Stratos (Greek: Στράτος), genitive. In honour of Stratos Asmanis in recognition of his warm-hearted hospitality during our work in the Michalos pit.

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Holotype. ~~ThyUM Thy~~ 0-30, a left M2. This and the paratype specimens are housed in the palaeontological collections of the University of Montpellier (Montpellier, France).

Paratypes. ~~ThyUM Thy~~ 0-9, left M1, ~~ThyUM Thy~~ 0-39, right m1; ~~ThyUM Thy~~ 0-2, right m2; ~~ThyUM Thy~~ 0-5, right m2; ~~ThyUM Thy~~ 0-145, right m3 (broken); ~~Thy 0-30, left M2;~~ ~~ThyUM Thy~~ 0-48 left M2; ~~ThyUM Thy~~ 0-54, left M2 (broken).

Type ~~locality~~ horizon and locality. Thymiana 0. Lowermost part of the Keramia Formation, SSE of the village of Thymiana, about 8 km from Chios city (Greece).

Age. late Early Miocene (MN4).

Diagnosis. Species of *Karydomys* characterized by having a backward paracone spur and long and narrow mesolophids on the M1 and M2, having labial spur of the anterolophule and lacking anterior protolophule and metalophule on the M1 but having double protolophules and metalophules on the M2; lower molars with ectomesolophid and long and narrow mesolophids.

Karydomys strati differs from ~~*Karydomys-Karydomys*~~ *debruijini* in lacking the posterior metalophulid on the m1, in having a well-developed ectomesolophid on some m2, a strong posterior spur of the paracone on the M1 and M2 and a double metalophule on the M2 (whereas it is either anteriorly connected or absent in ~~*Karydomys-Karydomys-*~~ *debruijini*). It differs from *Karydomys dzerzhinskii* in lacking the anterior protolophule on the M1, in having the anterior and posterior protolophule unequally developed and in showing a double metalophule on the M2 (in ~~*Karydomys-Karydomys-*~~ *dzerzhinskii* the single metalophule is usually anteriorly located). It can be distinguished from *Karydomys symeonidisi* in lacking the anterior protolophule on the M1, which is present in most of the M1 of ~~*Karydomys-*~~ *symeonidisi*, and in having a double metalophule on the M2. It is unlike *Karydomys boskosi* in being larger, lacking a posterior ridge of the metaconid and having a strong metalophulid and longer and narrower mesolophid on the m1. It differs from *Karydomys wigharti* in being

noticeably smaller (Fig. 4), in lacking the anterior protolophule on the M1, having a backward paracone spur on the M1 and M2 and a double protolophule on the M2. It is different from *Karydomys zapfei* in being significantly smaller (Fig. 4), in having ectomesolophid on the m1, a long mesoloph on the M1, a distinct backward paracone spur on the M1 and M2, and a; markedly ~~-bendingbent-~~ double metalophule on the M2.

Description

m1 The m1 has a small and single oval anteroconid. Both labial and lingual anterolophids are distinct. The labial anterolophid is of medium length and it does not reach the base of the protoconid, whereas the lingual one is short and encloses a rounded anterosinusid. The anterior metalophulid that connects the metaconid with the anteroconid is well-developed, whereas the posterior one is absent. The long and narrow mesolophid reaches the lingual side of the tooth, where it forms a mesostylid. The ectomesolophid is long and narrow. The entoconid is located anteriorly to the hypoconid and the hypolophid is close to the mesolophid. The posterolophid is long and reaches the posterior side of the entoconid lingually, closing the posterosinusid. The roots of this tooth are not preserved.

m2 Two lower second molars, of which one is ~~in~~ very well preserved and the other is damaged, have been found. The occlusal outline of these teeth is rectangular. Both show well-developed labial and lingual anterolophids. The labial anterolophid is longer than the lingual one. The metalophulid connects to the anteroconid. The anterolophulid is very short. The mesolophid is nearly transverse, either long and narrow (~~ThyUM Thy~~ 0-5) ~~or-but it can~~ be short (~~ThyUM Thy~~ 0-2). It can reach the lingual border of the tooth, where it finishes in a mesostylid (~~ThyUM Thy~~ 0-5). The metaconid and the mesolophid are connected by a longitudinal ~~and~~ thin crest. The ectomesolophid is long (~~ThyUM Thy~~ 0-5) or absent (~~as~~ in

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6 the damaged specimen (~~Thy~~UM Thy 0-2). The entoconid is anteriorly located with respect to
7 the hypoconid. The strong hypolophid, very close to the mesolophid, ~~bents~~ bends forward
8 anteriorly ~~and it is located very close to the mesolophid~~. The long posterolophid joins with the
9 posterolingual side of the entoconid. It encloses a deep and large posterosinusid. The roots of
10 these teeth are not preserved.
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18 m3 The most anterior part of the single m3 ~~found in Chios~~ is missing. Its occlusal outline is
19 sub-triangular, its posterior part being ~~as it is~~ reduced and rounded. The metalophid is
20 connected to the anterior arm of the protoconid and the mesolophid is absent. The well-
21 developed hypolophid is slightly oblique and encloses the much reduced entoconid. The
22 hypoconid is large although somewhat smaller than the protoconid. The posterolophid is long
23 and joins with the posterolabial side of the entoconid, enclosing a large and circular
24 posterosinusid. The roots of this tooth are not preserved.
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33 M1 ~~The anterocone of the A~~ single first upper molar found ~~has been found. The anterocone~~ is
34 slightly divided. The lingual anteroloph is a very thin crest that runs to meet the anterior side
35 of the protocone, enclosing the protosinus. The strong anterolophule connects the protocone
36 to the middle part of the anterocone. This tooth shows a distinct labial spur on the
37 anterolophule. The anterosinus is labially closed by a low ridge, which runs from the labial
38 side of the anterocone to the anterior part of the paracone. This tooth has no anterior
39 protolophule (protolophule I) and the posterior protolophule (protolophule II) connects to the
40 entoloph well-posteriorly to the protocone. The protocone and the entoloph are firmly
41 connected. The tooth shows a short but very distinct backward paracone spur. The mesoloph
42 is long and narrow, reaching the labial border of the tooth. The sinus is closed by a ridge that
43 connects the anterolingual side of the hypocone to the base of the protocone. The
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6 metalophule is short and joins with the posteroloph. This latter connects to the metacone,
7 enclosing a small posterosinus. The roots of this tooth are not preserved.
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12 M2 Three teeth, two of them complete ([ThyUM Thy 0-30](#) and [ThyUM Thy 0-48](#)) and the
13 other one damaged ([ThyUM Thy 0-54](#)), have been found. The teeth show well-developed
14 labial and lingual anterolophs. The labial anteroloph is connected to the base of the paracone,
15 enclosing a narrow anterosinus, whereas the lingual one reaches the base of the protocone
16 enclosing the protosinus. The protolophule is double, but its degree of development varies
17 from one specimen to another. Specimen [ThyUM Thy 0-30](#) shows the anterior protolophule
18 slightly interrupted and weaker than the posterior one. [ThyUM Thy 0-48](#) has the anterior
19 protolophule strong, whereas the posterior one is weaker and interrupted. [ThyUM Thy 0-54](#)
20 has both anterior and posterior protolophules complete. All specimens have a long and
21 narrow mesoloph that ends with a mesostyle at the labial border of the teeth. The backward
22 paracone spur is short but strong and reaches the mesostyle in two out of the four specimens
23 [available](#). The teeth have a double metalophule with the posterior one stronger than the
24 anterior one. Both the anterior and the posterior metalophules are nearly longitudinal and they
25 can even form an additional longitudinal crest on their own (specimen [ThyUM Thy 0-30](#)).
26 The posteroloph is short and connects to the posterior metalophule. It nearly reaches the
27 metacone, enclosing a small posterosinus. The roots of these teeth are not preserved.
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44 *Cladistic analysis*

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46 The cladistic analysis including all species of *Karydomys* as well as relevant species currently
47 placed in the genera *Democricetodon* and *Cricetodon* yielded a single most parsimonious tree
48 with a length of 86 and a relatively high degree of homoplasy (CI = 0.512; RI = 0.806). Our
49 results (Fig. 5) evidence two ~~main lineages that groups~~ separated ~~from one another~~ at the most
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basal node. The first one corresponds to all the species of *Cricetodon* included in this analysis, ~~which form a monophyletic group,~~ whereas the second ~~is formed~~ by includesencompasses the various species of *Democricetodon* taken into account in this work and all known species of *Karydomys*. However, while *Karydomys* forms a clade within the latter lineage, *Democricetodon* constitutes an array of successive sister-species to *Karydomys*. ~~Besides~~Further, two lineages diverge at the basal node of *Karydomys*: one constituted by the western ~~Eurasiate-Eurasian~~ species (*Karydomys wigharti* + *Karydomys zapfei*) and the other by the eastern ~~Eurasiate-Eurasian~~ ones (*Karydomys debruijini* + more derived species).

DISCUSSION

The examination of the new rodent remains from Chios has ~~allowed to evidence the presence ofrevealed~~ eight molars (Figs 2-3) belonging to a middle sized *Karydomys* (Fig. 4) but different from the molars ~~in all theof any~~ species of this genus known so far. *Karydomys strati* ~~sp. nov.~~ is morphologically close to the two known species from Karydia. However, it shows some important differences, particularly concerning the protolophule and the metalophule on the M1 and M2 and the degree of development of the mesolophids, which prevent to consider it as belonging to either of them. The presence of a double metalophule on the M2 (Fig. 6) may suggest that the new species from Chios could be, in fact, slightly older than *Karydomys symeonidisi* and *Karydomys boskosi*, in which the anterior metalophule is lost not only on the M1 but also on the M2. The absence, on the M1 of *Karydomys strati*, of the anterior protolophule, which is present in *Karydomys symeonidisi*, and the presence of a spur on the anterolophule on the M1, a primitive character absent in ~~*Karydomys*~~ *Karydomys* ~~*boskosi*~~, is consistent with this hypothesis. The presence of a posterior metalophule on the M2 of *Karydomys strati* suggest that it is more evolved than ~~*Karydomys*~~

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6 *Karydomys dzerzhinskii* and *Karydomys-Karydomys debrijni* (Fig. 6), which are the oldest
7 species of *Karydomys*. In addition, *Karydomys* from Chios is distinct from Middle Miocene
8 species such as *Karydomys-Karydomys wigharti* and *Karydomys-Karydomys zapfei* in being
9 noticeably smaller, in lacking the anterior protolophule on the M1 (present in *Karydomys-K.*
10 *wigharti*), in having a well-developed posterior paracone spur on the M1 and M2 as well as in
11 the presence of the ectomesolophid on the m1 (Fig. 6).
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17 The genus *Karydomys* was erected by Theodoropoulos (2000) on the basis of some
18 characters such as the presence of a small posterosinus and well-developed ectolophs on the
19 first two upper molars (in some of the taxa), the reduction of the size of the third molars and
20 the presence of a small, blade-like anteroconid situated very close to the protoconid and the
21 metaconid on the first lower molar. However, as pointed out by Maridet et al. (2011), some of
22 these characters, such as the presence of a small posterosinus, resulting from a posterior
23 position of the metalophule, as well as the development of the ectolophs (posterior paracone
24 spur in the present work), are not present in all the species of the genus. Therefore, Maridet et
25 al. (2011) suggested that the diagnosis of the genus had to be revised when more material
26 would become available. Even though we concur with Maridet et al. (2011) that there are a
27 number of issues related to the diagnosis of the genus *Karydomys*, we are inclined to maintain
28 this taxon in its current specific composition as the species of *Karydomys* form a
29 monophyletic grouping in our analysis. The clade *Karydomys* shares indeed one exclusive
30 synapomorphy: ~~which is to have~~ a slightly divided or "crest-like" anterocone on the M1 (3
31 (0→1)). ~~In fact, the M1 of *Karydomys* are ALSO characterized by a wider and flatter~~
32 ~~anterocone more independent from the anteroloph than those of in *Democricetodon*, in which~~
33 ~~it is a well-defined cusp that may fuse with the anteroloph by with wear.~~ The presence of a
34 short lingual anterolophid (23 (0→1)) on the m1 supports also the clade, but this ~~is shown by~~
35 ~~some occurs in some~~ species of *Democricetodon* as well (e.g. *Democricetodon*
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6 *D-emocricetodon* *anatolicus* of our ingroup). A very interesting synapomorphy is ~~found in the~~
7 connection of the anterior metalophulid ~~anterior~~ on the m1. ~~Thus, it~~ This crest joins ~~the a~~
8 distinct anterolophulid in *Democricetodon* (24(0→1)), ~~whereas it but connects~~ directly
9 connects to the anteroconid or to a tiny anterolophulid in *Karydomys* (24 (1→2)). This latter
10 synapomorphy feature is ~~also~~ shared by the members of the genus *Cricetodon*.

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16 According to our results *Karydomys* split early into two different lineages. One
17 constituted by the central Asiatic-Asian (*Karydomys debruijini* and *Karydomys dzerzhinskii*)
18 and Greek ~~species~~ (*Karydomys symeonidisi*, *Karydomys boskosi* and *Karydomys strati* ~~sp.~~
19 ~~nov.~~) species, which we term here ~~in~~ the "eastern lineage", and the other one formed by the
20 species from Germany and France (~~*Karydomys*~~ *K-arydomys* *wigharti* and ~~*Karydomys*~~
21 *K-arydomys* *zapfei*), the "western lineage". Maridet et al. (2011) had pointed out ~~the~~
22 morphological differences between ~~the the~~ species of *Karydomys*, those -from western and
23 central Europe (France and Germany) and south-eastern Europe (Greece), ~~on~~ the one side,
24 and ~~those the species~~ from central Asia (Kazakhstan and north-western China) on the other,
25 ~~on the other side~~. The latter were considered the least derived particularly on the basis of the
26 morphology of the M2. Our results show a basal position of the two central Asiatic-Asian
27 species of *Karydomys* (~~*Karydomys*~~ *K-arydomys* *debruijini* and ~~*Karydomys*~~ *K-arydomys*
28 *dzerzhinskii*) with respect to the Greek ones, but not regarding the western European species
29 ~~*Karydomys*~~ *K-arydomys* *wigharti* and ~~*Karydomys*~~ *K-arydomys* *zapfei*, which belong to a
30 separate lineage. The cladogram shows sister group relationships between *Karydomys*
31 *dzerzhinski* from Kazakhstan and the clade composed by the three Greek species (~~*Karydomys*~~
32 *Karydomys* *symeonidisi* (~~*Karydomys*~~ *Karydomys* *strati* ~~sp. nov.~~ + ~~*Karydomys*~~ *Karydomys*
33 *boskosi*)). These results are consistent with the suggestion of Kordikova and de Bruijn (2001)
34 about a close relationship between ~~*Karydomys*~~ *Karydomys* *dzerzhinski* and ~~*Karydomys*~~
35 *Karydomys* *symeonidisi*, with the former a plausible ancestor of the later. Our results also
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show that *Karydomys wigharti* is sister species of ~~*Karydomys*~~ *Karydomys zapfei*. Mörs and Kalthoff (2004) emphasized the morphological affinities between ~~these two species~~ them. Some synapomorphies of the species of *Karydomys* for central Asia and south-eastern Europe allow for differentiating them from the taxa from western and central Europe. In particular, the presence of a short but distinct backward paracone spur on the M1 (8 (0→1)), a derived character state, and the presence of a well-developed ectomesolophid on the m1 (27 (0→1)), another derived character state, are ~~characters~~ features that are usually lacking on the two western and central European species *Karydomys wigharti* and *Karydomys zapfei*. However, these are not clear-cut discriminators as ~~the several~~ M1 of *Karydomys debruijini* show a backward paracone spur that varies from more or less short to absent altogether, and the ectomesolophid is equally variable in ~~the its~~ degree of development on the m1 ~~of in~~ *Karydomys wigharti*. Besides morphology, the western and central European species are also larger than the other species of *Karydomys* and, indeed, *Democricetodon*. The grouping of the Greek species of *Karydomys* is supported by stout cusps (2 (0→1)), which is a parallelism with the western and central European species. The Greek species also show a well-developed backward paracone spur on the M2 (15 ((0→1))), which is a character state incipient in *Karydomys dzerzhinski*.

The diagnostic characters provided by Theocharopoulos (2000) to differentiate *Karydomys* from *Democricetodon* are not valid for all ~~taxa~~ species. ~~On one side,~~ †The presence of a small anteroconid, which was used to discriminate the two genera, is a character also ~~shared seen with in~~ various species of *Democricetodon*. ~~On the other side~~ Further, the alleged presence of better developed ectolophs in *Karydomys* than in *Democricetodon*, is actually lacking in the two western and central European members of *Karydomys* (~~*Karydomys*~~ *Karydomys wigharti* and ~~*Karydomys*~~ *Karydomys zapfei*) but present in some species of *Democricetodon* (e.g. ~~*Democricetodon*~~ *Democricetodon anatolicus*),

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6 | ~~whose which have the~~ ectolophs are well -developed. As mentioned above, only one
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8 | exclusive synapomorphy backs up the clade *Karydomys*, which is a slightly divided or "crest-
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10 | like" anterocone on the M1. We have reservations about the adequacy of such a unique
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12 | character to justify the legitimacy of the genus *Karydomys*. However, the differences between
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14 | *Democricetodon* and *Karydomys* regarding the nature of the connection of the anterior
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16 | metalophulid ~~anterior~~ should also be taken into account. The species currently attributed to
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18 | *Karydomys* may as well be seen as pertaining to *Democricetodon*, as derived members of the
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20 | genus. At this point, however, we refrain for formally synonymising *Karydomys* with
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22 | *Democricetodon* given the incomplete nature of our ingroup. Should a future, more
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24 | comprehensive, phylogenetic analysis of the species of *Democricetodon* and *Karydomys*
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26 | yield a pattern of results in line with our own (i.e. *Democricetodon* forming a paraphyletic
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28 | array of species relative to a *Karydomys* clade) then the merits of the recognition of the genus
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30 | *Karydomys* will have to be seriously questioned. In any case, the close relationships between
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32 | the genera *Karydomys* and *Democricetodon* suspected by Theocharopoulos (2000) are
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34 | confirmed.

35 | The teeth of the taxa belonging to *Cricetodon* are morphologically quite different
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37 | from those of *Democricetodon* and *Karydomys*. Our cladogram clearly supports the
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39 | monophyly of *Cricetodon*. The species of *Cricetodon* included in the ingroup share some
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41 | exclusive synapomorphies. They have the anterocone strongly divided (3 (0→1)) and a short
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43 | mesoloph (9 (0→1)) on the M1. Their m1 are characterized by having a large anteroconid
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45 | (22(0→1)) and by usually lacking the lingual anterolophid (23 (0→1)). With respect to the
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47 | m2, the less derived members of the group they have a weak lingual anterolophid ~~in the less~~
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49 | ~~derived members of the group~~ (28 (0→1)), which completely disappear in the more evolved
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51 | ~~members-representatives~~ of the clade (28 (1→2)). Their m3 show a more or less circular
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53 | protosinusid (31 (0→1)) instead of having it retracted and directed forward as is the case in
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Democricetodon and *Karydomys*. However, to confirm or refute the monophyly of this clade, a more comprehensive cladistic analysis that would include all the species belonging to

~~Cricetodon and closely related genera such as Hispanomys or Byzantiniathe subfamily Cricetodontinae~~ is necessary.

CONCLUSION

The new species *Karydomys strati* ~~sp. nov.~~ has been erected in this work to accommodate ~~new~~ remains of *Karydomys* recently recovered from the Miocene of Chios. According to our phylogenetic analysis, the genus *Karydomys* split early into two different lineages, an “eastern stock” that includes the central Asian and Greek species and a “western lineage”, which is constituted by the western and central European species of the genus. *Karydomys strati* belongs to the ~~so-called~~ “eastern lineage” stock. This ~~quite-relatively~~ large-sized democricetodontine rodent is characterized by ~~having~~ a labial spur on the anterolophule and ~~the lacking~~ of the anterior protolophule on the M1 ~~and-as well as~~ by the presence of a double metalophule on the M2. This latter character suggests that *Karydomys strati* is more evolved than ~~*Karydomys-K-arydomys*~~ *dzerzhinskii* and ~~*Karydomys-K-arydomys*~~ *debruijini*, which ~~are~~ are both ~~lacking~~ devoid of the posterior metalophule, but less evolved than the Greek species ~~*Karydomys-K-*~~ *symeonidisi* and ~~*Karydomys-K-*~~ *boskosi*, which ~~are~~ are both lacking the anterior metalophule.

The presence of *Karydomys* is of interest from a biostratigraphical point of view. The Keramia Formation has been usually given a Middle Miocene age. However, the evolutionary stage of the new species of *Karydomys* that it yields suggests that ~~the-its~~ stratigraphical level ~~it-comes from~~ could be, in fact, slightly older than those from which ~~*Karydomys-K-arydomys*~~ *symeonidisi* and ~~*Karydomys-K-arydomys*~~ *boskosi* were collected (MN4). The lowermost part

of the Keramia Formation may, therefore, ~~well~~ be late Early Miocene in age (MN4), which would be in accordance with the latest published magnetostratigraphical data of the area.

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This work is dedicated to the memory of my beloved father, M-~~anuel~~ López Gálvez, who will live forever in our hearts.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural act it contains, have been registered in

ZooBank: <http://zoobank.org/References/81D56B1D-2B00-4FCB-90D7-2C1D15EA0B7B>

Data for this study are available in the Dryad Digital Repository:

<http://datadryad.org/review?doi=doi:10.5061/dryad.m086rm8> [please note that the

data for this paper are not yet published and this temporary link should not be

shared without the express permission of the author]

REFERENCES

- AGUSTÍ, J., CABRERA, L., GARCÉS, M., KRIJGSMAN, W., OMS, O., and PARÉS, J.M., 2001. A calibrated mammal scale for the Neogene of Western Europe. State of the art. *Earth-Science Reviews*, **52**, 247–260.
- BESENECKER, H. 1973. Neogen und Quartär der Insel Chios (Ägäis). Unpublished PhD thesis, Universität Berlin, Berlin, 184 pp.
- BONIS, L. de and KOUFOS, G.D. 1999. The Miocene large mammal succession in Greece; pp. 205–237, in Agustí, J., Rook, L., and Andrews, P. (eds), *The Evolution of Neogene terrestrial ecosystems in Europe*. Cambridge university press, Cambridge.
- BONIS, L. de, KOUFOS, G.D. and SEN, S. 1998. Ruminants (Bovidae and Tragulidae) from the middle Miocene (MN5) of the island of Chios, Aegean sea (Greece). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **210**, 399–420.
- BONIS, L. DE, KOUFOS, G.D. and SEN, S. 1997a. The Sanitheres (Mammalia, Suoidea) from the Middle Miocene of Chios island, Aegean Sea, Greece. *Revue de Paléobiologie*, **16**, 259–270.
- BONIS, L. DE, KOUFOS, G.D. and SEN, S. 1997B. A giraffid from the middle Miocene of the island of Chios, Greece. *Palaeontology*, **40**, 121–123.
- [BOWDICH, T. E. 1821. An analysis of the natural classifications of Mammalia for the use of students and travellers. J. Smith, Paris, 115 pp.](#)
- BREMER, K., 1994. Branch support and tree stability. *Cladistics*, **10**, 295–304.
- BRUIJN, H. DE, DAAMS, R., DAXNER-HÖCK, G., FAHLBUSCH, V., GINSBURG, L., -MEIN, P. and MORALES, J. 1992. Report of the RCMNS working group on fossil mammals, Reisenburg 1990. *Newsletters on Stratigraphy*, **26**, 65–118.

1
2
3
4
5
6 BRUIJN, H. DE, FAHLBUSCH, V., SARAC, G., and ÜNAY, E. 1993. Early Miocene
7 Rodent Faunas from the Eastern Mediterranean Area .3. The Genera *Deperetomys* and
8 *Critetodon* with a Discussion of the Evolutionary History of the Cricetodontini.
9 *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen, Ser. B*, **96**,
10 151–216.

11
12 DAAMS, R., and VAN DER MEULEN, A. J. 1984. Paleoenvironmental and paleoclimatic
13 interpretation of micromammal faunal successions in the upper Oligocene and Miocene of
14 north central Spain. *Paléobiologie continentale*, **14**, 241–257.

15
16 FISCHER VON WALDHEIM, G. 1817. Adversaria zoologica. Mémoires de la Société
17 Impériale des Naturalistes de Moscou, 5, 357–471.

18
19 FREUDENTHAL, M., HUGUENEY, M. and MOISSENET E. 1994. The genus
20 *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of
21 Teruel (Spain). *Scripta Geologica*, **104**, 57–114.

22
23 GOLOBOFF, P. and FARRIS, J., 2001. Methods for quick consensus estimation. *Cladistics*,
24 **17**, 26–34.

25
26 GOLOBOFF, P., FARRIS, J. and NIXON, K.C., 2008. TNT, a free program for phylogenetic
27 analysis. *Cladistics*, **24**, 774–786.

28
29 HILGEN, F.J., LOURENS, L.J. and VAN DAM, J.A. 2012. The Neogene Period: pp. 923–
30 978. in Gradstein, F.M., Ogg, J. G., Schmitz, M.D., and Ogg, G.M. (eds), Geological Time
31 Scale 2012. Elsevier, Oxford.

32
33 KAYA, O., ÜNAY, E., GÖKTAS, F. and SARAÇ, G. 2007. Early Miocene stratigraphy of
34 Central West Anatolia, Turkey: implications for the tectonic evolution of the Eastern Aegean
35 area. *Geological Journal*, **42**, 85–109.

- 1
2
3
4
5
6 KORDIKOVA, E. G. and BRUIJN, H. de 2001. Early Miocene rodents from the Aktau
7 Mountains (south-eastern Kazakhstan). *Senckenbergiana Lethaea*, **81**, 391–405.
8
9
10 KONDOPOULOU, D., DE BONIS, L., KOUFOS, G. D. and SEN, S. (1993):
11 Palaeomagnetic data and biostratigraphy of the middle Miocene vertebrate locality of
12 Thymiana (Chios island, Greece). *Proceedings of the second congress of the Geophysical*
13 *Society of Greece*, **2**, 626–635.
14
15
16 KONDOPOULOU, D., SEN, S., AIDONA, E., HINSBERGEN, D. and KOUFOS, G. 2011.
17 Rotation history of Chios Island, Greece since the Middle Miocene. *Journal of*
18 *Geodynamics*, **51**, 327–338.
19
20
21 KOUFOS, G. D., BONIS, L. de. and SEN, S. 1995. *Lophocyon paraskevoidisi*, a new
22 viverrid (Carnivora, Mammalia) from the Middle Miocene of Chios Island, Greece.
23 *Geobios*, **28**, 511–523.
24
25
26 KOUFOS, G.D., KOSTOPOULOS, D.S., and VLACHOU, T.D. 2005. Neogene/Quaternary
27 mammalian migrations in Eastern Mediterranean. *Belgian Journal of Zoology* **135**, 181–
28 190.
29
30
31 KOUFOS, G. D. 2006. The Neogene mammal localities of Greece: faunas, chronology and
32 biostratigraphy. *Hellenic Journal of Geosciences*, **41**, 183–214.
33
34
35 KREATRAS, K. 1963. The Neogene of the SE region of Chios (Greece). *Bulletin of the*
36 *Geological Society of Greece*, **4-5**, 92–107. [in Greek, English summary].
37
38
39 LEHMANN, U. and TOBIEN, H. 1995. Artiodactyle fossilien (Mammalia) aus dem Miozän
40 von Thymiana, Chios. *Annales de Géologie des Pays Helléniques*, **36**, 403–414.
41
42
43 LINDSAY, E. H. 1987. Cricetid rodents of Lower Siwalik deposits, Potwar Plateau, Pakistan
44 and Miocene mammal dispersal events. Proceedings of the VIIIth RCMNS
45 Congress. Annales Instituti Geologici Publici Hungarici, 70, 483–488.
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6 LÓPEZ-ANTOÑANZAS, R., SEN, S. and KOUFOS G. D. 2005. Presence of a ctenodactylid
7 (Rodentia) in the Keramaria Formation (Middle Miocene) of Chios Island (Greece).
8 *Geobios*, **38**, 113–126.
9
10 LÓPEZ-ANTOÑANZAS, R., PELÁEZ-CAMPOMANES, P., ÁLVAREZ-SIERRA, M. A.
11 and GARCÍA-PAREDES, I. 2010. New species of *Hispanomys* (Rodentia, Cricetidae)
12 from the Upper Miocene of Batallones (Madrid, Spain). *Zoological Journal of the Linnean*
13 *Society*, **160**, 725–747.
14
15 LÓPEZ-ANTOÑANZAS, R. and KNOLL, F. 2011. New insights into the vertebrate fauna
16 from the Miocene of Chios (Greece). *Journal of Vertebrate Paleontology*, **31**, 146–147.
17
18 MADDISON, W.P. and MADDISON, D.R., 2009. Mesquite: A Modular System for
19 Evolutionary Analysis, ver. 2.6. Mesquite Project, Vancouver.
20
21 MADE, J. VAN DER. 1999. Intercontinental relationship Europe-Africa and the Indian
22 Subcontinent. 457–472. In RÖSSNER, G. H.; and HEISSIG, K. (eds). *The Miocene land*
23 *mammals of Europe*. Dr. Friedrich Pfeil, München, 483 pp.
24
25 MARIDET, O., WU, W. Y., YE, J., BI, S. D., NI, X. J. and MENG, J. 2011. Early Miocene
26 cricetids (Rodentia) from the Junggar basin (Xinjiang, China) and their biochronological
27 implications. *Geobios*, **44**, 445–459.
28
29 MEIN, P. 1989. Updating of MN zones. 73–90. In LINDSAY, E. H., FAHLBUSCH, V., and
30 MEIN, P. (eds). *European Neogene mammal chronology*. Plenum Press, New York, 628
31 pp.
32
33 MEIN, P. and FREUDENTHAL, M. 1981. Les Cricetidae (Mammalia, Rodentia) du
34 Néogène Moyen de Vieux-Collonges Partie 2 Cricetodontinae incertae sedis,
35 Melissiodontinae, Platacanthomyinae, et Anomalomyidae. *Scripta Geologica*, **60**, 1–11.
36
37 MELENTIS, J. K. and TOBIEN, H. 1967. Paläontologische Ausgrabungen auf der Insel
38 Chios (eine vorläufige Mitteilung). *Praktika tes Akademias Athenon*, **42**, 147–152.
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MELENTIS, J. K. and TOBIEN, H. 1968. Paläontologische Ausgrabungen auf der Insel Chios (eine vorläufige Mitteilung). *Annales de Géologie des Pays Helléniques*, **19**, 647–652.

MEULEN VAN DER, A.J. VAN DER, and DAAMS, R., 1992. Evolution of Early–Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **93**, 227–253.

MÖRS, T. and KALTHOFF, D. 2004. A new species of *Karydomys* (Rodentia, Mammalia) and a systematic re-evaluation of this rare Eurasian Miocene hamster. *Palaeontology*, **47**, 1387–1405.

OLIVER, A. and PELÁEZ-CAMPOMANES, P. 2016. Early Miocene evolution of the rodent *Megacricetodon* in Europe and its palaeobiogeographical implications. *Acta Palaeontologica Polonica*, **61**, 211–219.

PARASKEVAIDIS, I. 1940. Eine obermiocäne fauna von Chios. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **83**, 363–442.

PRIETO, J. 2012. The rare cricetid rodent *Karydomys* Theocharopoulos, 2000 in the fissure filling Petersbuch 6 (Middle Miocene, Germany). *Zitteliana*, **52**, 67–70.

PRIETO, J. 2013. First record of *Karydomys* (Rodentia, Mammalia) from the German part of the North Alpine Foreland Basin. *Swiss Journal of Geosciences*, **106**, 303–307.

RÖGL, F. 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geologica carpathica*, **50**, 339–349.

ROTHAUSEN, K. 1977. Die mittelmiozänen Wirbeltierfundstellen südlich Thymiana (Insel Chios, Ägäis, Griechenland). 2. Teil: Geologie: Die Fundstellen und ihre Abfolge. *Annales de Géologie des Pays Helléniques*, **28**, 495–515.

STEININGER, F. F., BERNOR, R. L. and FAHLBUSCH, V. 1989. European Neogene marine/continental chronologic correlations. 15–46. In LINDSAY, E. H., FAHLBUSCH, V., and MEIN, P. (eds). *European Neogene mammal chronology*. Plenum Press, New York, 628 pp.

THEOCHAROPOULOS, K. D. 2000. Late Oligocene—Middle Miocene *Democricetodon*, *Spanocricetodon* and *Karydomys* n. gen. from the Eastern Mediterranean area. *Gaia*, **8**, 1–92.

TOBIEN, H. 1968. ~~Palaeontologische~~ ~~Paläontologische~~ Ausgrabungen nach jungtertiären Wirbeltieren auf der Insel Chios (Griechenland) und bei Maragheh (NW-Iran). *Jahrbuch der Vereinigung "Freunde der ~~Universität~~ ~~Universität~~ Mainz"*, 51–58.

TOBIEN, H.-1969. Wirbeltiergrabungen im Miozän der Insel Chios (Ägäis). *Praktika tes Akademias Athenon*, **43**, 151–157.

TOBIEN, H. 1977. Die mittelmiozänen Wirbeltierfundstellen südlich Thymiana (Insel Chios, Ägäis, Griechenland). *Annales de Géologie des Pays Helléniques*, **28**, 489–494.

TOBIEN, H. 1980. A note on the skull and mandible of a new choerolophodont mastodon (Proboscidea, Mammalia) from the middle Miocene of Chios (Aegean Sea, Greece). 299–307. In JACOBS, L. L. (ed.). *Aspects of Vertebrate History: essays in honor of Edwin Harris Colbert*. Museum of Northern Arizona Press, Flagstaff, 412 pp.

ÜNAY, E. and GÖKTAŞ, F. 1999. Late Early Miocene and Quaternary small mammals in the surroundings of Söke (Aydm): Preliminary results. *Geological Bulletin of Turkey*, **42**, 99–114.

VAN DEN HOEK OSTENDE, L. W., MAYDA, S., OLIVER, A., MADERN, A., HERNÁNDEZ-BALLARÍN, V., and PELÁEZ-CAMPOMANES, P. 2015. Aliveri revisited, a biogeographical appraisal of the early Miocene mammals from the eastern Mediterranean. *Palaeobiodiversity and Palaeoenvironments*, **95**, 271–284.

VAN DE WEERD, A. 1976. Rodent fauna of the Mio–Pliocene continental sediments of the Teruel–Alfambra region, Spain. *Utrecht Micropaleontological Bulletins, Special Publication*, **2**, 1–185.

Appendix S1

Character list used in this analysis

1-Size of the M1: (0) small, 1.2-1.8 mm; (1) medium size, 1.8-2.6 mm; (2) large >2.6 mm

2-Cusps: (0) slender; (1) stout

M1

3-Anterocone: (0) single; (1) slightly divided or crest like; (2) divided

4-Anterolabial cingulum: (0) present; (1) absent

5-Labial spur of the anterocone: (0) absent; (1) present

6-Labial spur on the anterolophule: (0) absent; (1) present

7-Anterior protolophule: (0) absent; (1) present

8-Backward paracone spur: (0) very weak or absent; (1) short but distinct; (2) long

9-Mesoloph: (0) long; (1) short or medium length; (2) absent

10-Metalophule: (0) anterior; (1) posterior

11-Posteroloph: (0) long; (1) continues beyond the metalophule; (2) does not continue beyond the metaloph; (3) absent

12- Roots: (0) three; (1) four

M2

13-Anterior protolophule: (0) complete; (1) weak; (2) absent

14-Posterior protolophule: (0) absent; (1) weak; (2) complete

15-Backward paracone spur: (0) absent; (1) present

16-Mesoloph: (0) long; (1) short or medium sized; (2) absent

17-Metaloph: (0) anterior; (1) double; (2) posterior

18-Roots: (0) three; (1) four

M3

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6 19-Relative size: (0) large, LM1/LM3 <1.7; (1) small, LM1/LM3 >1.7

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8 20-Neoentoloph: (0) absent; (1) present

9
10 21-Mesoloph: (0) absent; (1) short; (2) long

11
12 m1

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14 22-Anteroconid: (0) small; (1) large

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16 23-Lingual anterolophid: (0) well developed; (1) short (2) absent

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18 24- Anterior metalophulid: (0) absent; (1) more or less transversely directed and connected to
19 the anterolophulid (2) very anteriorly directed and generally connected to the anteroconid

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21 25-Posterior metalophulid: (0) present; (1) mostly absent

22
23 26-Mesolophid: (0) absent; (1) short to medium length (length<1/3 of the distance between
24 ectolophid and lingual border); (2) long to medium length

25
26 27-Ectomesolophid: (0) very weak or absent; (1) present

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29 m2

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31 28-Lingual anterolophid: (0) developed; (1) very weak or not developed

32
33 29-Posterior metalophulid: (0) present; (1) weak or absent

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35 30-Mesolophid: (0) short (length<1/3 of the distance between ectolophid and lingual border); (1)
36 long

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38 m3

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40 31-Protosinusid: (0) retracted and directed forward; (1) circular

41
42 32-Mesolophid: (0) present; (1) absent

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8 **Figure captions**
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12 **TEXT-FIG. 1.** Simplified geological map of Chios Island (redrawn from Kondopoulou *et al.*
13 1993) and location of the fossiliferous site Thy 0.
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18 **TEXT-FIG. 2.** Lower cheek teeth of *Karydomys strati* sp. nov. A-D. SEM photographs of
19 the occlusal surface of the teeth. A, [ThyUM Thy 0-39](#), right m1. B, [ThyUM Thy 0-5](#), right
20 m2. C, [ThyUM Thy 0-2](#), right m2. D, [ThyUM Thy 0-145](#), right m3. E-H. CT-[Sean-scan](#)
21 images of [ThyUM Thy 0-39](#), right m1; E, occlusal view; F, lingual view; G, labial view; H,
22 anterior view. I-L. CT-[Sean-scan images views](#) of [ThyUM Thy 0-5](#), right m2. I, occlusal view;
23 J, lingual view; K, labial view; L, anterior view. M-P. CT-[Sean-scan images views](#) of [ThyUM](#)
24 [Thy 0-2](#), right m2; M, occlusal view; N, lingual view; O, labial view; P, anterior view. Q-S.
25 CT-[Sean-scan images views](#) of [ThyUM Thy 0-145](#), right m3. Q, occlusal view; R, lingual
26 view; S, labial view. The scale bar equals 1 mm for the SEM images (CT-[Sean-scan](#) images
27 have been approximately scaled).
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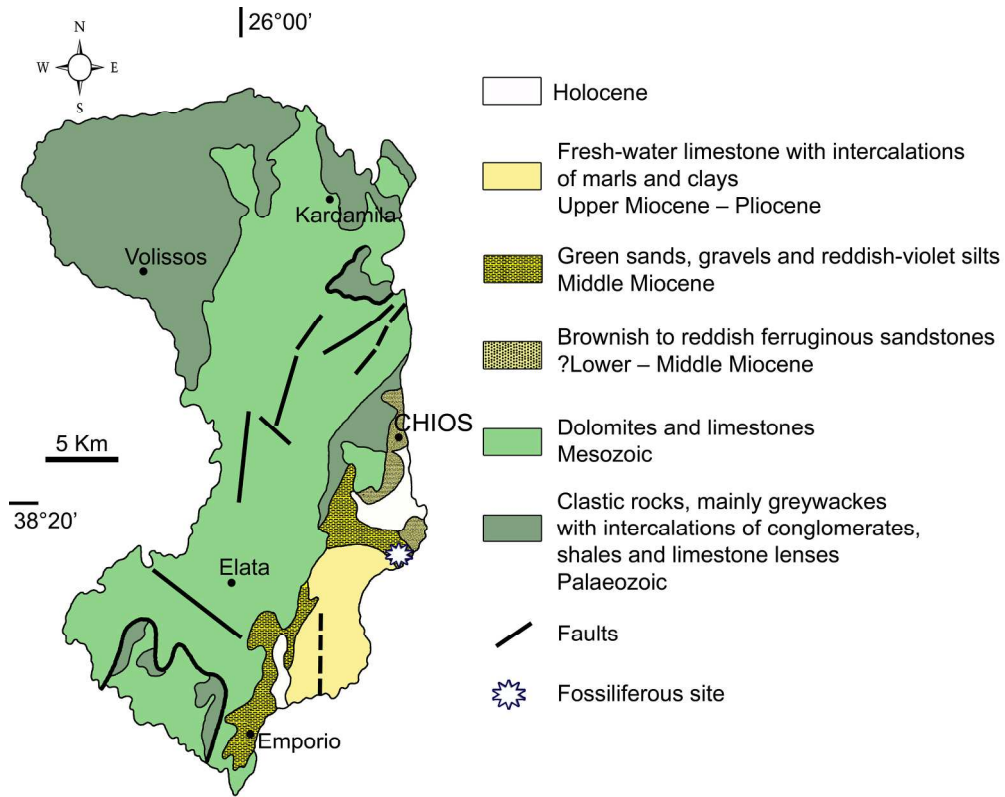
38 **TEXT-FIG. 3.** Upper cheek teeth of *Karydomys strati* sp. nov. A-D. SEM photographs of the
39 occlusal surface of the teeth. A, [ThyUM Thy 0-9](#), left M1; B, [ThyUM Thy 0-30](#), left M2;
40 [ThyUM Thy 0-48](#) left M2; [ThyUM Thy 0-54](#), left M2 (broken). E-H. CT-[Sean-scan](#) images
41 of [ThyUM Thy 0-9](#), left M1; E, occlusal view; F, lingual view; G, labial view; H, anterior
42 view. I-L. CT-[Sean-scan images views](#) of [ThyUM Thy 0-30](#), left M2. I, occlusal view; J,
43 lingual view; K, labial view; L, anterior view. M-P. CT-[Sean-scan views images](#) of [ThyUM](#)
44 [Thy 0-48](#) left M2; M, occlusal view; N, lingual view; O, labial view; P, anterior view. Q-S.
45 CT-[Sean-scan images views](#) of [ThyUM Thy 0-54](#), left M2. Q, occlusal view; R, labial view;
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6 S, anterior view. The scale bar equals 1 mm for the SEM images (CT-~~Scan~~-scan images have
7 been approximately scaled).
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12 **TEXT-FIG. 4.** Length/width scatter diagram of the two first upper and lower molars of the
13 different species belonging to the genus *Karydomys*.
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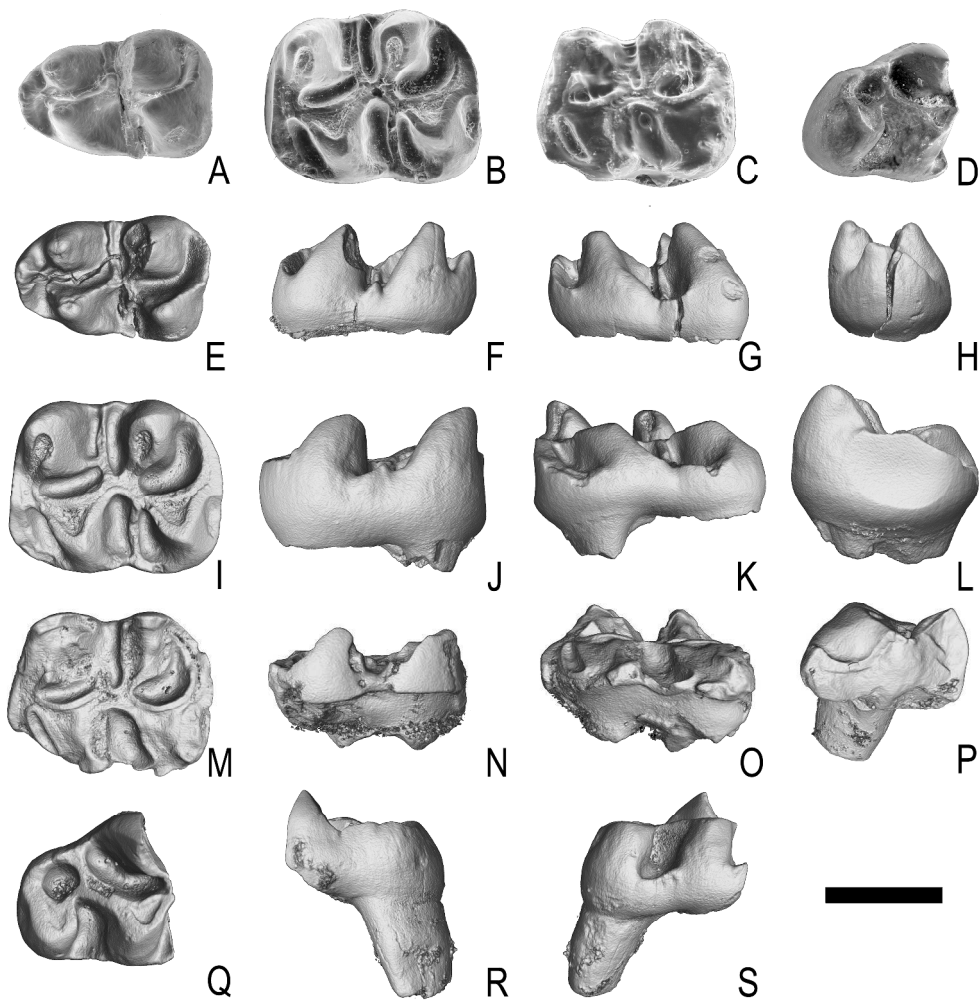
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17 **TEXT-FIG. 5.** Cladogram showing the relationships among all known species of *Karydomys*
18 as well as selected ~~ones of~~ *Democricetodon* and *Cricetodon* and the phylogenetic position of
19 *Karydomys strati* sp. nov. (data matrix in [Dryad Digital Data Repository: López-Antoñanzas](#)
20 [et al. 2018Supplementary File 2](#)). [Nodes show](#) Bremer and Relative Bremer Indices ~~are~~
21 ~~showed at the appropriate nodes.~~
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29 **TEXT-FIG. 6.** Evolutionary stage of various species of *Karydomys* with some important
30 structures signaled. A-C, *K-[arydomys](#) dzerzhinskii* (taken from Kordikova & de Bruijn,
31 2001); D-F, *Karydomys strati* sp. nov.; G-I, *K-[arydomys](#) wigharti* (taken from Mörs &
32 Kalthoff, 2004). The scale is not included as the morphology only is considered.
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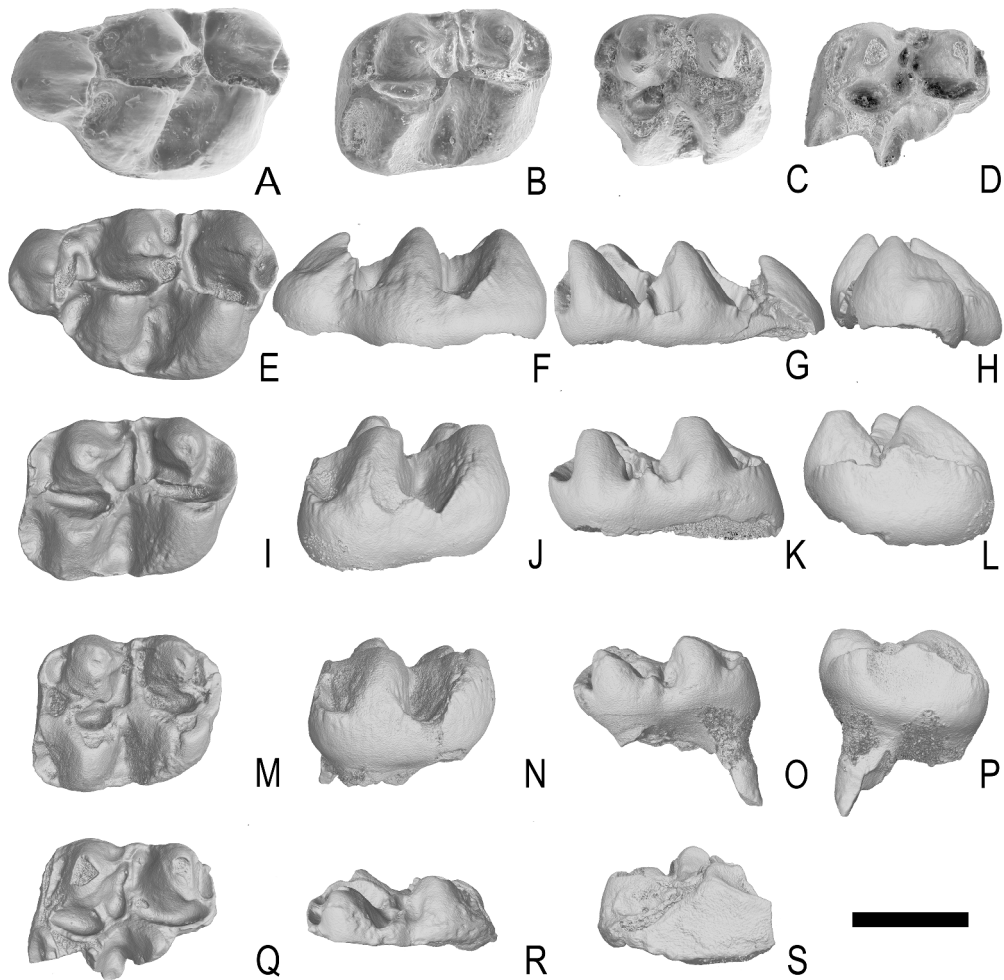


Simplified geological map of Chios Island (redrawn from Kondopoulou et al. 1993) and location of the fossiliferous site Thy 0.

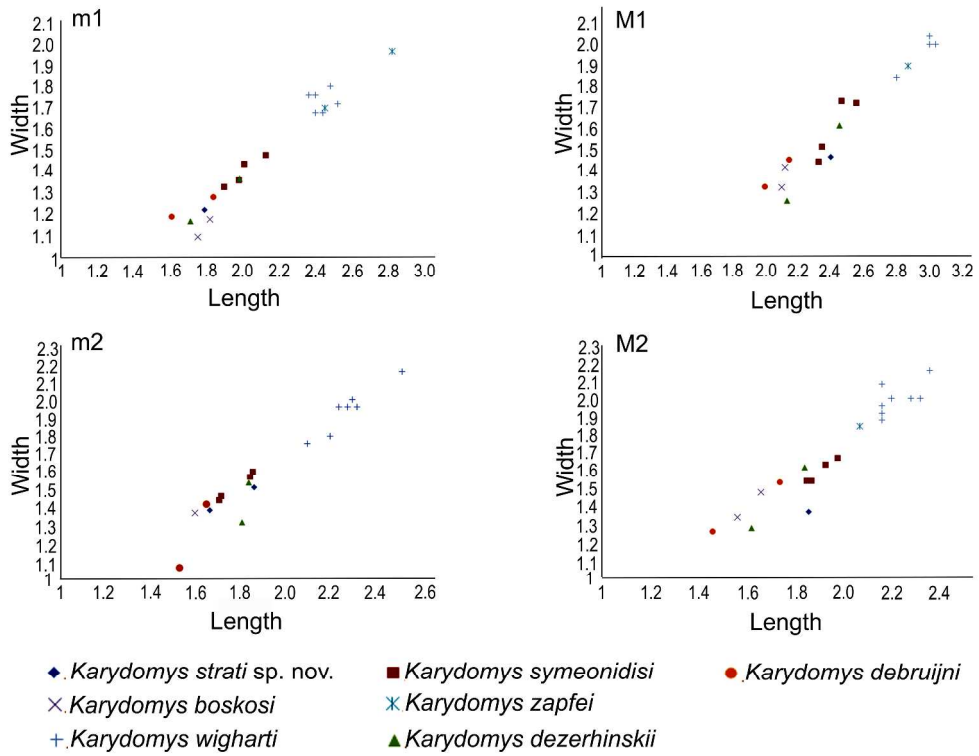
209x175mm (300 x 300 DPI)



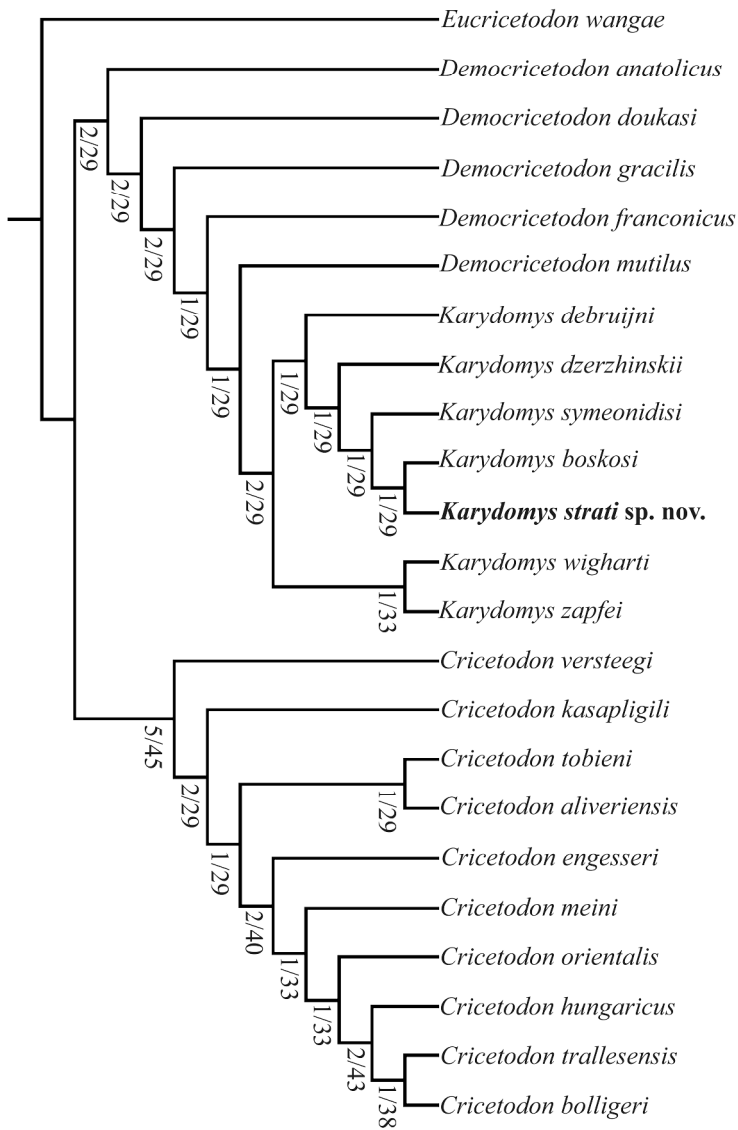
Lower cheek teeth of *Karydomys strati* sp. nov. A-D. SEM photographs of the occlusal surface of the teeth. A, UM Thy 0-39, right m1. B, UM Thy 0-5, right m2. C, UM Thy 0-2, right m2. D, UM Thy 0-145, right m3. E-H. CT-scan images of UM Thy 0-39, right m1; E, occlusal view; F, lingual view; G, labial view; H, anterior view. I-L. CT-scan images of UM Thy 0-5, right m2. I, occlusal view; J, lingual view; K, labial view; L, anterior view. M-P. CT-scan images of UM Thy 0-2, right m2; M, occlusal view; N, lingual view; O, labial view; P, anterior view. Q-S. CT-scan images of UM Thy 0-145, right m3. Q, occlusal view; R, lingual view; S, labial view. The scale bar equals 1mm for the SEM images (CT-scan images have been approximately scaled).



Upper cheek teeth of *Karydomys strati* sp. nov. A-D. SEM photographs of the occlusal surface of the teeth. A, UM Thy 0-9, left M1; B, UM Thy 0-30, left M2; UM Thy 0-48 left M2; UM Thy 0-54, left M2 (broken). E-H. CT-scan images of UM Thy 0-9, left M1; E, occlusal view; F, lingual view; G, labial view; H, anterior view. I-L. CT-scan images of UM Thy 0-30, left M2. I, occlusal view; J, lingual view; K, labial view; L, anterior view. M-P. CT-scan images of UM Thy 0-48 left M2; M, occlusal view; N, lingual view; O, labial view; P, anterior view. Q-S. CT-scan images of UM Thy 0-54, left M2. Q, occlusal view; R, labial view; S, anterior view. The scale bar equals 1 mm for the SEM images (CT-scan images have been approximately scaled).

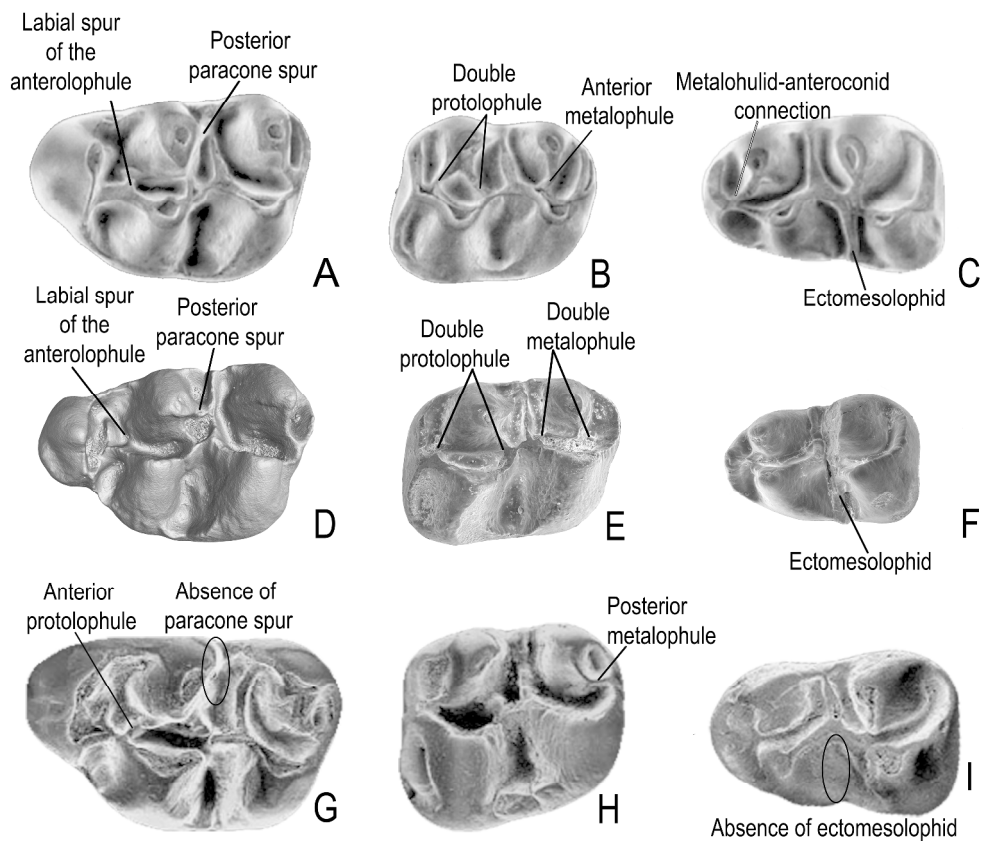


Length/width scatter diagram of the two first upper and lower molars of the different species belonging to the genus *Karydomys*.



Cladogram showing the relationships among all known species of *Karydomys* as well as selected *Democricetodon* and *Cricetodon* and the phylogenetic position of *Karydomys strati* sp. nov. (matrix in Supplementary File 2). Nodes show Bremer and Relative Bremer Indices.

203x276mm (600 x 600 DPI)



Evolutionary stage of various species of *Karydomys* with some important structures signaled. A-C, *Karydomys dzerzhinskii* (taken from Kordikova & de Bruijn, 2001); D-F, *Karydomys strati* sp. nov.; G-I, *Karydomys wigharti* (taken from Mörs & Kalthoff, 2004). The scale is not included as the morphology only is considered.

			Length	Width	
1	<i>Karydomys strati</i>	Thy 0-39	m1	1.79	1.224
2	<i>Karydomys strati</i>	Thy 0-2	m2	1.667	1.385
3	<i>Karydomys strati</i>	Thy 0-5	m2	1.865	1.513
4	<i>Karydomys strati</i>	Thy 0-145	m3 (broken)	/	/
5	<i>Karydomys strati</i>	Thy 0-9	M1	2.398	1.477
6	<i>Karydomys strati</i>	Thy 0-30	M2	1.857	1.372
7	<i>Karydomys strati</i>	Thy 0-48	M2 (eroded)	1.527	1.316
8	<i>Karydomys strati</i>	Thy 0-54	M2 (broken)	/	/

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3 Appendix S1
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5 Character list used in this analysis
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8
9 1-Size: (0) small, 1.2-1.8 mm; (1) medium size, 1.8-2.6 mm; (2) large >2.6 mm
10

11 2-Cusps: (0) slender; (1) stout
12

13
14 M1
15

16 3-Anterocone (0) single; (1) slightly divided or crest like; (2) divided
17

18 4-Anterolabial cingulum (0)present; (1)absent
19

20 5-Labial spur of the anterocone: (0) absent; (1) present
21

22 6-Labial spur on the anterolophule: (0) absent; (1) present
23

24 7-Anterior Protolophule: (0) absent; (1) present
25

26 8-Backward paracone spur: (0) very weak or absent; (1) short but distinct; (2) long
27

28 9-Mesoloph: (0) long; (1) short or medium length; (2) absent
29

30 10-Metalophule: (0) anterior; (1) posterior
31

32 11-Posteroloph: (0) long; (1) continues beyond the metalophule; (2) does not continue beyond
33

34 the metaloph; (3) absent
35

36 12- Roots: (0) 3; (1) 4
37

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39
40 M2
41

42 13-Anterior Protolophule: (0) complete; (1) weak; (2) absent
43

44 14-Posterior Protolophule: (0) absent; (1) weak; (2) complete
45

46 15-Backward paracone spur: (0) absent; (1) present
47

48 16-Mesoloph: (0) long; (1) short or medium sized; (2) absent
49

50 17-Metaloph: (0) anterior; (1) double; (2) posterior
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52 18-Roots: (0) three; (1) four
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55 M3
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1
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3 19-Relative size: (0) large, LM1/LM3 <1.7; (1) small, LM1/LM3 >1.7
4

5 20-Neoentoloph: (0) absent; (1) present
6

7 21-Mesoloph: (0) absent; (1) short; (2) long
8

9 m1
10

11 22-Anteroconid: (0) small; (1) large
12

13 23-Lingual anterolophid: (0) well-developed; (1) short (2) absent
14

15 24-Metalophulid anterior: (0) absent; (1) connected to the anterolophid (2) connected to the
16 anteroconid
17

18 25-Metalophulid posterior: (0) present; (1) mostly absent
19

20 26-m1-Mesolophid (0) absent; (1) short to medium length (length < 1/3 of the distance between
21 ectolophid and lingual border); (2) long to medium length
22

23 27-Ectomesolophid: (0) very weak or absent; (1) present
24

25 m2
26

27 28-Lingual anterolophid: (0) developed; (1) very weak or not developed
28

29 29-Posterior metalophulid: (0) present; (1) weak or absent
30

31 30-Mesolophid: (0) short (length < 1/3 of the distance between ectolophid and lingual border); (1)
32 long
33

34 m3
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36 31-Protosinusid: (0) retracted and directed forward; (1) circular
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38 32-Mesolophid: (0) present; (1) absent
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