

Early Miocene evolution of the rodent *Megacricetodon* in Europe and its palaeobiogeographical implications

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The *Megacricetodon* material from Aliveri (Isle of Evia, Greece) was previously assigned to *Megacricetodon primitivus*, implying palaeobiogeographical relationship between south-eastern and south-western Europe. The material from Aliveri is here assigned to the new species *Megacricetodon hellenicus* sp. nov. This form has significant morphological differences compared to other Early Miocene species from Europe. This new evolutionary hypothesis of this genus has implications on the Early Miocene paleobiogeography of Europe. This work presents a new interpretation on the earliest European representative of the genus *Megacricetodon* from Aliveri localities. Analyses of the *Megacricetodon* material from MN 4 and MN 5 localities enable to propose a new palaeobiogeographical framework in which there are three main migration events of the genus *Megacricetodon* into Europe, each corresponding to different lineages that evolved independently. The new Greek taxon is considered the first migration wave from Anatolia, representing an endemic lineage different from any other European *Megacricetodon*.

Key words: Mammalia, Rodentia, Cricetodontidae, migrations, endemism, Miocene, Greece.

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Introduction

Southeastern Europe has always been regarded as an important paleogeographic area because of its crucial role on the mammal exchanges between Asia, Africa, and Europe (Pickford and Morales 1994; Rögl 1999; Koufos et al. 2005; Wessels 2009; Álvarez-Sierra et al. 2013; De Bruijn et al. 2013). Asia Minor has been an important source of European micromammals during the Early Miocene and especially for Muroidea rodents. In this way, there are abundant genera of Miocene cricetids, such as *Cricetodon*, *Democricetodon*, *Karydomys*, and *Megacricetodon*, that occurred in Anatolia much earlier than in Europe (Klein Hofmeijer and De Bruijn 1988; Theocharopoulos 2000; Doukas 2003). Even though results on insectivores and eomyids may indicate a connection between Greece and western Europe around MN 3 (Van den Hoek Ostende 2001), the presence in Greece of the earliest representatives of many of these genera in Europe supports the generally accepted idea that this area was connected to Asia Minor during the Early Miocene but that the connection with central and western Europe, probably through the Dinarids was not possible till Middle Miocene

(Popov et al. 2004; Koufos et al. 2005; Wessels 2009). While the earlier Cricetodontini and Democricetodontinae from Europe have been studied from a paleogeographical point of view (De Bruijn et al. 1993; Theocharopoulos 2000; Álvarez-Sierra et al. 2013) much less is known about the genus *Megacricetodon*, despite it being one of the most diverse and abundant rodent during the Early and Middle Miocene in Europe.

The goal of this work is the study of the earliest European *Megacricetodon* material from the Greek locality of Aliveri (North and South quarries). Based on this study, and the new results and interpretations proposed by Oliver and Peláez-Campomanes (2013, 2014) on the early representatives of the central and western European record of the genus *Megacricetodon*, a palaeobiogeographical framework for the evolution of the group is proposed.

The site of Aliveri (Island of Evia, Greece) is situated in the Neogene sedimentary basin of Aliveri-Kymi. It was discovered by Hans De Bruijn, Albert J. Van der Meulen, and George Katsikatsos in 1977. The basin of Aliveri-Kymi is a very well-studied basin (De Bruijn et al. 1980; Katsikatsos et al. 1981; Benda and De Bruijn 1982), which contains an important fossil assemblage of small mammals (De Bruijn

and Van der Meulen 1979; De Bruijn et al. 1980; Van der Meulen and De Bruijn 1982; Klein Hofmeijer and De Bruijn 1985; Doukas 1986; López-Martínez 1986; Álvarez-Sierra et al. 1987; De Bruijn et al. 1987; Klein Hofmeijer and De Bruijn 1988), carnivores (Schmidt-Kittler 1983) and pollen (Benda and De Bruijn 1982).

Klein Hofmeijer and De Bruijn (1988) described the cricetids from Aliveri. They assigned the *Megacricetodon* material to *M. primitivus* after comparison with the type material from Valtorres. Nevertheless, they pointed out several differences between the material from these localities. Based on these differences in dental characteristics, they interpreted the Aliveri material as more primitive than the material from Valtorres, suggesting the earlier occurrence of *Megacricetodon* in the eastern Mediterranean than in the Western area. However, Oliver and Peláez-Campomanes (2014), considered that those differences between the *Megacricetodon* from Aliveri (specially the North quarry) and *M. primitivus* from Valtorres, are strong enough to place the material from these Greek localities in a new species different from *M. primitivus*.

Institutional abbreviations.—IAUU, Instituut voor Aardwetenschappen, Utrecht University, The Netherlands.

Other abbreviations.—AFF, Affalterbach; AL-N, Aliveri North Quarry; AL-S, Aliveri South Quarry; ANT, Antonios; ART, Artesilla; BEZ, Bézia; COL D, La Col D; DOL3, Dolnice 3; FRZ, Franzensbad; LAN1, Langenau 1; LANG, Langenmoosen; MUN3A, Munébraga 3A; NIE, Niederaichbach; OFF2, Offingen 2; ORE, Ořechov; PEL, Pellecahus; PUTT, Puttenham; SE, Sérido; SS, Sandelzhausen; STR, Strakonice; THC, Thymiana; VA8A, Valdemoros 8A; VLT, Valtorres.

Material and methods

According to the locality descriptions by De Bruijn et al. (1980) *Megacricetodon hellenicus* sp. nov. was recovered from two different exposures of the same horizon (North and South quarries) situated in a clay bed directly underlying the lignite in the open-cast mine of Aliveri, in the Aliveri-Kymi Basin, on the Island of Evia (Greece).

The nomenclature of the cheek teeth of *Megacricetodon* is based on Oliver and Peláez-Campomanes (2013). The definitions of character states for morphological structures are from Oliver and Peláez-Campomanes (2013) and Oliver and Peláez-Campomanes (2014). Notation M/m is used for upper/lower molars respectively. The images of the occlusal surface of the cheek teeth were made with a Scanning Electron Microscope Fei, model Quanta 200 using a large field detector (LFD). The 3D images were made using a Micro-CT scanner Nikon XTH 160 and processed using the ImageJ software (Fiji, version 1.48r; Rasband, 1997–2014).

Measurements of the cheek teeth are after Oliver and Peláez-Campomanes (2013). They have been taken using a Nikon Kosata KK measuring microscope (10× and 15×) and are given in millimetres. Length and width represent the maximum antero-posterior and bucco-lingual distances, taken perpendicular to each other.

The specimens from Aliveri North (AL-N) and South (AL-S) quarries are stored at the IAUU.

Systematic palaeontology

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Cricetodontinae Schaub, 1925

Genus *Megacricetodon* Fahlbusch, 1964

Type species: *Megacricetodon gregarious* (Schaub, 1925), La Grive M, Upper Miocene.

Megacricetodon hellenicus sp. nov.

Figs. 1, 2.

1979 *Megacricetodon primitivus* (Freudenthal, 1963); De Bruijn and Van der Meulen 1979: 209, fig. 1.

1980 *Megacricetodon primitivus* (Freudenthal, 1963); De Bruijn et al. 1980: 243.

1981 *Megacricetodon primitivus* (Freudenthal, 1963); Katsikatsos et al. 1981: 511.

1982 *Megacricetodon primitivus* (Freudenthal, 1963); Benda and De Bruijn 1982: 130.

1988 *Megacricetodon primitivus* (Freudenthal, 1963); Klein Hofmeijer and De Bruijn 1988: 185, 192, 193, 196, 198, 199, text-fig. 4, pl. 2.

Etymology: After Hellenic i.e., Ancient Greek *Megacricetodon*.

Type material: Holotype: m1 dextral, IAUU AL-N-2096 (Fig. 10; SOM 1, 2, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Oliver_PelaezCampomanes_et_al_SOM.pdf). Paratypes: M1: IAUU AL-N-2051–2063, 2069; M2: IAUU AL-N-2071–2073, 2076–2078; m1: IAUU AL-N-2091–2093, 2097, 2098; m2: IAUU AL-N-2101–2107, 2111–2114; m3: IAUU AL-N-2126.

Type locality: Aliveri North quarry, Island of Evia, Aliveri-Kymi Basin, Greece.

Type horizon: Underclay of the lignite occurring North of Aliveri along the eastern edge of the basin where the lignite wedges out against Mesozoic limestone (De Bruijn et al. 1980); Early Miocene (MN4).

Other material.—Isolated teeth from Aliveri South quarry: 4 M1, 1 M2, 3 M3, 2 m1, 3 m3 (Fig. 2A–I).

Diagnosis.—Small-sized species of *Megacricetodon*. It shows slender crests and well-developed mesoloph and mesolophids (generally of medium length). Lower first molars with rounded and simple anteroconid, being lower than the other four main cusps. Upper molars with long and angular entoloph and transverse sinus.

Megacricetodon hellenicus sp. nov. differs from the medium- and large-sized group of *Megacricetodon* defined by Peláez-Campomanes and Daams (2002) by its significantly smaller dimensions.

Megacricetodon hellenicus sp. nov. differs from *M. de-*

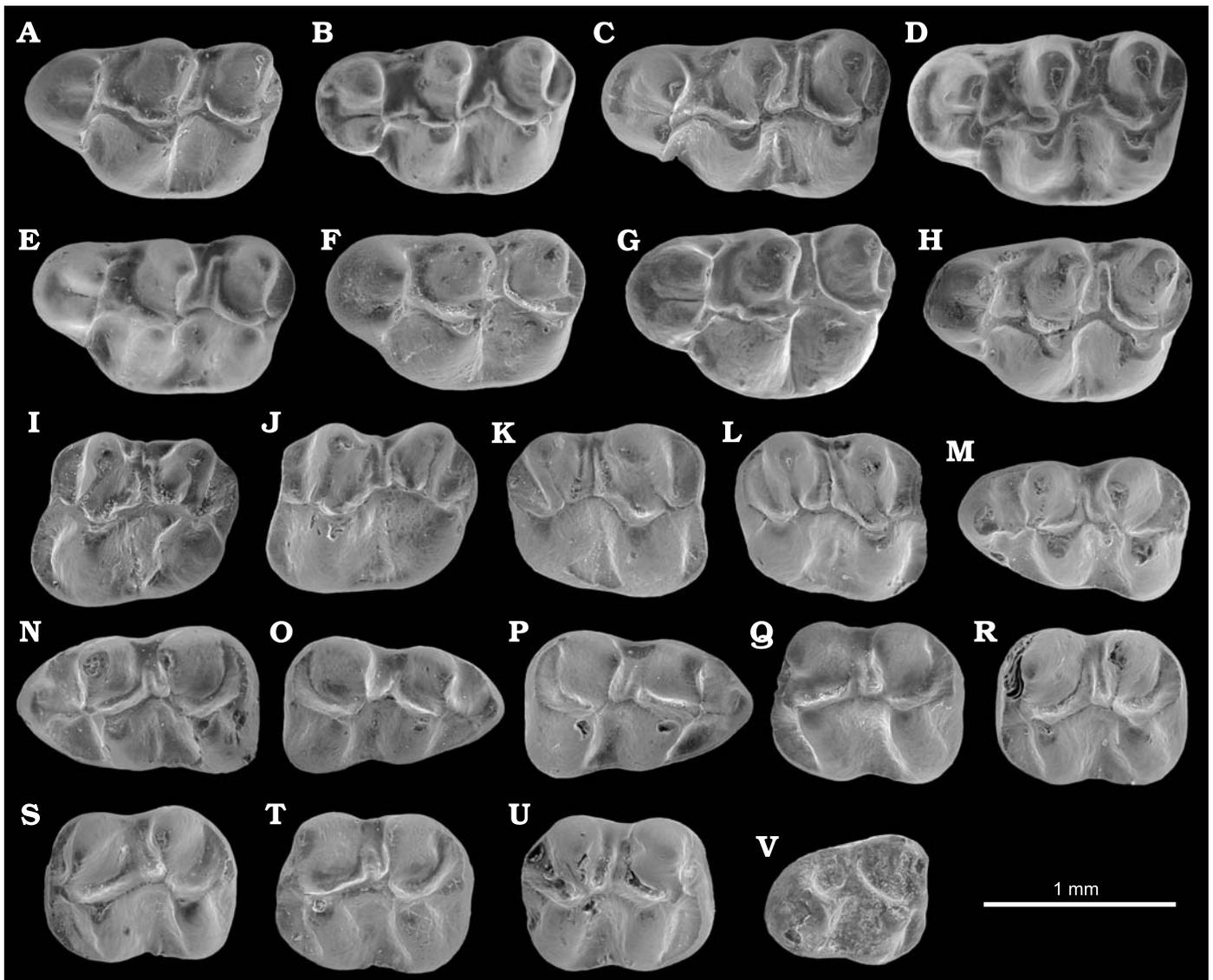


Fig. 1. Cricetodontid rodent *Megacricetodon hellenicus* sp. nov. from type locality Aliveri North quarry, Greece (MN4, Early Miocene). **A.** IAUU AL-N-2051, M1 left. **B.** IAUU AL-N-2052, M1 left. **C.** IAUU AL-N-2053, M1 left. **D.** IAUU AL-N-2055, M1 left. **E.** IAUU AL-N-2056, M1 left. **F.** IAUU AL-N-2057, M1 left. **G.** IAUU AL-N-2059, M1 left. **H.** IAUU AL-N-2060, M1 left. **I.** IAUU AL-N-2071, M2 left. **J.** IAUU AL-N-2072, M2 left. **K.** IAUU AL-N-2077, M2 right. **L.** IAUU AL-N-2078, M2 right. **M.** IAUU AL-N-2091, m1 left. **N.** IAUU AL-N-2092, m1 left. **O.** Holotype IAUU AL-N-2096, m1 right. **P.** IAUU AL-N-2097, m1 right. **Q.** IAUU AL-N-2101, m2 left. **R.** IAUU AL-N-2102, m2 left. **S.** IAUU AL-N-2104, m2 left. **T.** IAUU AL-N-2105, m2 left. **U.** IAUU AL-N-2111, m2 right. **V.** IAUU AL-N-2126, m3 right.

bruijni Freudenthal, 1968, *M. freudenthali* García Moreno (in Álvarez-Sierra and García-Moreno, 1986), *M. minutus* Daxner, 1967, and *M. pussillus* Qiu, 1996 by its bigger dimensions.

Megacricetodon collongensis (Mein, 1958) is similar in size to *M. hellenicus* sp. nov., but, it differs from it by the frequent presence of double anteroconid and double protolophule and metalophule in the M1 and M2.

The medium-sized *Megacricetodon*, *M. sinensis* Qiu, Li, and Wang, 1981 has a similar size to *Megacricetodon hellenicus* sp. nov., however, differs by the morphology of the anterocone (anterocone deeply split in more than 75% of the specimens), shorter mesolophid in the m1, m3 with longer lingual anterolophid and absent mesolophid.

Megacricetodon minor (Lartet, 1851) has a similar size to *M. hellenicus* sp. nov., but differs from it by having the M1 with a higher percentage of ectolophs connected with the mesoloph; M2 with a higher percentage of double protolophules; and m1 with a higher percentage of double anteroconids and longer mesolophids.

Megacricetodon tautavelensis Lazzari and Aguilar, 2007 differs from *Megacricetodon hellenicus* sp. nov. by its smaller size, in the M1 with a lower percentage of labial spurs of the anterolophule and the higher percentage of posterior protolophules; M2 with more variability in the morphotypes of the metalophule and protolophule; m1 with a higher percentage of subdivided anteroconid and more variability in the mesolophid.

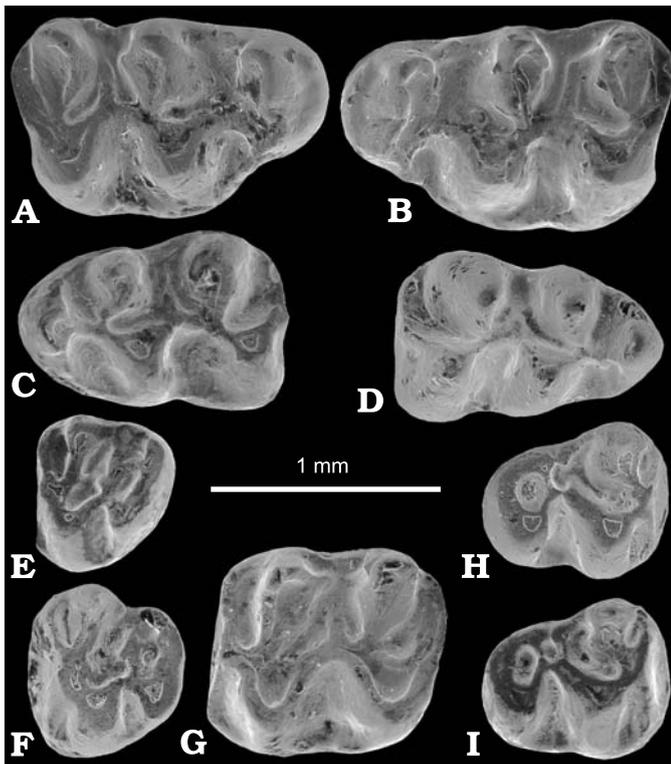


Fig. 2. Cricetodontid rodent *Megacricetodon hellenicus* sp. nov. from the Aliveri South quarry, Greece (MN4, Early Miocene). A. IAUU AL-S-1112, M1 right. B. IAUU AL-S-1114, M1 left. C. IAUU AL-S-1118, M3 left. D. IAUU AL-S-1119, M3 left. E. IAUU AL-S-1122, m1 left. F. IAUU AL-S-1124, m1 right. G. IAUU AL-S-1115, M2 left. H. IAUU AL-S-1128, m3 right. I. IAUU AL-S-1129, m3 right.

Megacricetodon primitivus (Freudenthal, 1963) has a similar size to *M. hellenicus* sp. nov., however, it differs by having M1 with deeply split anterocone, shorter mesoloph and short entoloph; M2 with a higher percentage of ectoloph absent; short entoloph in the M3; in the lower molars all the cusps of the m1 have the same height, shorter mesolophids in the m1 and m2, and a shorter lingual anterolophid of the m2.

Measurements.—See Table 1.

Description.—*M1*: The anterocone is slightly subdivided in five (5/12), it is slightly subdivided with a small platform in front of the furrow in two (2/12), the anterocone is

deeply split with a small platform in front of the furrow in four (4/12) or it is deeply split with a small cingulum ridge in front of it in one (1/12). The labial cone of the anterocone is larger than the lingual one in seven specimens, the two cones are equal in size in four specimens and in the remaining one the lingual cone is larger than the labial. In 12 out of 14 specimens, the anterolophule is connected to the lingual cone of the anterocone, and it is connected between the two lobes of the anterocone in two. The labial spur of the anterolophule is present in eight specimens (in three of them there are two labial spurs) and absent in four. In two teeth, there is a forward paracone spur. The protolophule is posterior (6/11), posterior almost double (4/11) or double (1/11). The entoloph is long and symmetrical, and the sinus is transverse. The ectoloph is strong in one specimen, short in six, and absent in the remaining six. One specimen shows a crest inside the sinus that starts from the entostyl. One out of 13 teeth has a lingual mesocingulum that connects the protocone to the hypocone. The mesoloph is long in two out of 13, medium in nine and short in two. The ectoloph and the mesoloph are never connected. The metalophule is posterior and points backwards in all the specimens (see SOM 3: tables 1–11).

M2: The protolophule is anterior in three specimens and it is anterior almost double in the remaining three. The entoloph is long and angular, with the posterior arm of the protocone better developed than the anterior arm of the hypocone. The sinus is transverse. The ectoloph is strong in four out of six and it is short in two. The mesoloph is long in one, medium in four (in one of them there are two medium mesolophs, Fig. 1J), and short in the remaining one. In three out of six, the ectoloph is connected with the mesoloph. One specimen shows a short crest inside the sinus that starts from the entostyl. The metalophule is anterior (5/6) or it is posterior and points backwards (1/6) (see SOM 3: tables 12–16).

M3: Klein Hofmeijer and De Bruijn (1988) attributed some very large specimens of M3 from North and South quarries to *Megacricetodon*. In our opinion, their morphology and large dimensions (M3 length > 0.80 mm) suggest that they belong to *Democricetodon franconicus* Fahlbusch, 1966 instead of to *Megacricetodon hellenicus*

Table 1. Measurements (in mm) of the upper and lower molars of *Megacricetodon hellenicus* sp. nov. from the North and South quarries, Greece (MN4, Early Miocene). TN, total number of teeth; N, number of teeth measured; min, minimum; max, maximum; σ , standard deviation.

Tooth	Locality	TN	Length					Width				
			N	min	mean	max	σ	N	min	mean	max	σ
M1	AL-N	14	11	1.44	1.49	1.54	0.03	10	0.92	0.96	1.01	0.03
	AL-S	4	4	1.46	1.5	1.53	0.03	3	0.98	0.99	1.01	0.02
M2	AL-N	6	1		1.1			1		0.98		
M3	AL-S	3	3	0.7	0.72	0.76	0.03	3	0.71	0.75	0.8	0.05
m1	AL-N	6	4	1.26	1.3	1.35	0.04	5	0.77	0.82	0.85	0.03
	AL-S	2	2	1.26	1.29	1.31	0.04	2	0.82	0.85	0.87	0.04
m2	AL-N	11	10	1.06	1.11	1.19	0.04	10	0.9	0.93	0.99	0.03
m3	AL-N	1	1		0.89			1		0.73		
	AL-S	2	3	0.87	0.89	0.9	0.02	3	0.76	0.77	0.79	0.02

sp. nov., therefore, there are no M3 known from the type locality. The following description refers to the material from Aliveri South quarry: the labial anteroloph is always present and extends to the paracone. The lingual anteroloph is incipient in one, and long but not connected to the protocone in two specimens. The paracone is well developed. The metacone is present in two out of three specimens. The hypocone is present in the three specimens. The metalophule is connected to the neo-entoloph in two specimens, and it is connected to the neo-entoloph and the protolophule in one. The mesoloph is absent in two out of three specimens. The second protolophule is present in one and incipient in the remaining two. The posterior arm of the protocone is absent. The neo-entoloph and the sinus are always present. The posterosinus is always present (see SOM 3: table 17).

m1: The anteroconid is always rounded and simple. The metalophulid is anteriorly connected in three specimens and is double in one. The lingual mesocingulid is incipient in two and absent in two specimens. The labial mesocingulid is present in three specimens (in one of them the mesocingulid is not connected to the hypoconid), and incipient in two. The mesolophid is medium (2/5) or short (3/5). In one out of six, there is an ectomesolophid. The hypolophulid is always anterior (see SOM 3: tables 18–22).

m2: The lingual anterolophulid is long (5/10) or short (5/10). The labial anterolophulid is long and connected to the protoconid in six specimens or long but disconnected in the remaining four. The lingual mesocingulid is present in four specimens (in three of them, the mesocingulid is not connected to the entoconid), incipient in two and absent in the remaining four. Only one specimen (1/10) has an incipient mesostylid. The labial mesocingulid is well-developed and connected to the hypoconid in two, well-developed and not connected to the hypoconid in four and incipient in the remaining four specimens. In one out of 11 the mesolophid is long, in four it is medium, and in six it is short. The hypolophulid is always anterior (see SOM 3: tables 23–24).

m3: As for the M3, Klein Hofmeijer and De Bruijn (1988) attributed some very large specimens of *m3* to *Megacricetodon*, that should be attributed to *Democricetodon* (*m3* L > 1 mm). Therefore, in our opinion, there is only one available tooth and it is highly corroded. The lingual anterolophulid is short and the labial anterolophulid is long, but not connected to the protoconid. The labial mesocingulid is incipient. The mesoloph is absent (see SOM 3: table 25). To complete the *m3* descriptions the material from Aliveri South quarry is included in the following paragraph: The lingual anterolophulid does not reach the antero-lingual corner of the metaconid in two specimens and reaches it in one specimen. The three specimens have mesolophid, one of them have two (one long, connected to the lingual mesocingulid and the other incipient).

Stratigraphic and geographic range.—Lower Aragonian, Lower Miocene, Greece.

Discussion

The *Megacricetodon* assemblage from the Aliveri South quarry shows similar size and morphology to *M. hellenicus* sp. nov. from the Aliveri North quarry. The small differences, in the relative abundance of some character states, observed between both assemblages, are interpreted as due to the scarce material available from the South quarry (see SOM 3: tables 1–25).

Despite the similar size between *Megacricetodon hellenicus* sp. nov. and *M. primitivus*, these two species show several differences: (i) *M. hellenicus* sp. nov. shows a dental pattern with longer and slender crests that give it a more lophodont aspect than in *M. primitivus*; (ii) *M. primitivus* has upper first molars with shorter mesoloph than *M. hellenicus*, and a short entoloph which posterior arm of the protocone poorly developed. By contrast, in *M. hellenicus* sp. nov. the mesoloph generally is of medium length and the entoloph is long and symmetrical, with transverse sinus; (iii) *M. primitivus* has M2 with a higher percentage of ectolophs absent and entolophs with equal development of the posterior arm of the protocone and the anterior arm of the hypocone. In contrast, in *M. hellenicus* sp. nov. the ectoloph is usually long, and the entoloph is long and angular, with the posterior arm of the protocone better developed than the anterior arm of the hypocone, (iv) the upper third molars of *M. primitivus* show a short neo-entoloph, while in *M. hellenicus* sp. nov. it is well developed (based on material from Aliveri South quarry); (v) in *M. primitivus* the five main cusps of the *m1* have similar height, whereas in *M. hellenicus* sp. nov. the anteroconid is notably lower than the other four cusps (see Fig. 3); (vi) the Spanish species has shorter mesolophids in the *m1* and *m2*, while the Greek species has mesolophids normally short or medium in length.

The study by Oliver and Peláez-Campomanes (2014) of all available material of *M. primitivus* from the Calatayud-Montalbán Basin (type area for the species) demonstrates the remarkable morphological stability shown by this Spanish taxon along the approximately one My of its distribution in the basin. Based on the low morphological variation of *M. primitivus* through time, we interpret the differences between the Spanish and Greek samples (SOM 3, 4) as important enough to consider them as belonging to two different taxa, contrary to the interpretation of Klein Hofmeijer and De Bruijn (1988). These authors assigned the *Megacricetodon* material from Aliveri (North and South quarries) to *M. primitivus*, although they actually recognized and pointed out several dental characters differentiating them. Their interpretation for these morphological differences is that the samples from Aliveri are more primitive than the sample from Valtorres, suggesting the earlier occurrence of *Megacricetodon* in the Eastern Mediterranean than in the Western.

This earlier occurrence of *Megacricetodon* in Greece is supported by different authors that have studied the Greek localities and suggested an early Middle Miocene (early

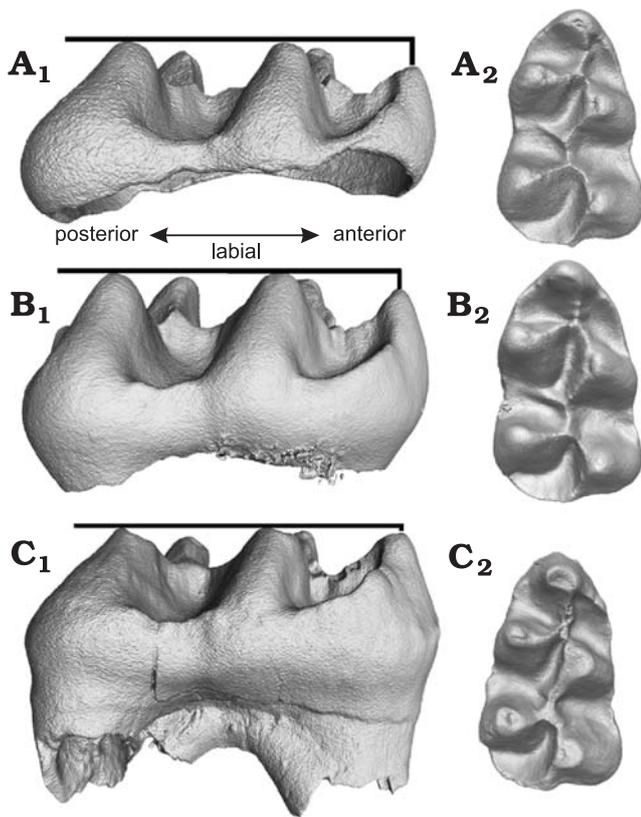


Fig. 3. Micro-CT images, showing the relative height of the five main cusps. In *Megacricetodon hellenicus* sp. nov. (A, IAUU AL-N-2096; B, IAUU AL-N-2097) from Aliveri South quarry, Greece (MN4, Early Miocene) the anteroconid is lower than the rest of the cusps. In *Megacricetodon primitivus* (Freudenthal, 1963) (C, VLT-167) from Valtorres, Spain (MN5, Middle Miocene) the anteroconid is of similar height than the other cusps. Labial (A₁–C₁) and occlusal (A₂–C₂) views.

MN 4) for the Aliveri assemblages (Álvarez-Sierra et al. 1987; Theocharopoulos 2000; Koufos 2006). The presence of the eomyid *Pseudotheridomys parvulus* (Schlosser, 1884) combined with the presence of the modern cricetids such as *Democricetodon*, *Megacricetodon*, and *Cricetodon* has been used to assign a MN 4 age to Aliveri (Álvarez-Sierra et al. 1987). Theocharopoulos (2000), studying the Democricetodontinae, argued that the *Democricetodon franconicus* Fahlbusch, 1966 from Aliveri is slightly more primitive than the material from Karydia and that both are more primitive than the material from Erkertshofen 1, type locality of *D. franconicus*, and Petersburg 2, thus implying an earliest MN 4 for the Aliveri fauna. The relative position between these two Greek localities is further confirmed by the evolutionary stage of *Cricetodon* and *Anomalomys*, and the presence of *Ligerimys* instead of *Pseudotheridomys* in Karydia, indicating a younger position for the latter assemblage (Doukas 2003; Koufos 2006). Based on recent studies on the biostratigraphy of Spanish Aragonian and its correlation to other European basins (Van der Meulen et al. 2011, 2012), the first *Megacricetodon* in the Calatayud-Montalbán Basin is from late MN 4, therefore, much later than the Aliveri fauna.

The Aliveri association is considered to have similar age to the Czech sites of Ořechov and Dolnice 3, based on the presence of *Democricetodon franconicus* and *Pseudotheridomys*. Nevertheless, the Czech *Megacricetodon* cannot be assigned to *M. hellenicus* sp. nov. based on its larger size and different dental morphology. It is remarkable that the first representatives of *Megacricetodon* from other European basins belong to the *Megacricetodon bavaricus* group as defined by Oliver and Peláez-Campomanes (2013). The first *Megacricetodon* from the Swiss and German Molasse are recorded in Langenau 1 and Rauscheröd (Reichenbacher et al. 2013), and assigned to *Megacricetodon* aff. *collongensis* (Mein, 1958) and in France from Pellecabus in the Aquitanian Basin (Ginsburg and Bulot 2000), assigned to *M. aff. bezianensis* Bulot, 1980. All those central European forms show close similarities such as the robustness of the teeth, the slender lower first molars, the long anterolophulid, and especially the elongated anteroconid, with a “crescent” shape, of the m1, as pointed out by Oliver and Peláez-Campomanes (2013), and are clearly different in dental proportions and morphology from the Aliveri material. The morphological differences observed between the early representatives of the *M. bavaricus* group and *M. hellenicus* sp. nov. are important enough to make us think that they represent a different lineage that evolved independently.

This hypothesis is supported by the presence of similar morphological characters, in the *Megacricetodon* material from Aliveri and other younger Greek localities, which are not common in other *Megacricetodon* forms. Vasileiadou and Koufos (2005) indicated that *Megacricetodon* from the locality of Antonios (Macedonia, Greece) shows many similarities with *Megacricetodon* from Aliveri and assigned this material to *M. primitivus*. They also said that *Megacricetodon* from Antonios shows morphological similarities with *M. primitivus* from Valtorres. We do not agree with the allotment of *Megacricetodon* from Antonios neither with *Megacricetodon* from Aliveri, nor with *M. primitivus* (Oliver and Peláez-Campomanes 2014). *Megacricetodon* from Antonios shows a less rounded anteroconid in the m1 and the anterocone is deeply split with a small cingulum ridge in front of it, in the M1, characters that differentiate it from both *M. hellenicus* sp. nov. and *M. primitivus*. Nevertheless, it shows a particular configuration of the sinus on the upper molars that is characteristic of the Greek forms, and that differentiates it from other supposedly contemporaneous European forms like *M. aff. collongensis* from central Europe, *M. bezianensis* from France or *M. primitivus* from Spain.

Therefore, after the detailed study on the assemblages of *Megacricetodon* from Greece and other European basins (Oliver and Peláez-Campomanes 2013, 2014), important differences have been pointed out that enable us to propose the existence of at least three migration events for the early *Megacricetodon* forms.

Figure 4 shows the temporal and geographic distribution of early *Megacricetodon* taxa, indicating the proposed

three distinct *Megacricetodon* forms, which reach Europe in different migration waves, and with different main distribution areas. The earliest European *Megacricetodon* form was endemic of the eastern Mediterranean area and was small sized. It represents a new species described here as *Megacricetodon hellenicus* sp. nov. from the Aliveri localities. The second wave of *Megacricetodon* reached Central-European basins. It involves large-sized forms, included in the *Megacricetodon bavaricus* group, which distributed towards Western Europe till Middle Miocene. And the third form, *Megacricetodon primitivus*, was also small-sized and restricted so far to south-western Europe (Iberian Peninsula and southern France).

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