Morphological analysis of Cricetodon aliveriensis (Rodentia, Mammalia) from the locality of Karydia (Rhodope, Northern Greece)

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RESEARCH PAPER

Morphological analysis of *Cricetodon aliveriensis* (Rodentia, Mammalia) from the locality of Karydia (Rhodope, Northern Greece)

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Abstract

Cricetodon is present in the early Miocene of Greece in six assemblages, *Cricetodon aliveriensis* Klein Hofmeijer and de Bruijn, 1988 in Aliveri and Karydia (both MN4) and *Cricetodon meini* Freudenthal, 1963 in the MN5 localities of Thymiana A and C, Antonios and Komotini. The two MN4 small mammal assemblages in Aliveri (Euboea island) and Karydia (Northern Greece) have several species in common and *Cricetodon aliveriensis* is one of them. The aim of this paper is to record and describe this species, the most abundant rodent in the Karydia assemblage, to compare the morphological variation and to discuss the differences in size between the material of Karydia and Aliveri. The results of this study indicate that we deal with one *Cricetodon* species in Karydia, although more advanced than *Cricetodon aliveriensis* from Aliveri. This study highlights the importance of a detailed morphological description to the size range of a species. The Karydia material shows a large range in length and width measurements that may indicate heterogeneity of samples. However, the morphological similarity and the normal distribution of the *Cricetodon* values support the assignment to only one species.

Keywords Micromammals · Rodentia · *Cricetodon* · Karydia · Greece · Miocene · Variability

Introduction

The tribe Cricetodontini Simpson (1945) "includes a well-distinguishable morphological unit of cricetids", including rodents with large-sized molars (Rummel 1999). Their representatives, throughout history tend to increase the hypsodonty and the simplicity of the molars (Rummel 1999). However, both characteristics seem to be independent which, during the Miocene epoch, led to three morphological phases (Basal, Mosaic and Derived morphology; López-Guerrero et al. 2015). Considering the record of the tribe in Europe and in Asia Minor, it seems to follow the Symmetrical Time Model of Jenkins (1994) where a new species originates as a small population, gradually scatters and expands geographically, undergoes a period of stasis, gradually diminishes and finally becomes extinct when the last small population disappears (Álvarez-Sierra et al. 2013).

Cricetodon has its origin in Anatolia in the locality of Inkonak (MP30) (Ünay et al. 2003) with *C. versteegi* (de Bruijn et al. 1993). In Greece, *Cricetodon* is present in six early Miocene assemblages, *C. aliveriensis* in Aliveri and Karydia (both MN4) and *C. meini* in the MN5 localities of Thymiana A and C (Koufos and Syrides 1997), Antonios and Komotini (de Bruijn et al. 1993; Vasileiadou and Koufos 2005). In Serbia, *Cricetodon* is present in two early Miocene assemblages, *C. aliveriensis* in Snegotin (MN4) and *C.* cf. *meini* in Paragovo (MN5) (Marković and Milivojević 2010). Remarkably, *Cricetodon* is absent from the MN4 locality of Sibnica (Marković et al. 2016). The absence of *Cricetodon*, *Mirrabella*, ground squirrels and ochotonids in Sibnica is interpreted as a signal of a more humid environment in Sibnica (Marković et al. 2016).

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The locality of Karydia (Fig. 1) was discovered by de Bruijn and Foussekis in 1989, located northeast of the town of Komotini (Doukas 2005). It includes three fossiliferous levels in a clay pit 800 m south from the village of Karydia, Karydia 1, Karydia 2 and Karydia 3 (Doukas 2005). All three of them are situated around a hill. All levels seem to be synchronous but the stratigraphy would point to a slightly older Karydia 3 (Doukas and van den Hoek Ostende 2006). Like Aliveri, the Karydia assemblage is attributed to MN 4 based on the presence of the cricetines *Democricetodon* and *Cricetodon* (Theocharopoulos 2000). Based on the evolutionary stage of the Muroidea and the presence of *Galerix kostakii* in Karydia (Doukas and van den Hoek Ostende 2006), which is considered a descendant of *Galerix symeonidisi* (Doukas 1986) firstly described in Aliveri, Karydia is interpreted as younger than Aliveri (Doukas 2003; van den Hoek Ostende et al. 2015). The fauna of Aliveri includes 30 micromammal species compared to the 25 of Karydia and the insectivores and the Spalacidae point to a humid environment (Doukas 2003).

Here, we present the most abundant rodent in all Karydia levels, which provides additional information about the early Miocene fossil record of Greece. Furthermore, we provide a detailed morphological analysis of the species that gives the opportunity to compare it with *Cricetodon* species of comparable age from geographically close localities. Finally, we discuss the morphological variability of its molars and how its abundance may affect it.

Methods

The samples were taken from a small hill southeast of the town of Karydia (41° 8′ 25.87″ N 25° 26′ 32.48″ E) located in the northeast of Greece, where clay was commercially excavated by the brick manufacturer Oxymachon. The first sampling in 1989 by Hans de Bruijn and Dimitri Foussekis was done on an outcrop on the western part of this small hill and yielded five bags of clay (KR1, ca. 75 kg). After processing, this small test sample contained a few rodent molars (ca. 10). In the early nineties, two other levels were sampled from lignitic clay beds on the eastern side of the small hill by Hans de Bruijn, Ioannis Dimitriou and Constantin Doukas (de Bruijn 2017). This provided sample sets KR2 and KR3 (Doukas 2003). KR2: 200 bags of in total circa 3000 kg of clayey sediment. The KR3 sample set is approximately half

Fig. 1 The locality of Karydia

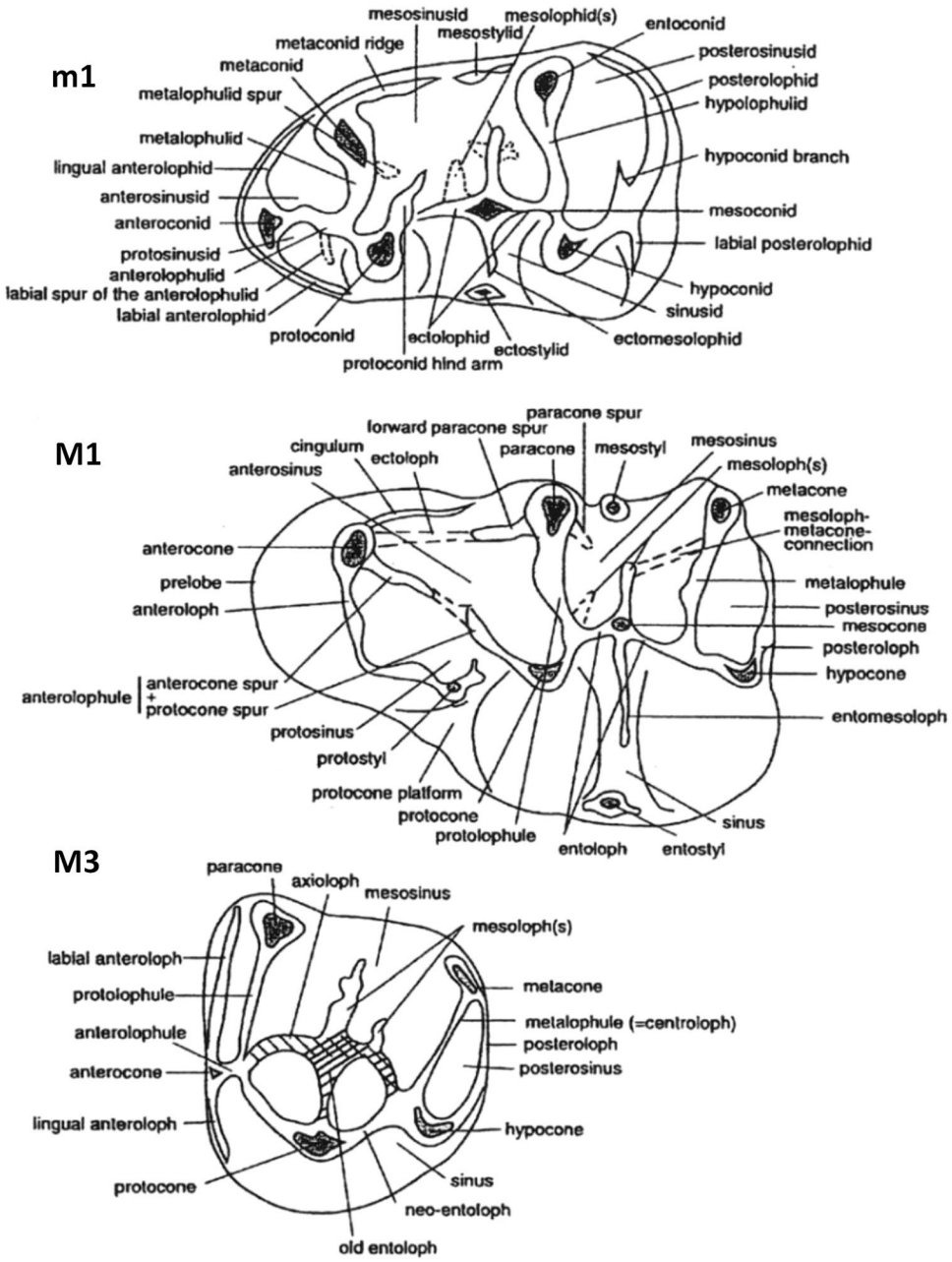

Fig. 2 Terminology of the molars (after Freudenthal et al. 1994)

this size. All material was collected by wet screening on a set of sieves with the finest mesh used being 0.5 mm (Theocharopoulos 2000). The collection from the Karydia locality is stored in the Department of Earth Sciences, Utrecht University. It includes 564 teeth of *Cricetodon* from all Karydia levels. The nomenclature (Fig. 2) used for the description of the molars is after Freudenthal et al. (1994). The dimensions, maximum length (L) and width (W) of the occlusal surface of cheek molars have been measured with a Leitz Ortholux microscope with a mechanical stage and measuring clocks and are given in mm following the procedure suggested by López-Guerrero et al. (2013).

Cricetodon aliveriensis from Karydia and Aliveri have been compared with species of comparable age from geographically close localities. These are, *C. tobieni* from Horlak (MN4, de Bruijn et al. 1993), *C. trallesensis* from Söke (MN4, Çinar Durgut and Ünay 2016), *C. fikreti* from Dededağ (MN4, Çinar Durgut and Ünay 2016), *C. yapintiensis* from Yapıntı (MN3 – 4, Çinar Durgut and Ünay 2016), *C. meini* from Komotini (MN5, de Bruijn et al. 1993), *C. meini* from Antonios (MN5, Vasileiadou and Koufos 2005), *C. kasapligili* from Keseköy (MN3, de Bruijn et al. 1993), *C. magnesiensis* from Kınık (MN3, Çinar Durgut and Ünay 2016) and *C. goklerensis* from Gökler 4A (MN2, Joniak

et al. 2017). The comparison of their dimensions was performed with the usage of their length and width values from the literature.

We tested the normality of the values using the Shapiro–Wilk W test. The Student's t-test was performed on the length of the molars between the *Cricetodon* populations from Karydia and Aliveri. The samples with less than ten molars, have been excluded. Furthermore, we compared the quotients between the average length of the first lower molars and the third from each of the two Greek localities (Lm1/Lm3). The variability values of the *Cricetodon* samples from Karydia were calculated based on M. Freudenthal and Cuenca Bescos (1984). They use coefficient of variability (V′), 100 R/M, where R is the range and M is the sum of the minimum and maximum values divided by 2 (Freudenthal and Martín Suárez 1990). Using this value, they calculated the means of $V'/\sqrt{(\log N)}$, where N is the number of the specimens, in the cricetines and murines.

Systematic paleontology

Order **Rodentia** Bowdich, 1821
Family **Muridae** Illiger, 1811
Subfamily **Cricetodontinae** Stehlin and Schaub, 1951

Genus ***Cricetodon*** Lartet, 1851

Type species. *Cricetodon aliveriensis* Klein Hofmeijer and de Bruijn, 1988

Comparative species. (Species similar in size with comparable age from localities of nearby areas): *Cricetodon meini* Freudenthal, 1963, *C. aliveriensis* Klein Hofmeijer and de Bruijn, 1988, *C. tobieni* de Bruijn et al. 1993, *C. kasapligili* de Bruijn et al. 1993, *C. fikreti* Çinar Durgut and Ünay, 2016, *C. trallesensis* Çinar Durgut and Ünay, 2016, *C. yapintiensis* Çinar Durgut and Ünay, 2016, *C. magnesiensis* Çinar Durgut and Ünay, 2016 and *C. goklerensis* Joniak et al. 2017.

Studied material. 563 teeth (*M*1: $n = 112$, *M*2: $n = 122$, *M*3: $n = 70$, *m*1: $n = 96$, *m*2: $n = 100$, *m*3: $n = 63$) (coll. KR1 501 – 552; KR2 421 – 494 and 1002 – 1422; KR3 1071 – 1290) from the early Miocene (MN4) locality of Karydia (KR) (KR1 + KR2 + KR3), Rhodope, Northern Greece.

Description. The width of the first upper molar is reduced on the antero-lingual part. M1 has strong and high cusps leaning to the posterior side. Protocone and hypocone lean towards the buccal side of the tooth. M1 has four long and wide roots and a strong and well-developed crown base, especially on the side borders of the molar. On the anterior part of the tooth, the anterocone is split and its two cusps are connected. A small linear fissure extends on their anterior side. The protostyle is not connected to the anterolophule in most specimens (Table 1: M1, A). If connected, it separates the protosinus into two parts. Furthermore, the protocone is connected to the double anterocone via the anterolophule (Table 1: M1, B). Most of the specimens have the anterior part of the anterolophule splitting into two ridges with the buccal branch of the anterolophule ending free in the anterosinus close to the anterocone spur. Additionally, the morphologies of the protocone and the paracone are variable with the spur of last appeared more often (Table 1: M1, C and D). Towards the posterior part of the tooth the entoloph reaches the meeting point of the protolophule and the protocone's posterior arm. Moreover, the mesoloph extends towards the buccal border of the tooth (Table 1: E) being connected almost half of the time to the metacone and the rest of them ending free at the mesosinus. On the posterior part of the tooth, the posteroloph is connected to the hypocone and, in the majority of the molars, to the posterior part of the metacone (Table 1: M1, F).

M2 is a square-shaped tooth with four long and wide roots. A strong base of the crown runs on the lingual side of the molar. The cusps are strong and high, leaning to the posterior side. Moreover, the protocone and the hypocone lean towards the buccal side of the tooth. On the anterior part of the tooth, the labial anteroloph is well developed and connected to the base of the paracone. On the other hand, the lingual anteroloph is variable in its development, but commonly relatively strong (Table 1: M2, A). Its connection to the protocone is also variable. In addition, the anterolophule, starting from the protocone, expands towards the labial side of the tooth and it ends at its anterior border of it. The entoloph meets the protolophule and the posterior arm of the protocone. The morphologies of the protocone and the paracone are variable with a robust protocone being developed in most of the molars (Table 1: M2, B and C). Moreover, the mesoloph extends towards the buccal border of the tooth (Table 1: M2, D). Most of the molars have a long mesoloph. However, there is a representative number of specimens with a short one. On the posterior part of the tooth, the posteroloph is thinner than in M1 and connects the hypocone with the metacone (Table 1: M2, E). Most of the molars have the posteroloph extending behind the metacone and ending at the buccal border of the tooth. The posterosinus is then divided into two parts.

M3 is the smallest of the three upper molars, with three roots. M3 has four cusps but the metacone is small and linear, placed on the buccal border of the tooth. The width of the tooth is reduced on the posterior part. Besides the metacone, the other three cusps are strong and high, leaning

Table 1 Morphological variations of the molars of *Cricetodon aliveriensis* from Aliveri and Karydia

Variation	M1	Karydia		Aliveri	
		n	%	*n*	%
A	The protostyle is connected to the anterolophule separating the protosinus in two parts	37	46.3	11	91.7
	The protostyle is not connected to the anterolophule	43	53.8	1	8.3
B	The protocone is connected to the lingual anterocone via a simple anterolophule	38	52.1	9	69.2
	The anterior part of the anterolophule splits in two ridges, one connecting to the lingual and the other one to the buccal anterocone	11	15.1	1	7.7
	The anterior part of the anterolophule splits in two ridges with only the lingual branch connecting to the lingual anterocone while the buccal one ending freely in the anterosinus	11	15.1	3	23.1
	The anterior part of the anterolophule splits in two ridges with the buccal branch of the anterolophule ending freely in the anterosinus close to the buccal anterocone spur	13	17.8	–	–
C	The posterior paracone spur is present	53	57.6	7	53.8
	The posterior paracone spur is absent	39	42.4	6	46.2
D	The protocone is robust	40	41.7	6	46.2
	The protocone is not robust	56	58.3	7	53.8
E	The mesoloph is connected to the metacone	48	51.6	3	25
	The mesoloph stops freely at the mesosinus	45	48.4	9	75
F	The posteroloph ends behind the metacone	61	80.3	9	69.2
	The posteroloph ends at the metacone	15	19.7	4	30.8
Variation	M2	Karydia		Aliveri	
		n	%	*n*	%
A	The lingual anteroloph is well developed	103	94.5	13	100
	The lingual anteroloph is not developed	6	5.5	–	–
B	The posterior paracone spur is present	39	36.5	8	61.5
	The posterior paracone spur is absent	68	63.6	5	38.5
C	The protocone is robust	67	63.8	8	61.5
	The protocone is not robust	38	36.2	5	38.5
D	The mesoloph is short ending freely in the mesosinus	38	33.6	3	23.1
	The mesoloph is long ending freely in the mesosinus	48	42.5	9	69.2
	The mesoloph ends at the base of the metacone	26	23	1	7.7
	The mesoloph ends at the buccal border of the tooth	1	0.9	–	–
E	The posteroloph crosses the metacon expanding towards the buccal border of the tooth and stops at the posterior base of the metacon separating the posterosinus in two parts	36	38.7	4	50
	The posteroloph continues behind of the metacone and ends at the buccal border of the tooth separating the posterosinus in two parts	39	41.6	4	50
	The posteroloph ends at the metacone	18	19.4	–	–
Variation	M3	Karydia		Aliveri	
		n	%	*n*	%
A	The anterolophule connects to the labial and the lingual anteroloph	56	98.3	14	100
	The anterolophule connects only to the labial anteroloph	1	1.7	–	–
B	Only the protocone has a posterior spur	17	27.9	1	6.7
	Only the paracone has a posterior spur	7	11.5	7	46.7
	The protocone is robust and the paracone has a posterior spur	26	42.6	5	33.3
	Neither of them is developed	11	18	2	13.3
C	The mesoloph has a medium size and ends freely in the mesosinus	16	25.4	6	46.2
	The mesoloph is long ending at the buccal border of the tooth near the metacone	33	52.4	6	46.2
	The mesoloph is short ending in the mesosinus opposite to another short ridge starting from the buccal border of the tooth without a connection	10	15.2	–	–
	The mesoloph is short without any connection	4	6.4	1	7.7

Table 1 (continued)

Variation	M3	Karydia		Aliveri	
		n	%	*n*	%
D	The posteroloph connects the hypocone with the metacone while the metalophule is well developed	58	66.7	9	69.2
	Only the posteroloph is present	14	16.1	1	7.7
	Only the metalophule is present	7	8.1	1	7.7
	The posteroloph connects the hypocone with the metacone while the metalophule is not well developed	6	6.9	2	15.4
	The posteroloph and the metalophule are underdeveloped	1	1.2	–	–
	An extra ridge is developed starting from the metalophule ending freely in the mesosinus	1	1.2	–	–
Variation	m1	Karydia		Aliveri	
		n	%	*n*	%
A	The labial spur of the anterolophulid is well developed	2	2.6	2	10.5
	The labial spur of the anterolophulid is not developed	76	97.4	17	89.5
	The anterolophulid is well developed and connected to the simple anteroconid while an underdeveloped metalophulid is present	4	5.7	1	5.3
	The anterolophulid and the metalophulid are well developed and connected to a single ridge that ends to the simple anteroconid	10	14.3	4	21.1
B	The anterolophulid and the metalophulid, separately from each other, connect to the simple anteroconid	28	40	12	63.2
	The anterolophulid and the metalophulid are well developed and connected to the simple anteroconid, both of them with an extra short ridge, opposite the other without a connection	13	18.6	–	–
	Only the metalophulid is present ending to the anteroconid	4	5.7	–	–
	The anterolophulid is connected to the metalophulid making a 90 degrees' angle with the latter connected to the anteroconid	5	7.1	1	5.3
	The metalophulid is connected to the anterolophulid making a 90 degrees' angle with the latter connected to the anteroconid	2	2.9	1	5.3
C	The ectomesolophid is present ending freely in the sinusoid	57	63.4	17	81
	The ectomesolophid is absent	33	36.7	4	19.1
	The mesolophid and the ectolophid are connected to the metaconid	22	28.2	2	11.8
	Only the ectolophid is connected to the metaconid	9	11.5	3	17.7
	The ectolophid connects with the metaconid but the mesolophid is underdeveloped ending freely at the mesosinus	31	39.7	12	70.6
D	The ectolophid connects with both the protoconid's hind arm and the metalophulid spur	8	10.3	–	–
	There is no connection to the metaconid	3	3.8	–	–
	There are two mesolophids with only the one being connected to the metaconid while the other one ending freely in the mesosinusid	1	1.3	–	–
	There is no connection to the metaconid but the mesolophid is well developed and ends freely in the mesosinusid	4	5.1	–	–
Variation	m2	Karydia		Aliveri	
		n	%	*n*	%
A	The ectomesolophid is short ending freely in the sinusid	13	14.3	3	37.5
	The ectomesolophid is long ending freely in the sinusid	5	5.5	–	–
	There ectomesolophid is absent	73	80.2	5	62.5
B	The mesolophid is small ending freely in the mesosinusid	28	32.2	6	75
	The mesolophid is long ending freely in the mesosinusid	36	41.4	–	–
	The mesolophid is connected to the base of the metaconid	23	26.4	2	25
C	The labial posterolophid is present	57	73.1	7	87.5
	The labial posterolophid is absent	21	26.9	1	12.5

Table 1 (continued)

Variation	m3	Karydia		Aliveri	
		n	%	*n*	%
A	The mesolophid is long ending freely in the mesosinusid	38	61.3	12	85.7
	There mesolophid is absent	3	4.8	–	–
	The mesolophid is connected to the base of the metaconid	21	33.9	2	14.3

n number of the molars

to the posterior side. Moreover, the protocone and the hypocone lean towards the buccal side of the tooth. The anterolophule, starting from the protocone, connects either to both the lingual and labial anterolophs or only to the labial one. The double connection is more common (Table 1: M3, A). Additionally, the development of the robust protocone, the paracone posterior spur, as well as the mesoloph varies (Table 1: M3, B and C). Most often the protocone is robust and the paracone has a posterior spur and the mesoloph is long, ending at the buccal border of the tooth near the metacone. Finally, the morphology of the posterior part of the tooth also alters (Table 1: M3, D). The dominant variation is this where the posteroloph connects the hypocone with the metacone while the metalophule is well developed.

The outline of the m1 is elongated. It has five strong and high cusps, leaning to the anterior side. In addition, it has two double and long roots. The simple anteroconid is symmetric with the lingual and labial anterolophid, well developed or not, surrounding the protosinusid and the anterosinusid. The morphology of the anterior part of the molar varies, especially those of the anterolophulid and the metalophulid (Table 1: m1, A and B). All the molars but two do not have the labial spur of the anterolophulid. The anterolophulid and the metalophulid most often connect independently to the simple anteroconid. An addition and posterior oriented metalophulid, weaker than the anterior, is present. The ectomesolophid may or may not be present (Table 1: m1, C). Most of the teeth have the ectomesolophid ending free in the sinusid. The development of the ectolophid and the mesolophid varies (Table 1: m1, D). The most common variation is the connection of the ectolophid with the metaconid and the underdeveloped mesolophid, ending freely at the mesosinusid. Finally, the posterolophid starts from the hypoconid and reaches the lingual border of the tooth encircling the posterosinusid.

The second lower molar is a square-shaped tooth with four strong and high cusps, leaning to the anterior side. The m2 has two double roots. The protoconid and the hypoconid lean towards the buccal side of the tooth. There is no anteroconid. The anterolophulid, starting from the protoconid, ends at the meeting point of the lingual and labial anterolophids. The ectolophid is developed towards the anterior part of the tooth and connects with the protoconid. The morphologies of the ectomesolophid and the mesolophid vary (Table 1: m2, A). The ectomesolophid is not developed in the majority of the molars. The mesolophid is most often long ending freely in the mesosinusid (Table 1: m2, B). On the posterior part, the posterolophid starting from the hypoconid, reaching the lingual border of the tooth and encircling the posterosinusid (Table 1: m2, C).

The posterior part of the m3 is reduced. It has a triangular outline with three wide roots. Its cusps lean towards the anterior side. The anterior half of the tooth that includes the anterolophulid, the labial and the lingual anterolophid, the protoconid and the metaconid, is similar to the m2. Furthermore, towards the posterior part, the ectolophid connects the protoconid to the base of the mesolophid. The morphology of the mesolophid in the middle part of the tooth varies (Table 1: m3, A). Most of the molars have a long mesolophid ending freely in the mesosinusid. In one of the specimens, the anterior wall of the entoconid is connected with the mesolophid which also connects to the metaconid. In the posterior part of the tooth the entoconid is connected to the ectolophid via the hypolophulid.

Remarks. From a morphological point of view, all *Cricetodon* specimens from the three fossiliferous levels belong to the same species. They have similar size (Tables 2, 3, 4) and share the wrinkled enamel, the presence of the double anterocone, the four roots and the absence of the ectoloph in M1 and the two, opposite oriented metalophulids in m1. The material includes one size group depicted by well-developed overlapping point clusters (Figs. 3, 4, 5, 6, 7, 8). Its large size range (Table 5) as well as that of Aliveri (Table 6) were tested using the Shapiro–Wilk W test. The populations from Karydia showed normally distributed values (Table 7; Figs. 9, 10). The only result below the critical value ($p = 0.05$) is that of the m1 from Karydia (1 + 2 + 3) ($p = 0.0498$). Furthermore, concerning Aliveri, M2 and m3 do not fit in a normal distribution ($p < 0.05$) but these results are based on its small specimen number.

The large similarity of *Cricetodon* from Karydia with the type material of Aliveri indicates that it belongs to

Cricetodon aliveriensis. The material from Karydia and Aliveri share the same root number, the double antero-cone without an ectoloph in M1 and the presence of two metalophulids in m1. Their cusps connected by long and transversal ridges, the mesoloph and the mesolophid are present and the enamel is thick and wrinkled. The cricetine from Karydia differs from Aliveri by its shorter or absent ectomesolophid and the shorter anterolophs. It is also larger than the specimens from Aliveri (Tables 5, 6) which fall in the lower range of the Karydia measurements. Although some larger molars are present in Aliveri such as the m3 AL648 and AL660 (Fig. 10). Dividing the average length of the first lower molars with the third from both localities results in almost identical ratios with 1.08 for Karydia and 1.05 for Aliveri. In contrast to the results so far, the Student's *t*-test performed on the length of all the molars comparing the two *Cricetodon* species from the two Greek localities gave a probability that the two samples come from a single population of less than 1 percent (Table 8). However, these statistical results are based on the small specimen number of Aliveri; thus, the true variation within the Aliveri specimens cannot be calculated.

Among the *Cricetodon* molars from the locality of Karydia (Figs. 11, 12), one distinct m3 (KR 2, 1001) has the size and all the morphological characters of the *Cricetodon* from Karydia but the posterior part of the tooth includes an extra ridge, not typical for *C. aliveriensis* (Fig. 12p).

Cricetodon aliveriensis from Karydia has been compared with species from geographically close localities with comparable age (Figs. 13, 14). The range in size of *Cricetodon aliveriensis* from Karydia overlaps many of the Turkish species, such as *C. tobieni* from Horlak (de Bruijn et al. 1993), *C. yapintiensis* from Yapıntı (Çinar Durgut and Ünay 2016), *C. kasapligili* from Keseköy (de Bruijn et al. 1993), *C. magnesiensis* from Kinik (Çinar Durgut and Ünay 2016) and *C. goklerensis* from Gökler (Joniak et al. 2017). However, their morphology differs. *Cricetodon aliveriensis* from Karydia differs from *C. tobieni* by the four roots of the M1, the shorter paracone spur and a more elongated M3. It differs from *C. yapintiensis* by the number of the roots

Table 2 Material and measurements of *Cricetodon* from the locality of Karydia 1 (mm)

	Length				Width			
	N	Min	Max	Mean	*N*	Min	Max	Mean
M1	–	–	–	–	2	1.45	1.56	1.51
M2	–	–	–	–	–	–	–	–
M3	2	1.70	1.79	1.75	2	1.46	1.46	1.46
m1	1	1.89	1.89	1.89	2	1.29	1.62	1.46
m2	1	1.84	1.84	1.84	2	1.55	1.56	1.56
m3	–	–	–	–	1	1.53	1.53	1.53

Table 3 Material and measurements of *Cricetodon* from the locality of Karydia 2 (mm)

	Length				Width			
	N	Min	Max	Mean	*N*	Min	Max	Mean
M1	33	2.20	2.76	2.49	47	1.43	1.85	1.66
M2	52	1.66	2.13	1.93	52	1.38	1.83	1.65
M3	63	1.48	1.93	1.73	64	1.35	1.66	1.52
m1	79	1.97	2.50	2.21	89	1.24	1.56	1.39
m2	72	1.70	2.23	2.00	75	1.44	1.81	1.59
m3	52	1.85	2.25	2.05	53	1.37	1.67	1.52

Table 4 Material and measurements of *Cricetodon* from the locality of Karydia 3 (mm)

	Length				Width			
	N	Min	Max	Mean	*N*	Min	Max	Mean
M1	48	2.25	2.88	2.52	59	1.39	1.90	1.65
M2	67	1.72	2.20	1.95	68	1.48	1.83	1.64
M3	1	1.87	1.87	1.87	1	1.59	1.59	1.59
m1	3	1.94	2.14	2.04	2	1.28	1.59	1.44
m2	13	1.87	2.11	1.96	20	1.46	1.86	1.61
m3	3	1.97	2.07	2.01	8	1.45	1.60	1.51

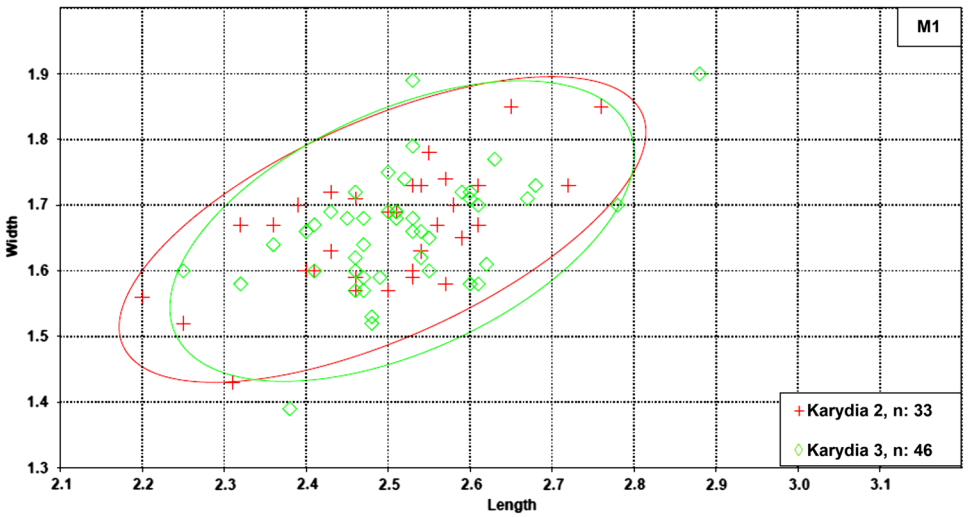

Fig. 3 L/W scatter plot of the M1 from *Cricetodon aliveriensis* from Karydia

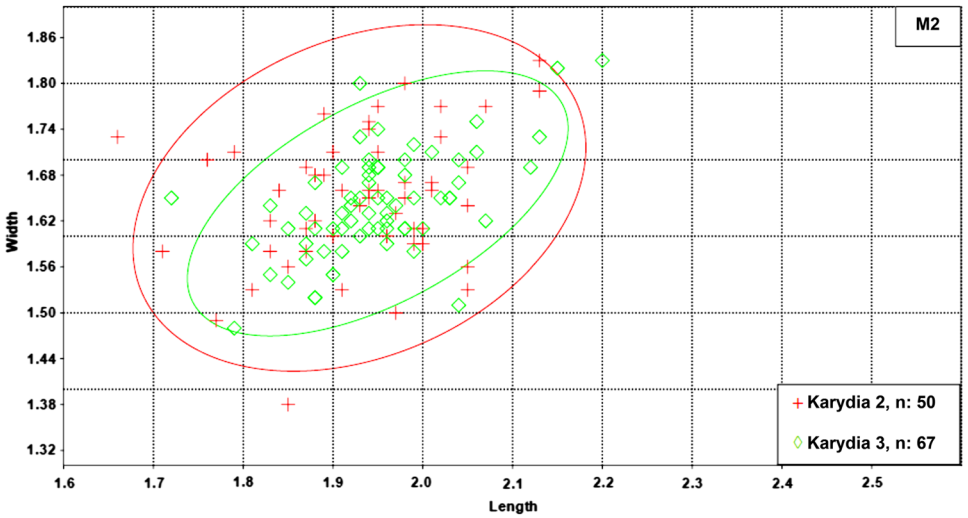

Fig. 4 L/W scatter plot of the M2 from *Cricetodon aliveriensis* from Karydia

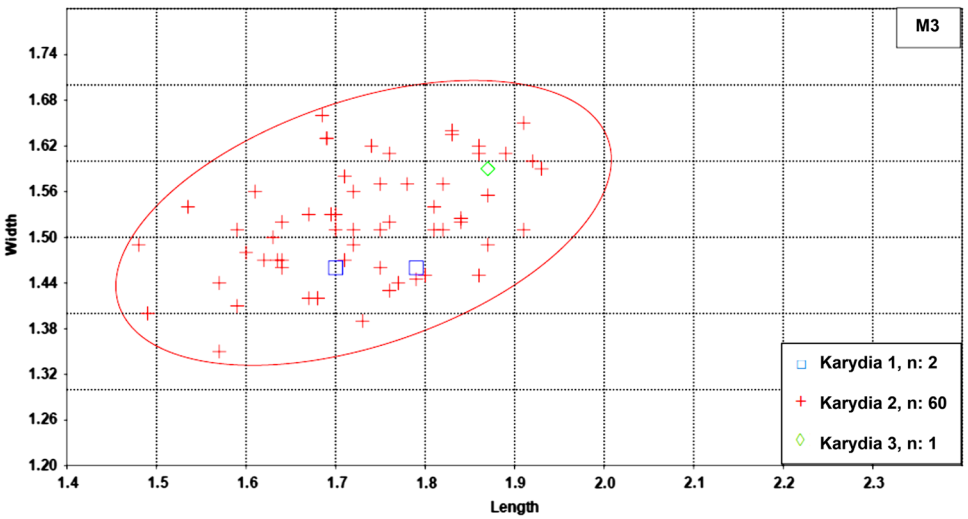

Fig. 5 L/W scatter plot of the M3 from *Cricetodon aliveriensis* from Karydia

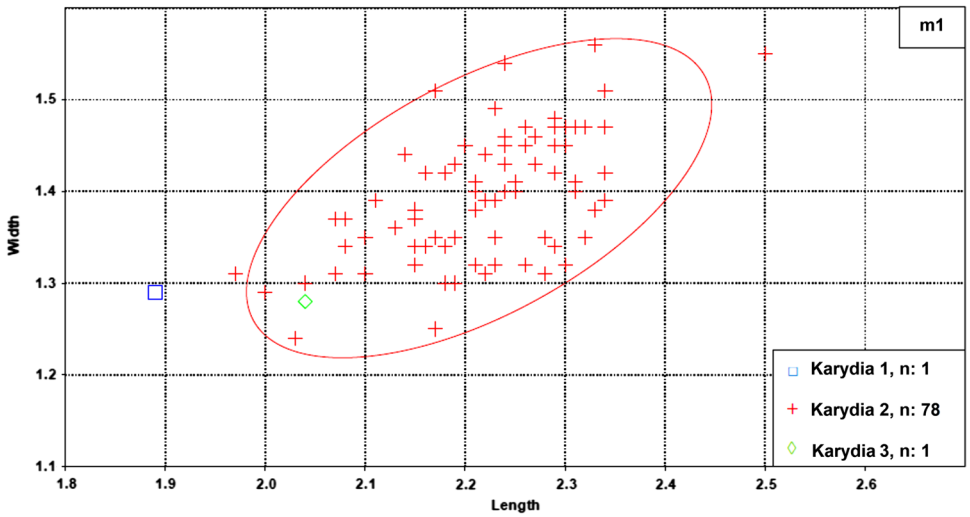

Fig. 6 L/W scatter plot of the m1 from *Cricetodon aliveriensis* from Karydia

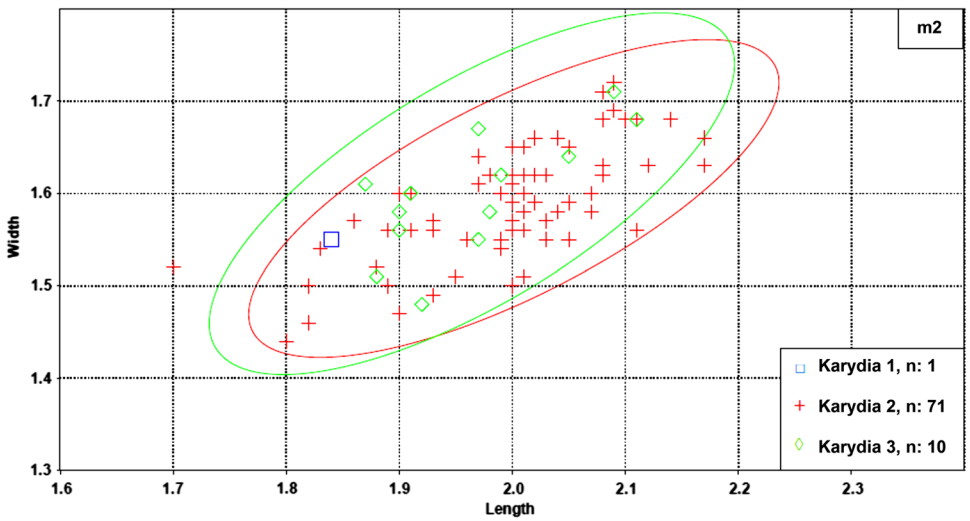

Fig. 7 L/W scatter plot of the m2 from *Cricetodon aliveriensis* from Karydia

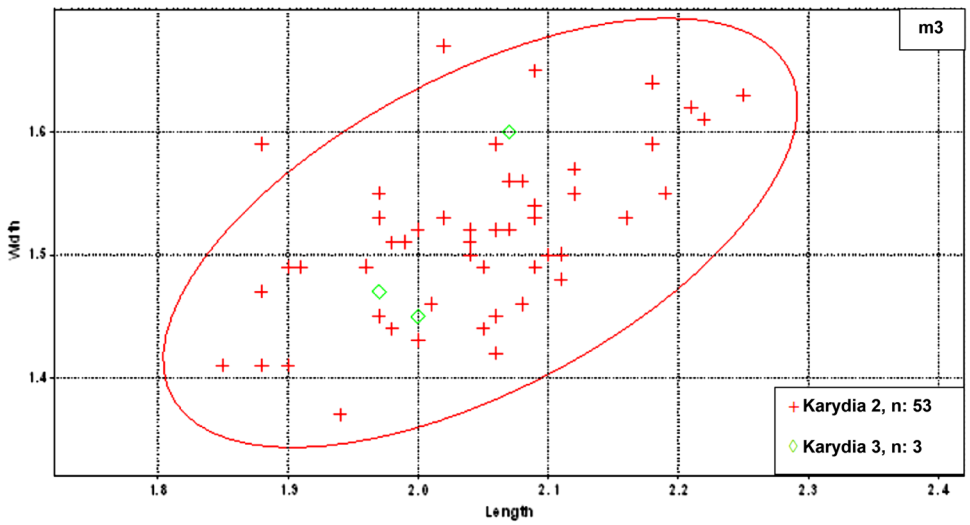

Fig. 8 L/W scatter plot of the m3 from *Cricetodon aliveriensis* from Karydia

Table 5 Material and measurements of *Cricetodon* from the locality of Karydia (1 + 2 + 3) (mm)

	Length				Width			
	N	Min	Max	Mean	*N*	Min	Max	Mean
M1	81	2.20	2.88	2.50	108	1.39	1.90	1.65
M2	119	1.66	2.20	1.94	120	1.38	1.83	1.64
M3	66	1.48	1.93	1.73	67	1.35	1.66	1.52
m1	83	1.89	2.50	2.21	93	1.24	1.62	1.39
m2	86	1.70	2.23	1.99	97	1.44	1.86	1.60
m3	55	1.85	2.25	2.05	62	1.37	1.67	1.52

Table 6 Material and measurements of *Cricetodon aliveriensis* from the locality of Aliveri South Quarry (Klein Hofmeijer et al. 1988) (mm)

	Length				Width			
	N	Min	Max	Mean	*N*	Min	Max	Mean
M1	13	2.23	2.52	2.35	13	1.46	1.63	1.53
M2	13	1.78	1.98	1.84	13	1.47	1.63	1.54
M3	15	1.51	1.71	1.63	15	1.39	1.53	1.45
m1	21	1.90	2.14	2.03	21	1.21	1.39	1.28
m2	9	1.72	1.94	1.84	9	1.41	1.54	1.48
m3	16	1.77	2.20	1.93	16	1.31	1.68	1.44

Table 7 Shapiro–Wilk normality test of Cricetodon from the locality of Karydia (1 + 2 + 3), Karydia 2, Karydia 3 and Aliveri

Locality	Length	M1	M2	M3	m1	m2	m3
Karydia 2	*N*	33	52	63	79	72	52
	Standard deviation	0.12	0.10	0.11	0.09	0.09	0.10
	Shapiro–Wilk W	0.9810	0.9864	0.9855	0.9784	0.9709	0.9804
	p (normal)	0.8146	0.8121	0.6676	0.2007	0.0941	0.5416
Karydia 3	*N*	48	67	1	3	13	3
	Standard deviation	0.11	0.08	–	–	0.08	–
	Shapiro–Wilk W	0.9526	0.9748	–	1	0.9097	0.9494
	p (normal)	0.0507	0.1916	–	1	0.1815	0.5665
Karydia (1 + 2 + 3)	*N*	81	119	66	83	86	55
	Standard deviation	0.11	0.09	0.11	0.10	0.09	0.09
	Shapiro–Wilk W	0.9756	0.9883	0.9848	0.9701	0.9842	0.9823
	p (normal)	0.1248	0.4041	0.5951	0.0498	0.3809	0.5923
Aliveri	*N*	13	13	15	21	9	16
	Standard deviation	0.09	0.07	0.06	0.07	0.07	0.10
	Shapiro–Wilk W	0.9165	0.7655	0.9666	0.9682	0.9737	0.8753
	p (normal)	0.2249	0.0027	0.8054	0.6925	0.9245	0.0328

in M1 and the well-developed lingual anteroloph in almost all of the specimens and a shorter ectomesolophid in m1. It differs from *C. kasapligili* by a more advanced morphology, the four-rooted M1, the anterocone is well separated and in m1 the lingual and labial anterolophids are better developed. It differs from *C. goklerensis* by the presence of a mesolophid and its longer ectomesolohpid in m1. Compared to *C. magnesiensis* it has lower cusps and a much weaker paracone spur in M1. *Cricetodon aliveriensis* is smaller than *Cricetodon meini* from the MN5 localities Antonios and Komotini, Greece (de Bruijn et al. 1993; Vasileiadou and Koufos 2005), with a well-separated anterocone in M1 and anteriorly developed metalophulid in m1. *Cricetodon aliveriensis* from Karydia is smaller than the Turkish *C. fikreti* (Çinar Durgut and Ünay 2016) with a weaker paracone spur and longer mesoloph in M1 and M2 and smaller than *C. trallesensis* (Çinar Durgut and Ünay 2016) by its lower cusps.

The method of Freudenthal and Cuenca Bescos (1984) is used to calculate the variability values of the length and width of the *C. aliveriensis* sample from Karydia and the results are presented in Table 9. This calculation does not

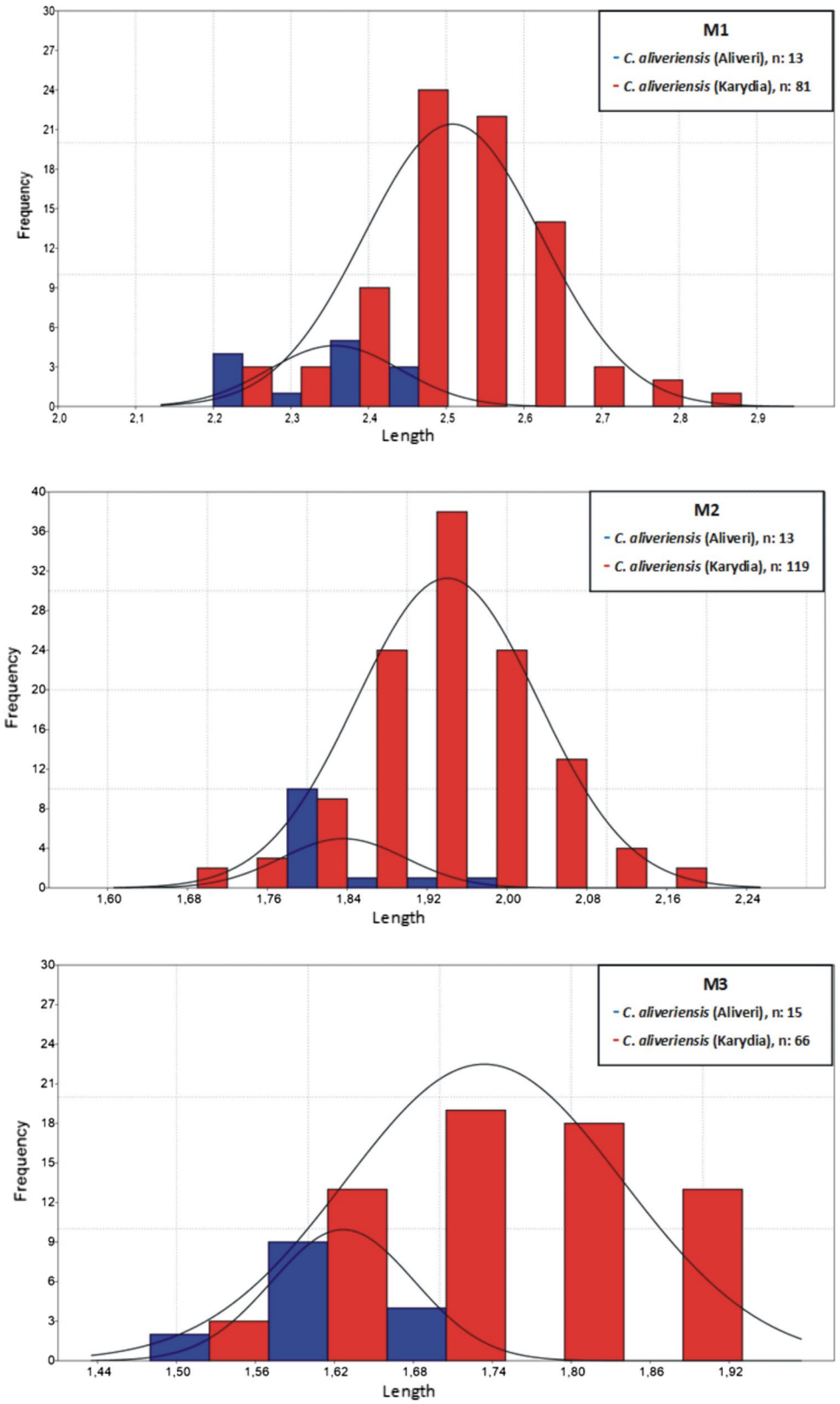

Fig. 9 Length distribution of the upper molars from *Cricetodon aliveriensis* of Aliveri and Karydia (1 + 2 + 3)

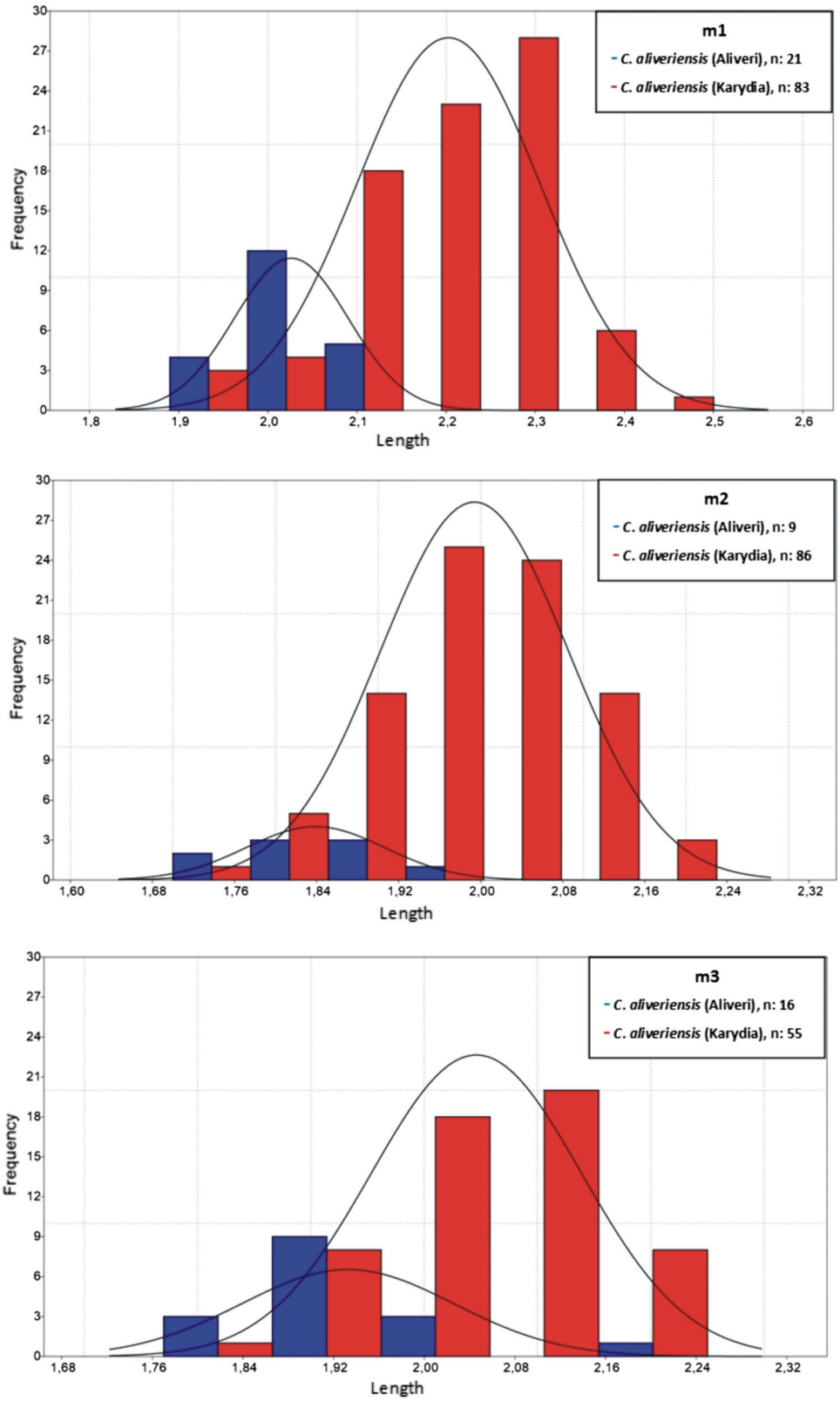

Fig. 10 Length distribution of the lower molars from *Cricetodon aliveriensis* of Aliveri and Karydia (1 + 2 + 3)

include elements with less than 5 samples and as a result Karydia 1 is not presented in the table. Karydia 2 as well as the combination of all three layers indicate that the variability is higher than the average values of the cricetines in M1, M2, m1 and m2 and normal in M3 and m3. Regarding Karydia 3, the variability of the M1 and M2 as

Table 8 Student's *t*-test comparing the average size values between the populations of Karydia and Aliveri

Width	Karydia (1 + 2 + 3)		Aliveri		*t*	*p*
	N	Variance	*N*	Variance		
M1	108	0.00907	13	0.00361	4.3824	< 0.05
M2	120	0.00603	13	0.00248	4.5924	< 0.05
M3	67	0.00541	15	0.00172	3.5149	< 0.05
m1	93	0.00588	21	0.00163	6.5738	< 0.05
m3	62	0.00440	16	0.00789	3.7698	< 0.05
Length	*N*	Variance	*N*	Variance	*t*	*p*
M1	81	0.01316	13	0.00781	4.5570	< 0.05
M2	119	0.00836	13	0.00423	3.9905	< 0.05
M3	66	0.01127	15	0.00314	3.7770	< 0.05
m1	83	0.01074	21	0.00427	7.4163	< 0.05
m3	55	0.00881	16	0.00938	4.2283	< 0.05
Width	Karydia 2		Aliveri		*t*	*p*
	N	Variance	*N*	Variance		
M1	47	0.00726	13	0.00361	4.9835	< 0.05
M2	52	0.00793	13	0.00248	4.0338	< 0.05
M3	64	0.00547	15	0.00172	3.5347	< 0.05
m1	89	0.00486	21	0.00163	7.0350	< 0.05
m3	53	0.00472	16	0.00789	3.6313	< 0.05
Length	*N*	Variance	*N*	Variance	*t*	*p*
M1	33	0.01515	13	0.00781	3.6617	< 0.05
M2	52	0.00991	13	0.00423	3.1293	< 0.05
M3	63	0.01144	15	0.00314	3.6568	< 0.05
m1	79	0.00867	21	0.00427	8.6163	< 0.05
m3	52	0.00915	16	0.00938	4.2066	< 0.05
Width	Karydia 3		Aliveri		*t*	*p*
	N	Variance	*N*	Variance		
M1	59	0.01008	13	0.00361	4.0674	< 0.05
M2	68	0.00465	13	0.00248	4.9861	< 0.05
Length	*N*	Variance	*N*	Variance	*t*	*p*
M1	48	0.01184	13	0.00781	4.9354	< 0.05
M2	67	0.00705	13	0.00423	4.6302	< 0.05

well as that of the m2 width is high. On the other hand, the variability of the m2 length and the m3 width is close to the average values.

Discussion and conclusions

This study highlights the importance of having sufficient fossil material in order to access the intraspecific variation. *Cricetodon* is the most abundant rodent in all Karydia levels. All its molars from all three levels share the elongated shape with the well-separated double anterocone, the distinguished, robust and strong cusps and cuspids with the wrinkled and thick enamel and the absence of the ectoloph in the M1, which are typical characteristics of *Cricetodon aliveriensis*. The Karydia material shows a large range in length and width measurement. The method of Freudenthal and Cuenca Bescos (1984) was used to further investigate the intraspecific variation of the species. The variability values of the first and second molars are higher than the average cricetine values and normal of the third, which can be interpreted by a variety of reasons, such as the initial separation into two species, relatively large time span or differences between measurements of fresh and worn specimens

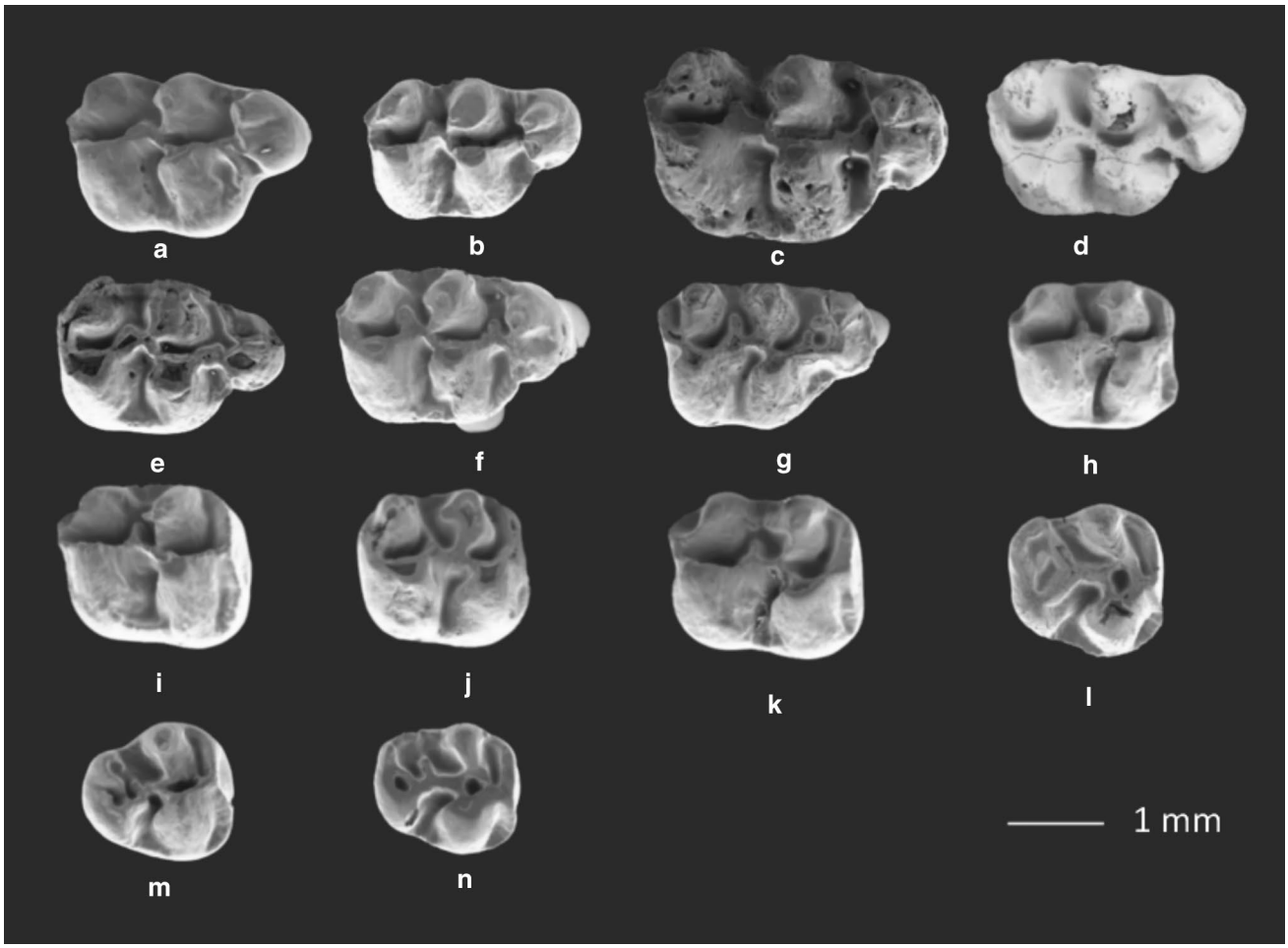

Fig. 11 *Cricetodon aliveriensis* upper molars from the locality of Karydia (M1: **a**: KR3, 1086/ **b**: KR3, 1090/ **c**: KR3, 1071/ **d**: KR3, 1091/ **e**: KR3, 1074/ **f**: KR3, 1082/ **g**: KR2, 1311/ M2: **h**: KR2, 1381/ **i**: KR2, 1363/ **j**: KR2, 1377/ **k**: KR2, 1381/ M3: **l**: KR2, 1407/ **m**: KR2, 1404/ **n**: KR2, 1056)

due to hypsodonty (Freudenthal and Martín Suárez 1990). The presence of a large m3 specimen in Aliveri, which is comparable with the larger values of Karydia, indicates that also some larger *C. aliveriensis* were present in Aliveri. The morphological similarity next to the normal distribution of the values of their dimension and the almost identical ratios from the division the average length values of the first and third lower molars despite the great difference between the number of specimens in Aliveri and Karydia do support the assignment to one species, *Cricetodon aliveriensis*. Apart from the overall morphological similarity of the two Greek *Cricetodon* occurrences in MN4, *Cricetodon aliveriensis* in Karydia appears to be more advanced than in Aliveri. In particular, some of the divergent characters of the specimens are the reduction or the disappearance of the ectomesolophid, the reduction of the anterolophs and the increase of the teeth size in Karydia. The different allotment of the morphological characters between the molars of Aliveri and Karydia may be correlated with the abundance of this species in the latter. Peláez-Campomanes et al. (2015) correlate environmental changes with to primary productivity.

In contrast to the previous assumptions indicating that the two *Cricetodon* species from Karydia and Aliveri belong to the same species, the Student's *t*-test performed on their molar length, gave a probability that the two samples come from a single population of less than 1 percent. However, these statistical results are based on the small specimen number of Aliveri; thus, the true variation within the Aliveri specimens cannot be interpreted, especially after taking into account the presence of the two larger m3 molars. Next to *Cricetodon aliveriensis* we see more species with a generally larger dentition in Karydia than in Aliveri. According to Doukas and van den Hoek Ostende (2006), *Heterosorex* sp. could be identified either as the

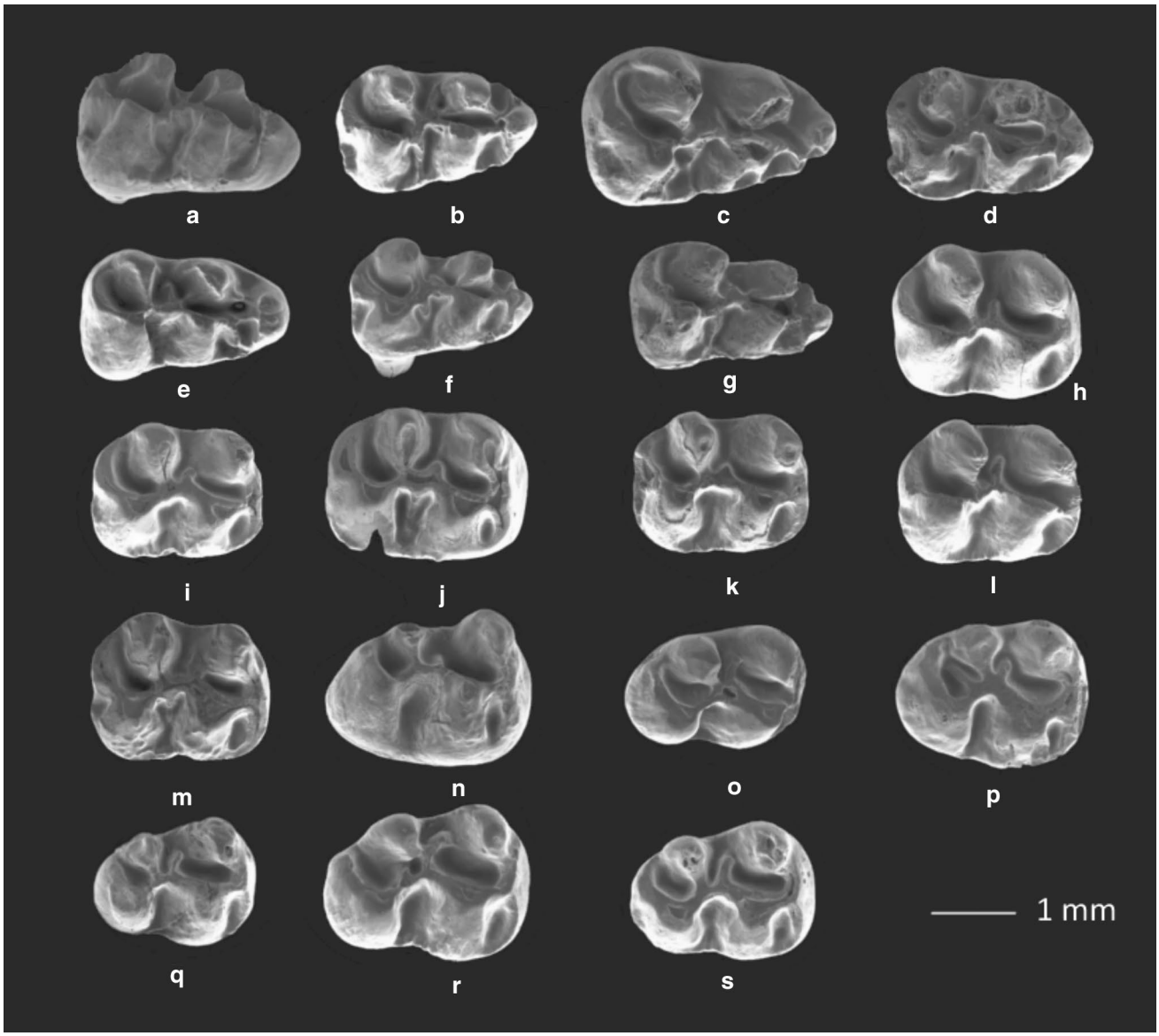

Fig. 12 *Cricetodon aliveriensis* lower molars from the locality of Karydia (m1: **a**: KR2, 1105/ **b**: KR2, 1118/ **c**: KR2, 1106/ **d**: KR2, 1108/ **e**: KR2, 1185/ **f**: KR2, 1116/ **g**: KR2, 1103/ m2: **h**: KR2, 1201/ **i**: KR2, 1206/ **j**: KR2, 1218/ **k**: KR2, 1214/ **l**: KR2, 1209/ **m**: KR2, 1215/ m3: **n**: KR2, 1018/ **o**: KR2, 1020/ **p**: KR2, 1001/ **q**: KR2, 1004/ **r**: KR2, 1006/ **s**: KR2, 1012)

Aliveri species *H. ruemkae* or as *H. neumayrianus*. Either way, "the representative from Karydia is somewhat larger than that in Aliveri" (Doukas and van den Hoek Ostende 2006). Duncan in her thesis (2012) mentions that *Pseudotheridomys parvulus* has similar width/length ratios, but the dentition of the Karydia assemblage are generally larger than Aliveri. In the same study we see that these differences reflect the early stages of the transition in the eomiyds, from *Pseudotheridomys* to *Ligerimys* described by Fahlbusch (1970, 1983). Furthermore, *Eumyarion latior* from Karydia shows an intraspecific variation in size and morphology but its insufficient specimen number

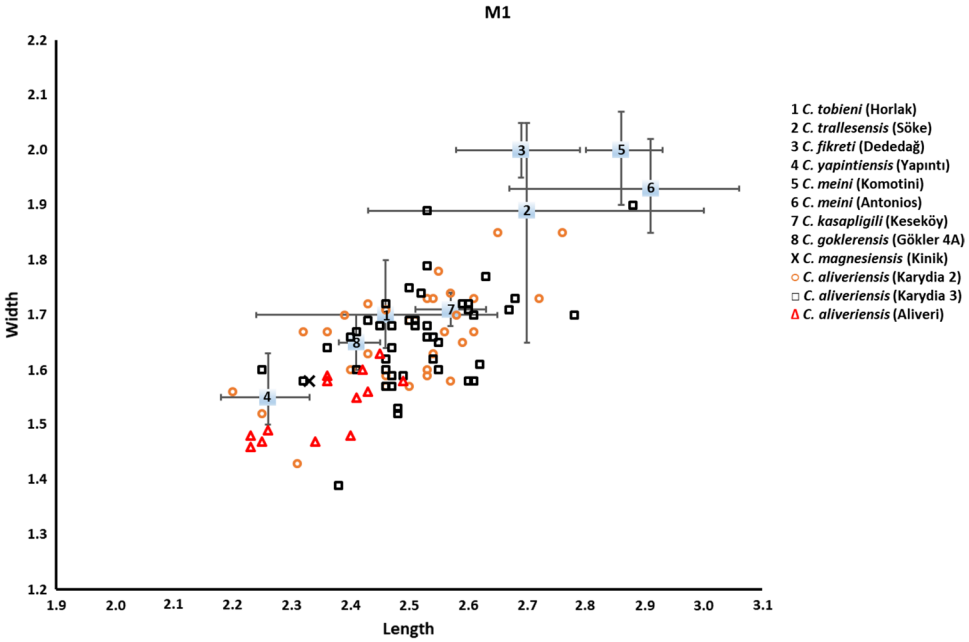

Fig. 13 L/W scatter plot of the M1 from *Cricetodon aliveriensis* from Karydia and Aliveri (Klein Hofmeijer et al. 1988), *C. tobieni* from Horlak (MN4, de Bruijn et al. 1993), *C. trallesensis* from Söke (MN4, Çinar Durgut and Ünay 2016), *C. fikreti* from Dededağ (MN4, Çinar Durgut and Ünay 2016), *C. yapintiensis* from Yapıntı (MN3 – 4, Çinar Durgut and Ünay 2016), *C. meini* from Komotini (MN5, de Bruijn et al. 1993), *C. meini* from Antonios (MN5, Vasileiadou and Koufos 2005), *C. kasapligili* from Keseköy (MN3, de Bruijn et al. 1993) and *C. goklerensis* from Gökler 4A (MN2, Joniak et al. 2017) and *C. magnesiensis* from Kınık (MN3, Çinar Durgut and Ünay 2016)

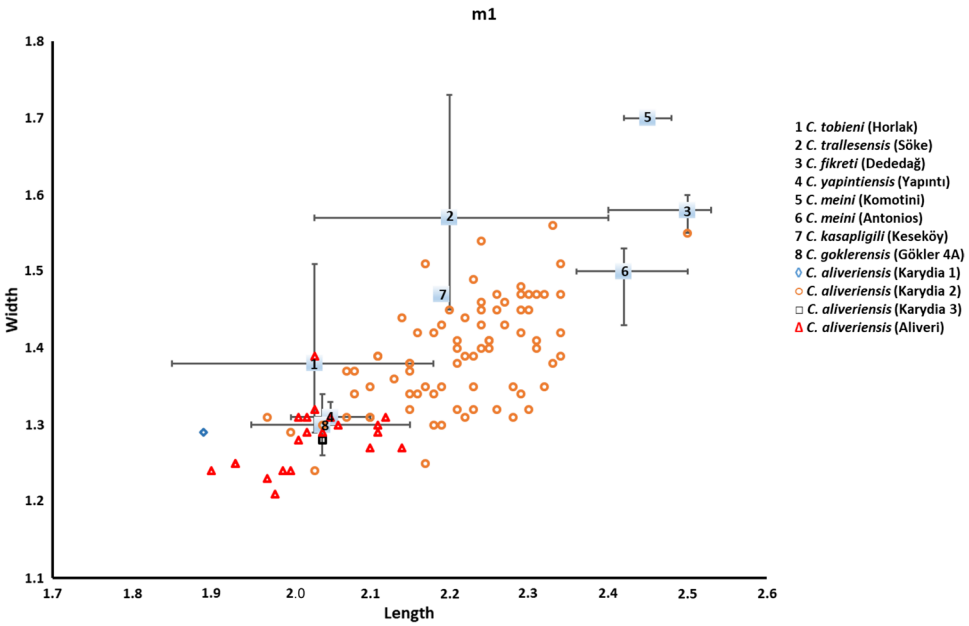

Fig. 14 L/W scatter plot of the m1 from *Cricetodon aliveriensis* from Karydia and Aliveri (Klein Hofmeijer et al. 1988), *C. tobieni* from Horlak (MN4, de Bruijn et al. 1993), *C. trallesensis* from Söke (MN4, Çinar Durgut and Ünay 2016), *C. fikreti* from Dededağ (MN4, Çinar Durgut and Ünay 2016), *C. yapintiensis* from Yapıntı (MN3 – 4, Çinar Durgut and Ünay 2016), *C. meini* from Komotini (MN5, de Bruijn et al. 1993), *C. meini* from Antonios (MN5, Vasileiadou and Koufos 2005), *C. kasapligili* from Keseköy (MN3, de Bruijn et al. 1993) and *C. goklerensis* from Gökler 4A (MN2, Joniak et al. 2017)

Table 9 List of the means of $V'/\sqrt{(\log N)}$ for *Cricetodon* from different levels of Karydia, compared to the mean values of Cricetodontinae from Freudenthal and Cuenca Bescos (1984)

Element	Cricetodontinae			Karydia 1 + 2 + 3		Karydia 2		Karydia 3	
	N	Mean of $\frac{V'/}{\sqrt{\log N}}$	Standard deviation	*N*	Mean of $\frac{V'/}{\sqrt{\log N}}$	*N*	Mean of $\frac{V'/}{\sqrt{\log N}}$	*N*	Mean of $\frac{V'/}{\sqrt{\log N}}$
LM1	118	13.38	3.38	81	19.38	33	18.32	48	18.94
WM1	118	15.18	3.62	108	21.74	47	19.80	59	23.30
LM2	113	14.82	3.69	119	19.42	52	18.93	67	18.12
WM2	113	15.15	3.66	120	19.44	52	21.40	68	15.62
LM3	85	19.61	5.36	66	19.57	63	19.68	1	–
WM3	85	16.51	5.12	67	15.24	64	15.33	1	–
Lm1	126	13.48	3.22	83	20.06	79	17.21	3	–
Wm1	126	15.30	3.90	93	18.94	89	16.37	2	–
Lm2	124	13.03	3.60	86	19.39	72	19.79	13	11.43
Wm2	124	14.55	3.77	97	18.06	75	16.63	20	21.13
Lm3	96	16.24	4.12	55	14.99	52	15.10	3	–
Wm3	96	15.77	4.76	62	14.52	53	14.80	8	10.35

L length, *W* width of the molars

prevents further comparison with *E. latior* from Aliveri (Duncan 2012). The cricetine from Karydia is assigned to *Cricetodon aliveriensis* but, like in *Pseudotheridomys parvulus*, we may witness a transition to a different species that may also justifies the high variability values and the large size range. We emphasize the need of additional future research focusing on this subject.

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