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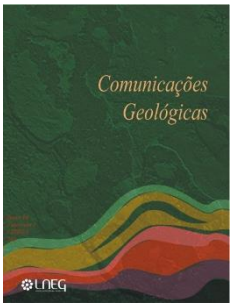
The oldest European marmots: Metrical study of the Marmota fossils from the Early and Middle Pleistocene of Sierra de Atapuerca sites (Burgos, Spain)

As mais antigas marmotas da Europa: Estudo métrico dos fósseis de Marmota do Plistocénico Inferior e Medio das jazidas de Sierra de Atapuerca (Burgos, Espanha)



D. Estraviz-López[1,2]*, G. Cuenca-Bescós[3], H. A. Blain[4,5], J. M. López-García[4,5], C. Núñez-Lahuerta[3], J. Galán[3]

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Abstract: The oldest European remains of marmots (Genus Marmota) are 0.8 my old and come from the site of Gran Dolina, Atapuerca. Dental measurements from the specimens recovered at Gran Dolina are compared with other Early Pleistocene fossil marmots from Croatia; as well as a set of Middle and Late Pleistocene marmots from France and Italy and Middle Pleistocene fossils from other sites at Sierra de Atapuerca. These fossils are also compared with four species of modern marmots, including? an extensive sample of Marmota marmota. Plotting the length of each dental piece of Gran Dolina versus its width, less than 25% of the Early Pleistocene specimens fall into the variability of Marmota marmota, meanwhile the Middle Pleistocene fossils fall within (or extremely close) to its variability. These Early Pleistocene marmots cannot be metrically assigned to the extant alpine marmot.

Keywords: Gran Dolina, Trinchera Galería, microvertebrates, rodents, Iberian Peninsula

Resumo: Os vestígios europeus mais antigos de marmotas (género Marmota) têm 0.8 milhões de anos e provêm da Gran Dolina, Atapuerca. As medições realizadas em peças dentárias de marmotas fósseis encontrados em Gran Dolina são comparadas com exemplares de marmotas provenientes do Pleistocénico inferior da Croácia e do Pleistocénico Médio e Superior de França e Itália, bem como com exemplares encontrados em outras localidades do Pleistocénico médio da Serra de Atapuerca. Estes fósseis também são comparados com quatro espécies de marmotas modernas, incluindo uma extensa amostra de Marmota marmota. Ao plotar o comprimento de cada peça dentária de Gran Dolina face a sua largura, menos do 25% dos exemplares do Pleistocénico Inferior caem dentro da variabilidade existente em Marmota marmota. Os exemplares do Pleistocénico Médio estão dentro (ou extremamente próximos) da variabilidade de Marmota marmota. Os exemplares de marmotas do Pleistocénico Inferior de Gran Dolina não podem ser metricamente atribuídos à marmota alpina.

Palavras-chave: Gran Dolina, Trinchera Galería, microvertebrados, roedores, Península Ibérica

[1] FCT-NOVA, Departamento de Ciências da Terra, 2829-516 Caparica, Portugal.
[2] Museu da Lourinhã, Rúa João Luis de Moura, Nº 95, 2530-158 Lourinhã, Portugal.
[3] Aragosaurus-IUCA-Universidad de Zaragoza, Spain.
[4] Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007, Tarragona, Spain.
[5] Área de Prehistòria, Universitat Rovira i Virgili, Facultat de Lletres, Avinguda Catalunya 35, 43002, Tarragona, Spain.

* Corresponding autor/Autor correspondente: estravizlopez.dario@gmail.com

1. Introduction

1.1. The marmots in Europe, an overview

Marmots are nowadays one of the biggest rodents in the Northern Hemisphere after beavers and porcupines. They are related to squirrels and belong to the family Sciuridae, being them classified in the tribe Marmotini. Today the genus *Marmota* includes 15 species, nine in Eurasia and six in North America (Armitage, 2000).

They first evolved during the Late Miocene of North America, being the oldest species of the genus (*Marmota vetus*), about 10 mya (Erbajeva and Alexeeva, 2009). This species dispersed into Eurasia during the Miocene, but the first Eurasian marmots appeared 3.4 mya near the Baikal Lake with *Marmota tologoica* (Erbajeva and Alexeeva, 2009) and in the Late Pliocene-earliest Pleistocene of Yushe Basin (North China) with *Marmota robusta* (Flynn *et al*., 1997; Qiu, 2017). During the rest of the Pliocene, it is safe to assume that Eurasia became a center of diversification for marmots, as numerous diversification events have been identified around this time for the group (Menéndez *et al*., 2021). By the end of the Pliocene, they appear in the fringes of Eastern Europe (Erbajeva and Alexeeva, 2009). During the Early Pleistocene in Europe, marmots are extremely rare, being recorded in a handful of sites and by scarce material (except in the Sierra de Atapuerca sites, Spain). They appear in Montoussé, France (Clot, 1975); Deutsch Altenburg, Austria (Maul, 1990); Akhalkalaki, Georgia (Tappen *et al*., 2002); and Podumci and Tatinja Draga, Croatia (Malez and Rabeder, 1984; Paunović and Rabeder, 2000). The only locality with Early Pleistocene as well as Middle Pleistocene marmot fossils in Europe is the Sierra de Atapuerca. These marmots (subject of the present work) had been previously referred to the alpine marmot, *Marmota marmota* (Gil, 1997) but later they were reclassified simply as Marmota sp. in base of morphological characters (Cuenca-Bescós *et al*., 2016).

In the Middle Pleistocene marmot remains become more common, but still rare compared to other rodents. They appear at the cave of Aragó, France, about 0.5 mya, being their representatives ascribed to *Marmota marmota primigenia* (Hanquet, 2011; Lebreton *et al*., 2016). In the French site of La Fage the subspecies, *Marmota marmota mesostyla* was named by Chaline (1972) in base of dental characters that he defined as intermediate between *Marmota bobak* and *Marmota marmota*, nevertheless molecular phylogenetic studies have shown that the alpine marmot (*Marmota marmota*) and the steppe marmot (*Marmota bobak*) are not sister taxa, therefore these similarities might be due to convergence (Armitage, 2014). In this time period, they also appear in Lazaret site (South of France), whose specimens have been traditionally classified as *Marmota marmota primigenia* (Desclaux, 1996; Valensi and Abbassi, 1998). In Iberia, *Marmota* is known from La Parte (Asturias, Spain), thanks to an isolated left humerus (Álvarez-Lao and García-García, 2006) and from remains found in El Castillo (Gerona, Spain) (Villalta, 1972), both attributed to *Marmota* sp.

The great majority of marmot fossils in Europe come from the Late Pleistocene, and most of them have been attributed either to *Marmota marmota* or *Marmota marmota primigenia*. In the Iberian Peninsula, they appear in the sites of Lezetxiki, Axlor (Basque country) or Buena Pinta (Madrid) (Laplana *et al*., 2016; Mariezkurena-Gastearena, 2011).

Despite these appearances in Iberia during the Late Pleistocene, the alpine marmot became extinct in the area during the Holocene and did not appear in historic times, until the introduction of specimens during the last 100 years (Barrio *et al*., 2013).

1.2. Sierra de Atapuerca: geological, chronological and paleoecological settings

The archaeological and paleontological sites of the Sierra de Atapuerca, located near the city of Burgos (North Spain), contain one of the world's most extraordinary accumulations of Pleistocene fossil humans and stone tools (Carbonell and Tristán, 2017). The Sierra de Atapuerca is a small Mesozoic-core hill connected to the Iberian Range, which constitutes a scarcely pronounced relief in the middle of the Neogene sediments of the Bureba Corridor, which connects the Ebro and Duero Basins (Benito-Calvo and Pérez-González, 2015). The Sierra de Atapuerca possesses three main cave systems, from East to West, these are: El Mirador, Cueva Mayor and Trinchera del Ferrocarril (Carbonell and Tristán, 2017). The third system, Trinchera del Ferrocarril, is an abandoned railway trench that exposed several fossiliferous caves, including the sites of Gran Dolina and Trinchera Galeria among others. In Trinchera Galería a marmot fossil, Middle Pleistocene in age, was recovered (García-Medrano *et al*., 2017). The Gran Dolina site contained some of the oldest hominin remains of Western Europe from level TD6, which in 1997 were recognized as a new species, *Homo antecessor* (Bermúdez de Castro *et al*., 1997). The sedimentary infilling of the cave of Gran Dolina, represents one of the longest stratigraphic sequences found in Atapuerca sites, comprising 18-19m of outer cave-filling sediments divided into 19 stratigraphic levels. Most of the marmot remains from Sierra de Atapuerca come from this site, concretely from levels TD5 and TD6, 0.8-1 mya in age. Some Middle Pleistocene marmot remains from TD11 have been also recovered (Parés *et al*., 2018). According to several proxies the environment during the time was warmer and more humid than today, with a landscape dominated by humid meadows and riparian woody habitats (Rodríguez *et al*., 2011; Blain *et al*., 2013).

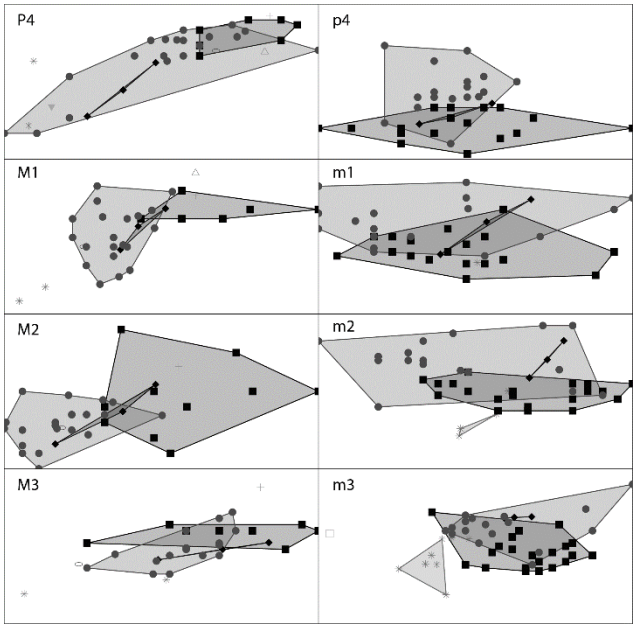

Figure 1. Bivariate graphics of length (x axis) versus width (y axis) of *Marmota* teeth. M: upper molars; m: lower molars; P: upper premolars; p: lower premolars. *, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Figura 1. Gráficos bivariados de cumprimento (eixo x) versus largura (eixo y) de dentes de *Marmota*. M: Dentes molares da mandíbula superior; m: dentes molares da mandíbula inferior; P: dentes pré-molares da mandíbula superior; p: dentes pré-molares da mandíbula inferior.

Table 1. Origin, age and number of specimens of each category of marmots considered in the study. The first four categories are marmots from Sierra de Atapuerca (Spain).

Tabela 1. Origem, idade e número de espécimenes de cada categoria de marmotas consideradas no estudo. As primeiras quatro categorias são marmotas provenientes de Sierra de Atapuerca (Espanha).

Species	Country	Layer/Site	Period	Number of specimens
Marmota sp.	Spain	Gran Dolina/ TD5	Early Pleistocene	14
Marmota sp.	Spain	Gran Dolina/ TD6	Early Pleistocene	5
Marmota sp.	Spain	Gran Dolina/ TD11	Middle Pleistocene	1
Marmota sp.	Spain	Trinchera Galeria	Middle Pleistocene	1
Marmota sp.	Croatia	Tatinja Draga	Early Pleistocene	1
Marmota sp.	Croatia	Podumci	Early Pleistocene	1
Marmota sp.	France	Lazaret	Middle Pleistocene	24
Marmota sp.	Italy	Parmorari	Late Pleistocene	114
Marmota marmota	Spain/France	Lizarra/Panticosa/Piedmont	Recent	146
Marmota marmota	Austria	Styria	Recent	4
Marmota caudata	Afganistan	Pandjir Valley	Recent	4
Marmota kastschenkoi	Russia	Novosibirsk	Recent	4
Marmota bobak	?	?	Recent	2

The aim of this work is to improve our knowledge on the origin and evolution of Western Europe marmots, with focus on the Early and Middle Pleistocene Sierra de Atapuerca marmots. As we have pointed above, they are exceptional in terms of the number and preservation quality of the specimens, making them paramount for our understanding of the group.

2. Material and methods

A sample of 321 individual teeth of fossil marmots, attached or not to mandibles, from Early, Middle and Late Pleistocene have been

considered for this study, as well as modern specimens of four species of marmots (Tab. 1).

For each tooth, length and width were measured (Appendix 3). The measurements of one *Marmota marmota*, and the specimens of *Marmota caudata* and *Marmota kastschenkoi* were obtained by measuring images from the bibliography (Kryštufek and Vohralík, 2013), with the software ImageJ (Schneider *et al*., 2012). The other measurements were obtained using the software of image acquisition of Olympus Imaging.

These measurements were analyzed using the software PAST 4.0 (Hammer, 2019). First a series of biplots of length versus width of each of the dental pieces were elaborated to give a qualitative idea of the dispersion of data (Fig. 1). Those were later quantified in base of the percentage of the specimens that fell in the variability of modern alpine marmots (Tab. 2). Then two PCAs were performed (Fig. 2). The first included the only specimen of Sierra de Atapuerca that has preserved two teeth, the P4 and the M1. Then the second PCA included a "reconstructed individual" with the average length and width of all the measurements of TD5 and TD6. These "reconstructed individuals" were generated for the other groups. Individuals for which it was possible to record as many measurements were included to test how "reconstructed individuals" deviated from the real ones.

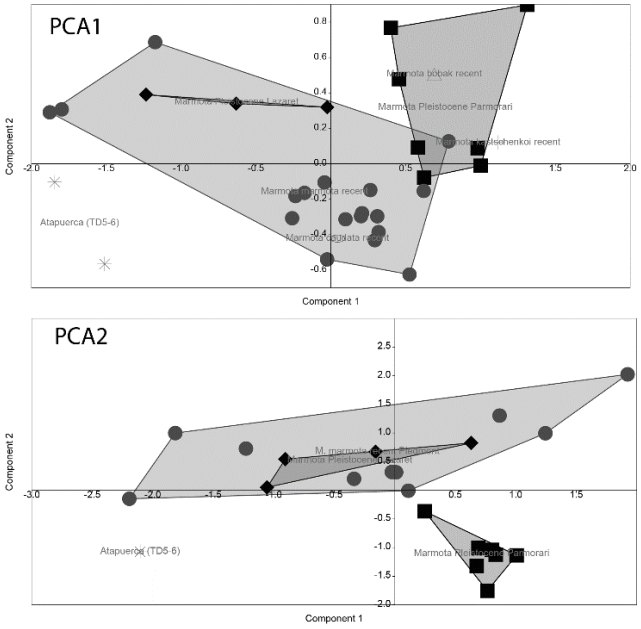

Figure 2. Top, principal component analysis (PCA) that includes the measurements of the fourth upper premolar and first upper molar of an Atapuerca specimen (td6t50h17ata96), as well as the averages for those teeth in TD5-TD6 specimens, compared with other marmots. Bottom, principal component analysis (PCA) that includes an average for all the measurements that could be recorded for TD5-TD6 specimens, compared with other marmots. Asterisks, Atapuerca (Spain); triangle, modern *Marmota bobak*; inverted triangle, modern *Marmota caudata*; grey filled square, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*. Reconstructed specimens are dashes.

Figura 2. Em cima, análise de componentes principais (PCA), que inclui as medidas do quarto pré-molar superior e o primeiro molar superior de um espécime de Atapuerca (td6t50h17ata96) assim como as médias para aqueles dentes de TD5-TD6, comparados com outras marmotas. Em baixo, análise de componentes principais (PCA) que inclui a média de todas as medidas que foram registados nos exemplares de TD5-TD6, comparados com outras marmotas. Espécimes reconstruídos são barras.

3. Results

The biplot results for the dentition are shown in Figure 1; a version with labels for each group and the axes of each biplots is available in Appendix 1. Table 2 quantifies the percentage of each group that falls in the variability of modern alpine marmots. In the first PCA, the PC 1 (75% of the variability) was positively related with all the measurements of P4 and M1; meanwhile the PC 2 (16% of the variability) was negatively related with the measurements of P4 and positively with those of M1. In the second PCA, the PC1 (42% of the variability) was positively correlated with all measurements; meanwhile the PC 2 (33% of the variability) was positively correlated with all lower teeth measurements except the m2 length and negatively correlated with the others. In Appendix 2 it is possible to visualize each principal component.

Table 2. Percentage of specimens of each category that fall within the morphospace of modern Marmota marmota for each tooth type and in total. M: upper molars; m: lower molars; P: upper premolars; p: lower premolars.

Tabela 2. Percentagem de espécimenes de cada categoria que caem no morfoespaço das Marmota marmota modernas para cada tipo de dente e no total. M: Dentes molares da mandíbula superior; m: dentes molares da mandíbula inferior; P: dentes pré-molares da mandíbula superior; p: dentes pré-molares da mandíbula inferior.

	P4	M1	M2	M3	p4	m1	m2	m3	Totals
Lazaret	100	100	66	100	100	66	100	100	91,50
Parmorari	50	16,6	20	14,29	38,8	50	57,14	31,82	34,83
M. caudata	100	100	100	0	_	_	_	_	75,00
M. bobak	100	0	_	_	_	_	_	_	50,00
M. kastschenkoi	0	0	0	0	_	_	_	_	0,00
Atapuerca TD5	50	0	_	0	_	100	0	0	25,00
Atapuerca TD6	_	0	_	_	_	_	0	50	16,67
Atapuerca TD11	_	_	_	_	_	_	100	_	100,0 0
Atapuerca TG3	_	_	_	_	_	_	_	0	0,00
Other Early Pleistocene	50	_	_	0	_	_	_	_	25,00

4. Discussion

Table 2 show that less than 25% of the TD5 and TD6 marmot fossils fall into the variability of modern *Marmota marmota*, meanwhile the one of TD11 falls into the variability of the modern alpine marmot and the one of TG3 falls extremely close (Fig. 1 and Appendix 1). The situation is even more pronounced in both PCAs; where neither the real specimen or both "reconstructed individuals" fit into the morpho-space of modern alpine marmot (Fig. 2). Therefore, just based in metrical characters it does not seem possible to attribute the TD5-TD6 specimens to *Marmota marmota*, as Cuenca-Bescós *et al*. (2016) found based in morphology, while the Middle Pleistocene specimens might be attributable to them.

The situation of the marmots of the Early Pleistocene of Atapuerca is relatively similar to that of the other two Early Pleistocene specimens of Croatia, although the m3 from Podumci falls far from any marmot in the sample (Fig. 1).

More than 90% of the times the specimens of the Middle Pleistocene of Lazaret fall into the variability of extant *Marmota marmota*, even when the sample size is bigger than that of Sierra de Atapuerca (Fig. 1). In both PCAs 100% of the specimens, real or virtual, fall into the morphospace of alpine marmots (Fig. 2). This makes the assignation to *Marmota marmota* likely (Tab. 2).

The specimens from Parmorari (Italy) are remarkable, with an extremely large sample of more than 100 individual teeth, they fall in the variability of modern *Marmota marmota* only about 1/3 of the times in the biplots (Tab. 2). In both PCAs only two specimens of 14 fit into the morphospace of alpine marmots (Fig. 2), and the reconstructed individuals fall outside *Marmota marmota* morphospace. This situation needs to be addressed with a stronger

corpus of data, since the more glacial conditions of the Late Pleistocene could make the marmots achieve greater sizes as the biplots at Figure 1 suggest.

No relevant data is extracted from the inclusion of specimens referred to other species of modern marmots, other than *Marmota caudata*, which is similar metrically to *Marmota marmota* and *Marmota bobak* but more divergent from *Marmota kastschenkoi* (Fig. 1).

More data on modern specimens should be included in future analysis, in particularly, the addition of data from *Marmota monax*, an asocial American species that is one of the most basally branching species of the clade (Armitage, 2014). Also, further work should include discrete morphological characters and measurements of other body parts that have also been found in TD5-TD6 layers of Gran Dolina, to provide a better understanding of the intraspecific and interspecific variation in marmots and the systematics and paleoecology of Early Pleistocene marmots of Sierra de Atapuerca.

5. Conclusions

The dental and mandibular marmot remains from the Early Pleistocene of Gran Dolina do not seem to be attributable to extant alpine marmots in base of metric data. The general trend is similar to the other European Early Pleistocene specimens, being them of smaller dimensions than extant alpine marmots. The Middle Pleistocene marmots from Sierra de Atapuerca could be metrically attributed to alpine marmots. The same can be said about the Middle Pleistocene marmots of Lazaret, France. The Late Pleistocene marmots of Parmorari, Italy, are particularly distinct metrically from extant Marmota marmota. This could point towards a size increase during glacial conditions. Further work is needed to definitively clarify the affinities of the marmots from Sierra de Atapuerca.

Appendixes

Only available online.

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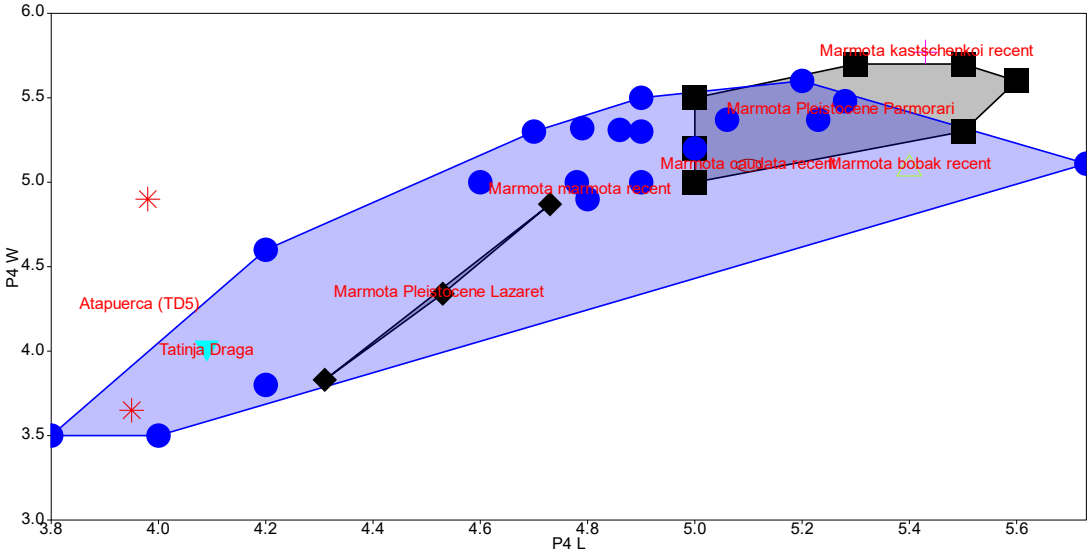
Appendix 1

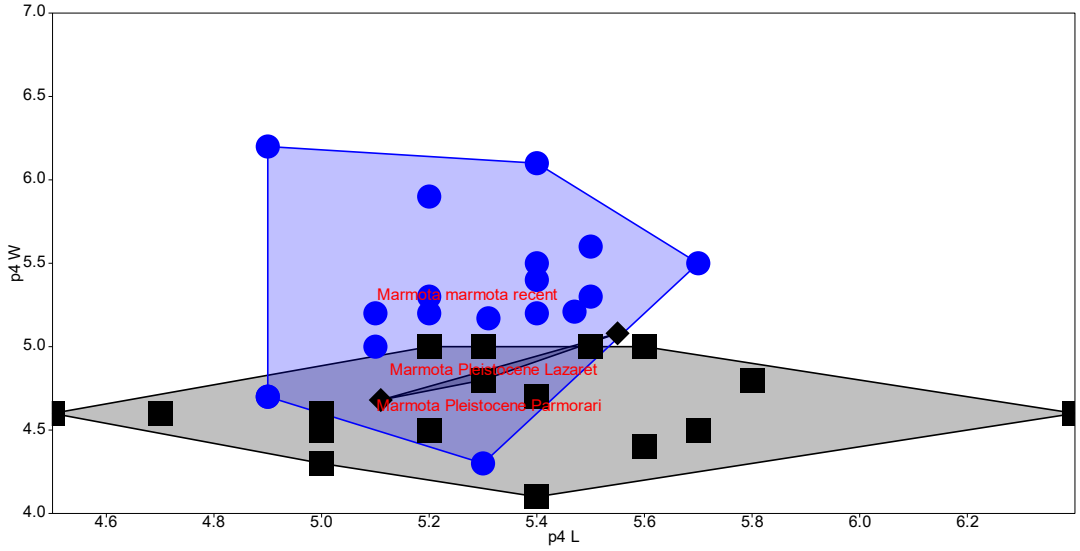
Appendix 1.1. Length versus width of P4 of marmots. Asterisks, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Anexo 1.1. Comprimento *versus* largura do P4 em marmotas. Asteriscos, Atapuerca (Espanha); triângulo invertido, Tatinja Draga (Croácia); quadrado, Podumci (Croácia); triangulo, atual *Marmota bobak*; oval, atual *Marmota caudata*; mais, atual *Marmota kastschenkoi*; losangos preenchidos, Lazaret (França); quadrados preenchidos, Parmorari (Itália); pontos, atual *Marmota marmota*.



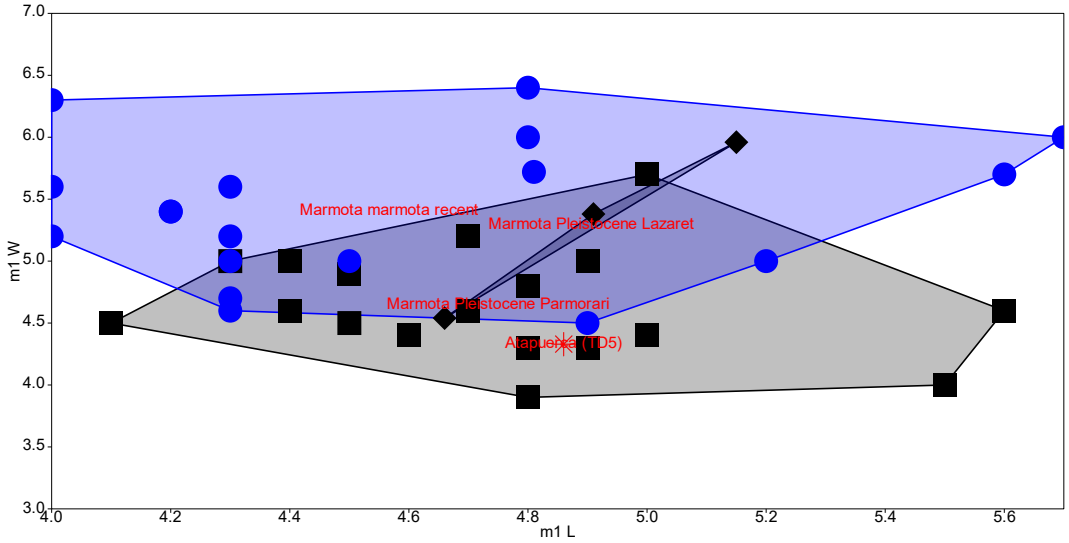
Appendix 1.2. Length versus width of p4 of marmots. Asterisks, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Anexo 1.2. Comprimento *versus* largura do p4 em marmotas. Asteriscos, Atapuerca (Espanha); triangulo invertido, Tatinja Draga (Croácia); quadrado, Podumci (Croácia); triangulo, atual *Marmota bobak*; oval, atual *Marmota caudata*; mais, atual *Marmota kastschenkoi*; losangos preenchidos, Lazaret (França); quadrados preenchidos, Parmorari (Itália); pontos, atual *Marmota marmota*.



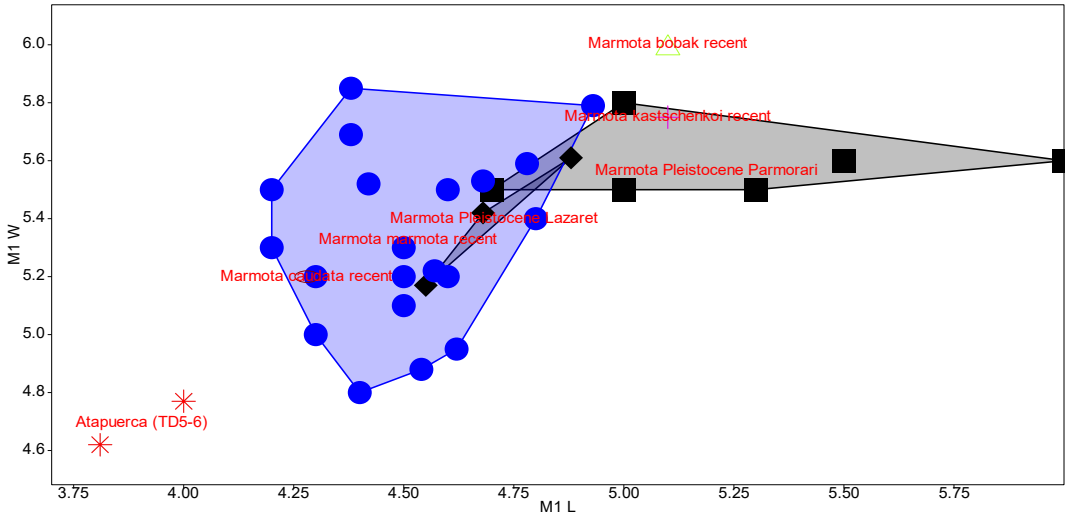
Appendix 1.3. Length versus width of m1 of marmots. Asterisks, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Anexo 1.3. Comprimento *versus* largura do m1 em marmotas. Asteriscos, Atapuerca (Espanha); triangulo invertido, Tatinja Draga (Croácia); quadrado, Podumci (Croácia); triangulo, atual *Marmota bobak*; oval, atual *Marmota caudata*; mais, atual *Marmota kastschenkoi*; losangos preenchidos, Lazaret (França); quadrados preenchidos, Parmorari (Itália); pontos, atual *Marmota marmota*.



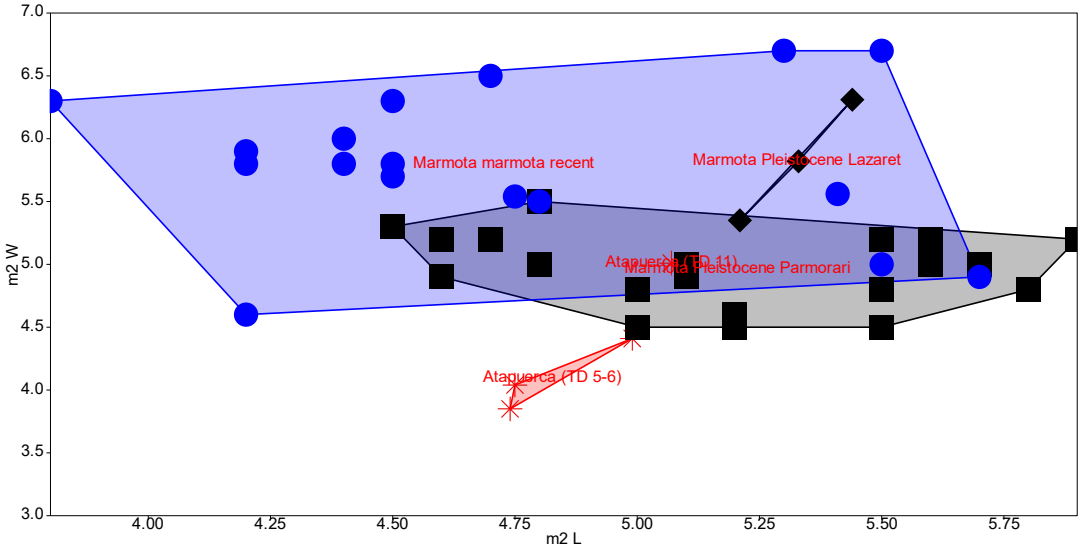
Appendix 1.4. Length versus width of M1 of marmots. Asterisks, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Anexo 1.4. Comprimento *versus* largura do M1 em marmotas. Asteriscos, Atapuerca (Espanha); triangulo invertido, Tatinja Draga (Croácia); quadrado, Podumci (Croácia); triangulo, atual *Marmota bobak*; oval, atual *Marmota caudata*; mais, atual *Marmota kastschenkoi*; losangos preenchidos, Lazaret (França); quadrados preenchidos, Parmorari (Itália); pontos, atual *Marmota marmota*.



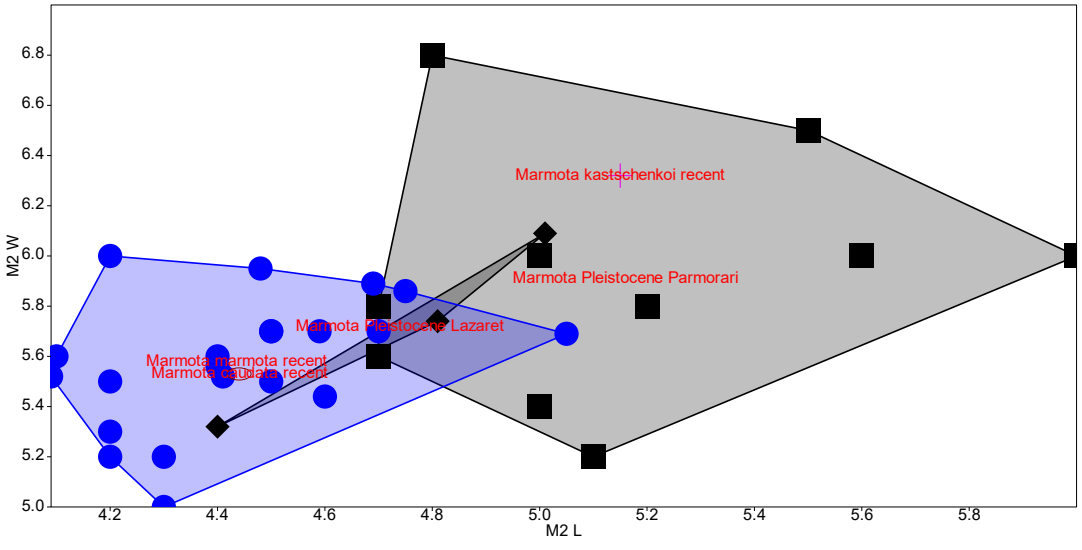
Appendix 1.5. Length versus width of m2 of marmots. Asterisks, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Anexo 1.5. Comprimento *versus* largura do m2 em marmotas. Asteriscos, Atapuerca (Espanha); triangulo invertido, Tatinja Draga (Croácia); quadrado, Podumci (Croácia); triangulo, atual *Marmota bobak*; oval, atual *Marmota caudata*; mais, atual *Marmota kastschenkoi*; losangos preenchidos, Lazaret (França); quadrados preenchidos, Parmorari (Itália); pontos, atual *Marmota marmota*.



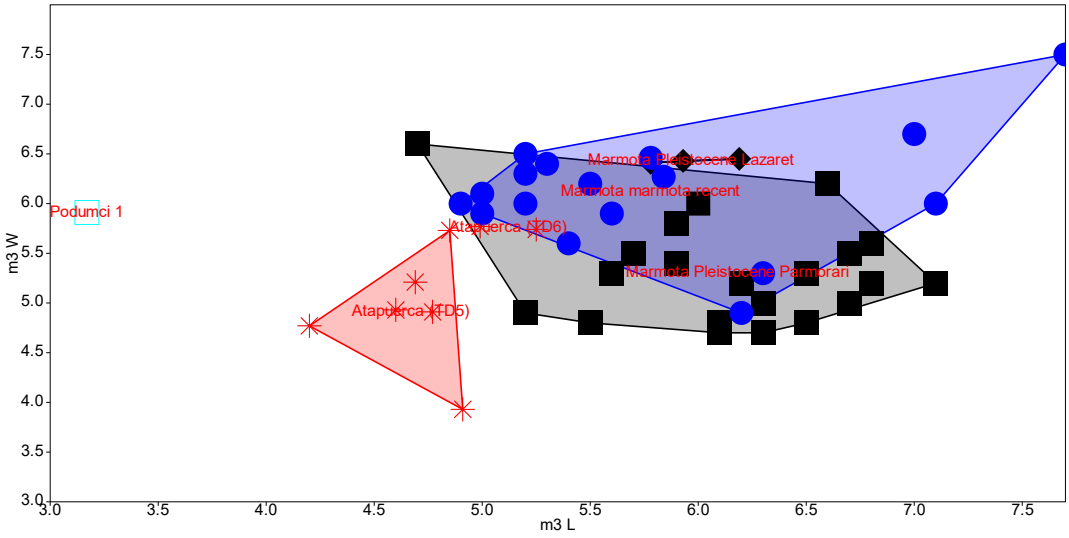
Appendix 1.6. Length versus width of M2 of marmots. Asterisks, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Anexo 1.6. Comprimento *versus* largura do M2 em marmotas. Asteriscos, Atapuerca (Espanha); triangulo invertido, Tatinja Draga (Croácia); quadrado, Podumci (Croácia); triangulo, atual *Marmota bobak*; oval, atual *Marmota caudata*; mais, atual *Marmota kastschenkoi*; losangos preenchidos, Lazaret (França); quadrados preenchidos, Parmorari (Itália); pontos, atual *Marmota marmota*.



Appendix 1.7. Length versus width of m3 of marmots. Asterisks, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Anexo 1.7. Comprimento *versus* largura do m3 em marmotas. Asteriscos, Atapuerca (Espanha); triangulo invertido, Tatinja Draga (Croácia); quadrado, Podumci (Croácia); triangulo, atual *Marmota bobak*; oval, atual *Marmota caudata*; mais, atual *Marmota kastschenkoi*; losangos preenchidos, Lazaret (França); quadrados preenchidos, Parmorari (Itália); pontos, atual *Marmota marmota*.



Appendix 1.8. Length versus width of M3 of marmots. Asterisks, Atapuerca (Spain); inverse triangle, Tatinja Draga (Croatia); square, Podumci (Croatia); triangle, modern *Marmota bobak*; oval, modern *Marmota caudata*; plus, modern *Marmota kastschenkoi*; filled rhombs, Lazaret (France); filled squares, Parmorari (Italy); dots, modern *Marmota marmota*.

Anexo 1.8. Comprimento *versus* largura do M3 em marmotas. Asteriscos, Atapuerca (Espanha); triangulo invertido, Tatinja Draga (Croácia); quadrado, Podumci (Croácia); triangulo, atual *Marmota bobak*; oval, atual *Marmota caudata*; mais, atual *Marmota kastschenkoi*; losangos preenchidos, Lazaret (França); quadrados preenchidos, Parmorari (Itália); pontos, atual *Marmota marmota*.