

First functional morphology comparison between two Miocene cricetid mandibles

Patricia María CARRO-RODRÍGUEZ^{1,2,*}, Paloma LÓPEZ-GUERRERO¹, Jérôme PRIETO³,
María Ángeles ÁLVAREZ-SIERRA^{1,2} & Pablo PELÁEZ-CAMPOMANES⁴

¹ Department of Geodynamics, Stratigraphy and Palaeontology (GEODESPAL), Universidad Complutense de Madrid, Madrid, Spain. patcarro@ucm.es*, palomalopez@geo.ucm.es

² Sedimentary Geology and Environmental Change, Geosciences Institute (CSIC, UCM), Madrid, Spain. masierra@ucm.es

³ Department of Earth and Environmental Science, Palaeontology & Geobiology, Ludwig-Maximilians-University Munich, Richard-Wagner-Str. 10, 80333 Munich, Germany. j.prieto@web.de

⁴ Department of Paleobiology, Museo Nacional de Ciencias Naturales, CSIC. C/ José Gutiérrez Abascal 2, 28006 Madrid. pablopelaez@mncn.csic.es

*Corresponding author

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ABSTRACT

Geometric morphometric allows characterizing complex morphologies in order to quantify the geometry of the structure and facilitate comparisons. It allows performing methods analysing differentiation pattern based on variance, such as the Principal Component Analysis (PCA). For that reason, it has been chosen as the method to analyse the mandibles of two extinct species of cricetid rodents: *Cricetodon* aff. *aureus* and *Megacricetodon minor* from the MN6, middle Miocene from Goldberg and Steinberg (Germany). We performed a digitisation of 18 landmarks that includes the most relevant characteristics of these mandibles. We also performed a measure of the mechanical advantage and potential of the mandibles. In that way, we have been able to quantify notorious morphological differences on the angular and condylar processes and the lower masseter

RESUMEN

La morfometría geométrica permite caracterizar formas completas para cuantificar la geometría de la estructura y facilitar las comparaciones. Permite llevar a cabo metodologías que analizan esos patrones de diferenciación como el Análisis de Componentes Principales (ACP), a través del cual se estudia la varianza de una manera simple. Por esta razón ha sido el método elegido para analizar las mandíbulas de dos especies extintas de cricétidos: *Cricetodon* aff. *aureus* y *Megacricetodon minor* de la MN6, Mioceno medio de los yacimientos de Goldberg y Steinberg (Alemania). Hemos llevado a cabo la digitalización de 18 puntos de referencia (*landmarks*) que resumen las características más relevantes de las mandíbulas. Además hemos realizado la medición de las ventajas y potencias mecánicas de estas. De esta manera, hemos podido cuantificar diferencias morfológicas

insertion and establish significant differences among the biomechanical behaviour of the mandibles. Later, we can relate the morphological and biomechanical information with speed and force biting.

Keywords: *Cricetodon*, *Megacricetodon*, geometric morphometric, middle Miocene, Germany

notorias en los procesos angular y condilar y en la inserción del masetero inferior y establecer diferencias significativas entre los comportamientos biomecánicos de las mandíbulas para después relacionarlo con la velocidad y la fuerza de la mordida de estos roedores.

Palabras clave: *Cricetodon*, *Megacricetodon*, morfometría geométrica, Mioceno medio, Alemania.

1. INTRODUCTION

Shape and shape changes have been studied to understand the way in which the organisms or their parts vary as a consequence to different biological processes (Richtsmeier *et al.*, 2002; Zelditch *et al.*, 2004). These shape changes could be the result of ontogenetic development, adaptation to environmental factors or evolutionary diversification (Zelditch *et al.*, 2004). In palaeontology, the study of shape is an essential requirement to carry out other analysis. For that reason, in recent years, geometric morphometric has revealed as a great tool to analyse and understand the morphological variation of fossils (Casanovas-Vilar & van Dam, 2013; Siver *et al.*, 2013; Gómez Cano *et al.*, 2017; Tokita *et al.*, 2017; Carro-Rodríguez *et al.*, 2018). Geometric morphometric is a multivariate method to quantify the morphology of an object. It is based on an analysis of selected points (landmarks and semilandmarks) (Rohlf & Marcus, 1993; Zelditch *et al.*, 2004) that correspond to Cartesian coordinates. In geometric morphometric, most analysis measurements imply biological homology and thus considering them as the same point in each specimen in the study (Bookstein, 1996; Hall, 2003; Klingenberg, 2008; Oxnard & O'Higgins, 2009) but not the position, scale and rotation of the object (Kendall, 1977; Baltanás *et al.*, 2003; Zelditch *et al.*, 2004; Toro Ibacache *et al.*, 2010; Klingenberg, 2016).

Mammal mandible is one of the anatomical parts most used in these analyses because of its characteristic modularity, integration and biomechanics (Atchley, 1983, 1993; Andresen *et al.*, 2000; Bastir *et al.*, 2004; Zelditch *et al.*, 2008; Menegaz & Ravosa, 2017). The present morphological analysis has focused on the well-preserved mandibles of two extinct species of cricetids rodents (Rodentia) belonging to the genera: *Cricetodon* Lartet, 1851 and *Megacricetodon* Fahlbusch, 1964. Both are commonly used in biostratigraphic and paleoecological studies in European continental deposits during the middle Miocene (Mein, 1975; Aguilar, 1995; De Bruijn & Ünay, 1996; Daams *et al.*, 1999; Oliver Pérez *et al.*, 2008; Prieto *et al.*, 2010; Van der Meulen *et al.*, 2011, 2012; López-Guerrero *et al.*, 2013, 2014; Van Dam *et al.*, 2014, Prieto & Rummel, 2016).

Studied mandibles were excavated in two close localities: Goldberg and Steinberg (formerly called Spitzberg) in the Nördlinger Ries of Southwest Germany. The Nördlinger Ries is a circular shallow depression formed due to a meteorite impact at ~15 Ma (Heizman & Fahlbusch, 1983). This crater was like an isolated lake where spring mounds of calcareous tufa rose (Arp, 2006; Göhlich & Ballmann, 2013). On the basis of small mammal remains, the faunas of Goldberg and Steinberg have been dated as upper Aragonian (MN6, middle Miocene) (Heizmann & Fahlbusch, 1983). More precisely, they correlate to a time ranging from ~15 to ~14.2 Ma (Prieto & Rummel, 2016; and reference therein) based on the evolutionary level of *Cricetodon* (Rummel, 2000). The abundant fossil remains of these localities display an exceptional preservation (Rachl, 1983; Ziegler, 1983; Heizmann & Fahlbusch, 1983; Göhlich & Ballmann, 2013), such as cranial structures, which are very uncommon in the fossil record. Heizmann & Fahlbusch (1983) published the faunistic list of Steinberg and pointed out the similarities with the Goldberg fauna. The material studied in this work was assigned to *Cricetodon sansaniensis* and *Megacricetodon schaubi* by Heizmann & Fahlbusch (1983). Later, Rummel (2000) assigned *C. sansaniensis* from Steinberg to *C. aff. aureus* and Freudenthal & Fahlbusch (1969) pointed out that *M. minor* is the senior synonymous of *M. schaubi*. In that way, the nomenclatural state of the art is respectively *C. aff. aureus* and *M. minor*.

Although the best diagnostic characteristics of *Cricetodon* and *Megacricetodon* are based on dental morphological traits, Mein & Freudenthal (1971a, 1971b) pointed out that there are some mandibular features that let establishing differences among these genera. These differences could be the result of generic level variation and/or a response to differential feeding behaviours (Atchley, 1993; Cox *et al.*, 2012; Renaud *et al.*, 2012; Anderson *et al.*, 2014; Kono *et al.*, 2017; Menegaz & Ravosa, 2017). In order to establish the morphologic regions that gather the greatest amount of variation, we performed a geometric morphometric analysis. Then, in order to analyse if there could be a relationship between these differences and dietary preferences, we measured the mechanical advantage of the mandibles through the lengths of four structures involved in biting.

2. MATERIAL AND METHODS

2.1. Samples

To carry out the analysis, 12 mandibles of *Cricetodon* aff. *aureus* and *Megacricetodon minor* (Table 1) were photographed from the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG; Munich, Germany). The specimens were photographed using the binocular microscope Leica 50x and its associated software from the same institution and a 12.3 megapixels Nikon D300S camera equipped with a Nikon 105mm f/2.8G IF-ED lens.

Table 1. List of mandibles studied of *Megacricetodon minor* from Goldberg and *Cricetodon* aff. *aureus* from Steinberg.

Species	Catalogue number
<i>Megacricetodon minor</i>	SNSB-BSPG 1966 XXXIV-3493
	SNSB-BSPG 1966 XXXIV-3498
	SNSB-BSPG 1966 XXXIV-3516
	SNSB-BSPG 1966 XXXIV-3528
	SNSB-BSPG 1966 XXXIV-3539
	SNSB-BSPG 1966 XXXIV-3546
	SNSB-BSPG 1966 XXXIV-3555
<i>Cricetodon</i> aff. <i>aureus</i>	SNSB-BSPG 1970 XVIII-8060
	SNSB-BSPG 1970 XVIII-8062
	SNSB-BSPG 1970 XVIII-8063
	SNSB-BSPG 1970 XVIII-8067
	SNSB-BSPG 1970 XVIII-8068

2.2. Morphometric and statistical analyses

To characterize the shape of the mandibles, we choose the lateral view and the labial region following Bi *et al.* (2008), Anderson *et al.* (2014), Astúa *et al.* (2015), Fabre *et al.* (2017), and Menegaz & Ravosa (2017). In order to eliminate the asymmetry between right and left mandibles, we rotate the pictures of the left mandibles, as if they were reflected in a mirror, and processed them as right mandibles. We included only the mandibles for which all structures were complete (Fig.1). Eighteen landmarks (Fig. 2, Table 2) were used to describe the shape of the mandible. Landmarks were digitized using tpsDig2 2.32 (Rohlf, 2010) and a Generalized Procrustes Analysis (GPA) was performed on the landmarks using MorphoJ (Klingenberg, 2011). These Procrustes-transformed landmarks were used to generate a covariance matrix with which we performed a Principal Component Analysis (PCA).

Following Anderson *et al.* (2014) and Fabre *et al.* (2017), we measured the mechanical advantage (MA,

Table 2. Landmarks locations in the hemimandible. Lm: landmark. Location of landmarks proposed by Anderson *et al.* (2014) and Fabre *et al.* (2017).

Lm	Location
Lm1	Most antero-ventral point of alveolus of the incisor
Lm2	Most antero-dorsal point of alveolus of the incisor
Lm3	Point at the maximum of curvature of the diastema
Lm4	Anterior point of the alveolar margin of the tooth row
Lm5	Boundary between the second and third lower molars
Lm6	Intersection between the ascending ramus and the posterior part of the lower third molar
Lm7	Dorsal-most point of the coronoid process
Lm8	Point at the maximum of concavity between the coronoid and the articular processes
Lm9	Antero-dorsal side of the articular condyle
Lm10	Dorsal-most point of the articular condyle
Lm11	Posterior-most point of the articular condyle
Lm12	Ventral-most point of the articular condyle
Lm 13	Point at the maximum of concavity between the articular and the angular processes
Lm14	Posterior-most point of the angular process
Lm15	Ventral-most point of the angular process
Lm16	Maximum point of concavity in the dorsal mandibular region
Lm17	Ventral-most point of the front lower part of the mandible
Lm18	Point of maximum of curvature of the deep masseteric insertion

efficiency of the mandible to transmit the muscular forces to the bite point) and the mechanical potential (MP, estimation of the biting force). These mechanical advantages and potentials are ratios based on lengths measured in the photographs of the mandibles using the ruler tool of Photoshop (Fig. 2). MA is the ratio between inlever or the distance from the jaw point to the point of muscle attachment and outlever or the distance from the jaw point to the bite point (Fig. 2). We calculated four MA ratios: $MA_{T/In}$ (inlever: temporal; outlever: incisor length), $MA_{Ms/In}$ (inlever: masseter length; outlever: incisor length), $MA_{T/Mo}$ (inlever: temporal length; outlever: molar length) and $MA_{Ms/Mo}$ (inlever: masseter length; outlever: molar length) (see Table 3). It can be observed in Figure 2 that most of the measured lengths have an origin and an end that correspond to a landmark; this fact essays the interpretation between the PCA and the ratios. Only the length for the distance between the condylar process and the lower first molar does not have a correspondence with

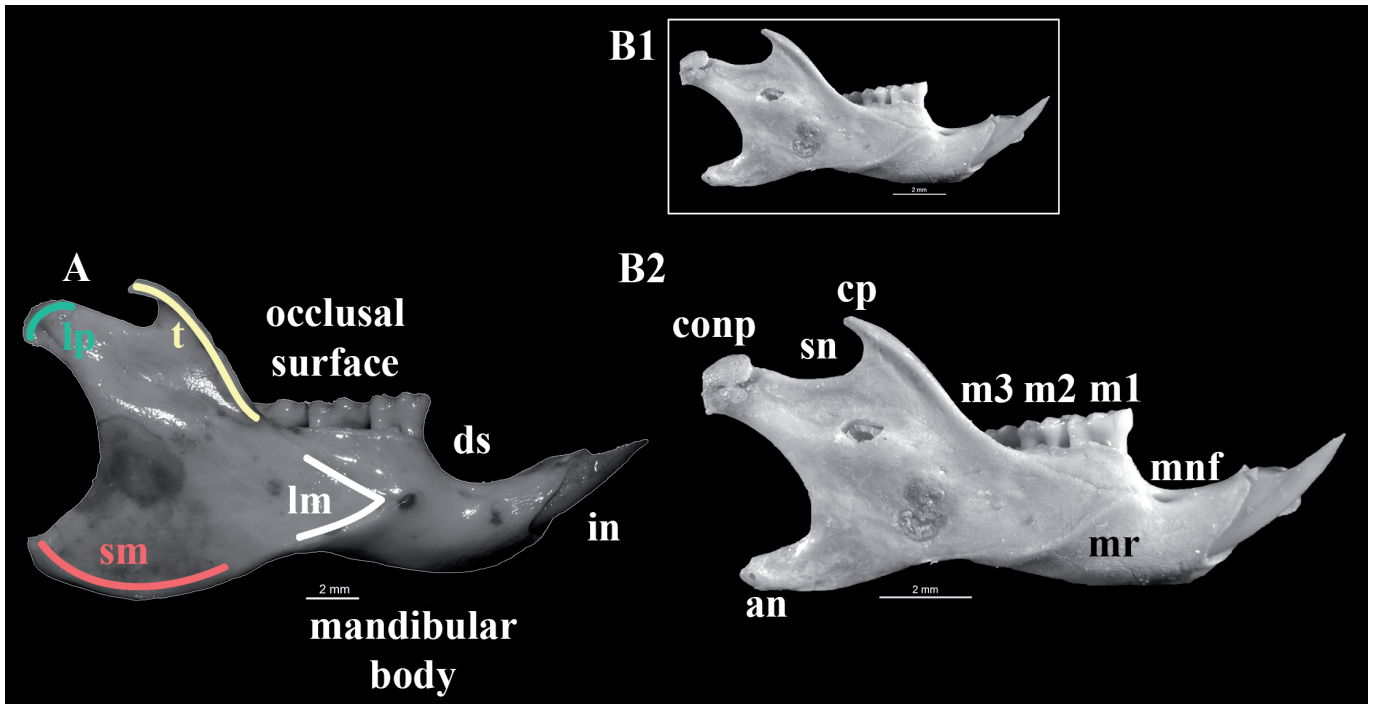
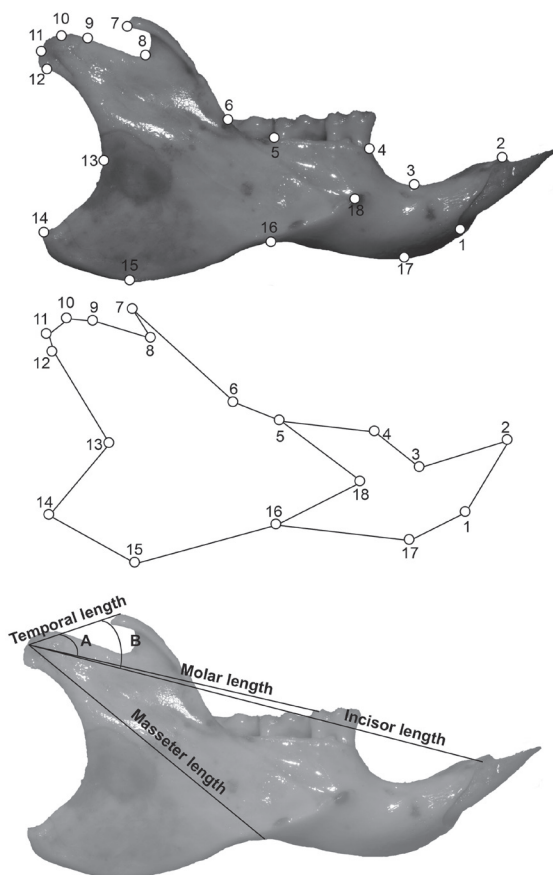


Figure 1. *Cricetodon* aff. *aureus* (SNSB-BSPG 1970 XVIII-8063) (a) and *Megacricetodon minor* (SNSB-BSPG 1966 XXXIV-3516) (b) at different scale to visualize the size differences. The nomenclature of the skeletal regions is the proposed by Mein & Freudenthal (1971a) and Bi *et al.* (2008). The musculature nomenclature is from Atchley *et al.* (1985). Abbreviations: an, angular process; cp, coronoid process; conp, condylar process; ds, diastema; mnf, mental foramen; mr, masseteric ridge; in, incisor; m1, m2, m3, first, second, third lower molars; sn, sigmoid notch. Coloured lines indicate the insertions for the muscles: lm, lateral masseter; lp, lateral pterygoid, sm, superficial masseter, t, temporal muscle.



any landmark. Anderson *et al.* (2014) measured the incisor length from the condylar process to the incisor tip. In our sample, some of the specimens do not present the incisor or this presents alterations in its position. Therefore, we use the anterior point of the alveolus of the incisor as the end of the incisor length. To calculate the MP firstly, we obtained the angle between the molar length and the temporal length (angle A) and between the incisor length and temporal length (angle B). Secondly, we calculated the two force angles (FA) through: $\text{radian}(90^\circ) - \text{radian}(\text{angle A or B})$. Finally, the $MP_{Mo} = MA_{T/Mo} \times \text{cosine}(\text{FA-A})$ and $MP_{In} = MA_{T/In} \times \text{cosine}(\text{FA-B})$ (Fig. 2; Table 3). With these ratios, we performed boxplots in order to visualize the variation of the sample among these species. To confirm if

Figure 2. Top: digitalized landmarks (see Table 3) of *Cricetodon* aff. *aureus* (SNSB-BSPG 1970 XVIII-8063). Middle: wireframe of this specimen used for visualized geometric variation of the shape. Bottom: lengths and angles measured on digital photographs. Temporal length: from LM11 to LM7; molar length: from LM11 to the tip of hipoconid of the lower first molar; incisor length: from LM11 to LM2; masseter length: from LM11 to LM17.

there were significant differences between the two species, we performed a non-parametric Mann-Whitney test due to the limited sample size.

Table 3. List of ratios obtained from the linear measurements.

Specimen	Species	MA _{T/In}	MA _{Ms/In}	MA _{T/Mo}	MA _{Ms/Mo}	MP _{In}	MP _{Mo}
3493		0.229	0.532	0.356	0.827	0.120	0.185
3498		0.269	0.536	0.413	0.825	0.121	0.177
3516		0.275	0.565	0.415	0.853	0.138	0.188
3528	<i>M. minor</i>	0.293	0.550	0.430	0.806	0.139	0.194
3539		0.259	0.549	0.384	0.815	0.172	0.233
3546		0.266	0.531	0.390	0.780	0.145	0.206
3555		0.251	0.575	0.358	0.822	0.145	0.199
8060		0.158	0.609	0.253	0.973	0.084	0.133
8062		0.237	0.584	0.385	0.949	0.099	0.163
8063	<i>C. aff. aureus</i>	0.197	0.617	0.312	0.982	0.101	0.157
8067		0.238	0.609	0.385	0.986	0.089	0.144
8068		0.205	0.594	0.328	0.951	0.119	0.186

3. RESULTS AND DISCUSSION

We computed a PCA using the landmark dataset and plot the results in a graph (Fig. 3). The PCA resumes the total variance into a few dimensions that allow us to explore the landmark position variation of the sample. The percentage of variance that gathers the first two principal components

(PC1 and PC2) is 70.7%. To represent the variation of the landmarks along the axis, we added the wireframes configurations of the extreme configuration (Fig. 3). The PC1 ordered the sample in two different groups characterized by a greater development of the angular process and lower development of the condylar process in *Cricetodon* aff. *aureus* and a greater development of the condylar process and more anterior position of the lower masseter in *Megacricetodon minor*. The PC2 gathers the morphological variation of the coronoid process from forms with lower development on it (negative values) to forms with greater development on this process. The PC1 gathers the interspecific variation of the sample establishing two different groups. The PC2 gathers the intraspecific variation within the two groups. The rest of the variance (29.3%) is mostly distributed among the PC3-PC6, which distributes the sample according to morphological differences without a clear relationship with biomechanical features.

This intraspecific variation could be related to the findings of Anderson *et al.* (2014), which described that part of the morphological variation is a result of the adaptive plasticity of the populations in response to environmental changes. To explore this morphological variability, we performed the biomechanical ratios by boxplots (Fig. 4). The results show differences between the species for the different ratios. To confirm that there are significant differences between the analysed ratios of the mandibles, we performed a Mann-Whitney analysis. The results indicate that all ratios, but one show significant differences (Fig. 4).

It can be noted on the PCA (Fig. 3) that we have been able to quantify morphological differences among these species. Unlike the descriptions proposed by Mein & Freudenthal (1971a) based on morphological variation of the mandible, the geometric morphometric analysis allows us to establish the amount of variation among the different parts of the mandibles. It is worth noting that the greater morphological variation is related to skull structures that are tightly related to biomechanical features (as angular and coronoid processes and low masseter insertion) (Satoh, 1999; Cox *et al.*, 2012; Anderson *et al.*, 2014; Fabre *et al.*, 2017).

Although diet is traditionally inferred based on molar morphologies (Coillot *et al.*, 2013; Lazzari *et al.*, 2015), there are other proxies that could be used to deduce the diet of these cricetid rodents, such as the mechanical advantage and potential (Anderson *et al.*, 2014; Fabre *et al.*, 2017). Boxplots (Fig. 4) show that *Megacricetodon minor* presents higher mechanical advantage values in the ratios MA_{T/In} and MA_{T/Mo}. These results coincide with those of the PCA in which the PC1 describes the mandibles of *M. minor* as mandibles with a post-displaced condylar process. Higher values of the length between the condylar and coronoid process result in an increase in the values of MA_{T/In} and MA_{T/Mo}. The result of MA_{T/Mo} must be interpreted

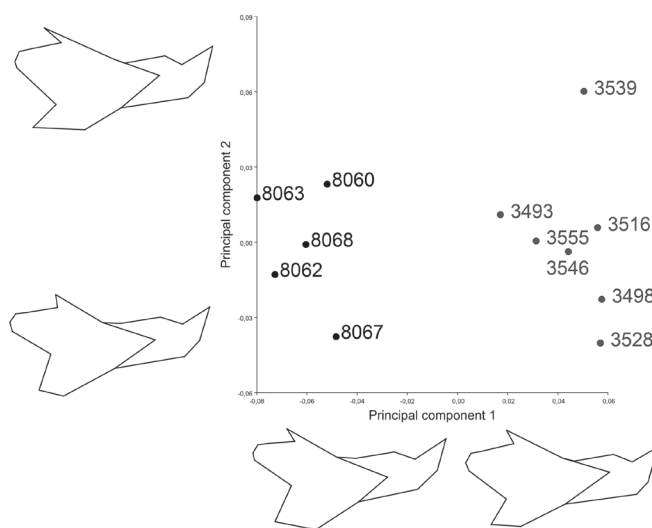


Figure 3. PCA and morphological transformation along the axis. Black dots represent *Cricetodon* aff. *aureus* and grey dots denote *Megacricetodon minor*. Numbers are the abbreviations of the catalogue numbers. Wireframes are representing the extreme morphology for each axis.

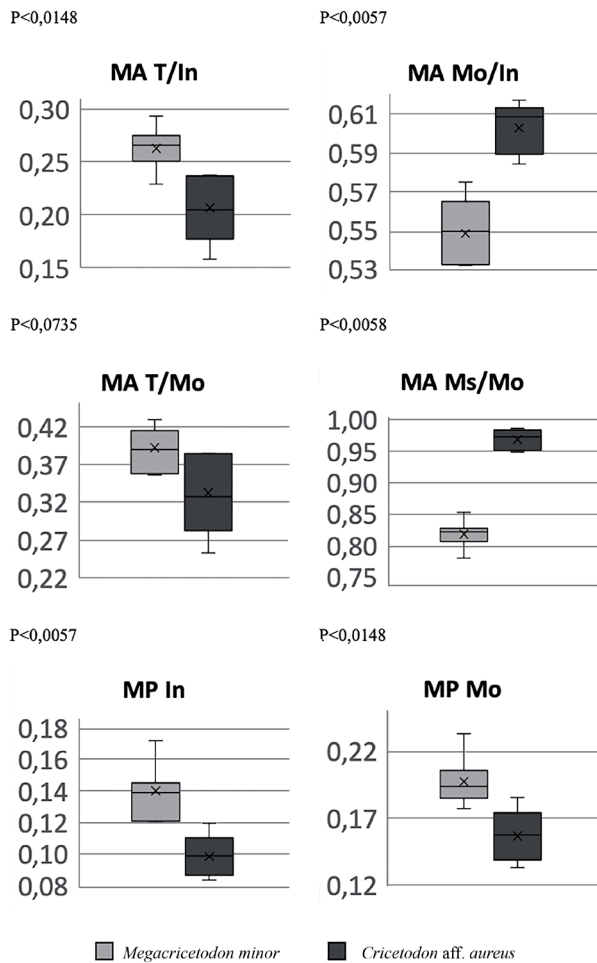


Figure 4. Boxplots of mechanical advantage and potential. On the top of the plots there are the p-values of the Mann-Whitney analysis for each ratio.

with caution since the statistical analysis does not show significant differences between the species in this ratio. In sum, *M. minor* possesses post-displaced condylar process and narrower masseteric areas; these position and reduction thus likely favour a quick jaw closure and weaker biting forces compatible with a faunivore diet (Fabre *et al.*, 2017). The morphological pattern shown by the mandible of *M. minor* is similar to extant faunivore rodents as the tribe Hidromiyini (see Helgen, 2005; Fabre *et al.*, 2017). As we have mentioned above, traditionally, dentition has been the proxy to infer the diet of the mammals. Dentition of *Megacricetodon* has been described as brachyodont and mesodont molar with bunodont dental pattern (van Dam & Weltje, 1999; Fejfar *et al.*, 2011) typical of an omnivore organism. However, and taking into account the morphometric and biomechanical analysis, the morphological pattern of *M. minor* could fit to an omnivore diet with faunivore preferences attending to the biomechanical behavior of its mandibles.

Cricetodon aff. aureus presents significant higher values in $MA_{Ms/In}$ and $MA_{Ms/Mo}$ related to the greater development of the angular process and its relative position with the condylar process indicative of the biting strength. The values of the mechanical potential are significantly higher in *M. minor*. The results of these ratios can be related with the post-displaced condylar process that triggers an increase in the ratios values. The results of the PC1 combined with the ratios of the mandibles show that *C. aff. aureus* presents a wider angular process and masseteric ridge areas that could be defined as a mandible with a slower closure (lower values of $MA_{T/In}$ and $MA_{T/Mo}$) and stronger biting force (higher values of $MA_{Ms/In}$ and $MA_{Ms/Mo}$) compatible with a harder diet (Fabre *et al.*, 2017). This mandibular morphology is comparable with extant rodent species to which a herbivorous diet is attributed as *Hapalomys*, *Melomys* and *Sundamys* among others (Camacho-Sánchez *et al.*, 2017; Fabre *et al.*, 2017; Gómez Cano *et al.*, 2017). These results coincide with the traditional interpretation of the molar pattern of *Cricetodon*, described as cricetids with bunodont molars and some high-crowned pattern in some of the species (De Bruijn & Ünay, 1996; van Dam & Weltje, 1999; Durgut & Ünay, 2016). This dental pattern and the mandibular morphology could correspond to a more herbivore organism.

As it is evident on the PC2, *M. minor* presents a greater amount of morphological variability, which could be related to the plasticity as defined in Anderson *et al.* (2014): “non-heritable morphological variation, enables organisms to modify the shape of their skeletal tissues in response to varying environmental stimuli”. This plasticity could be the origin of the ecological success of this ubiquitous species, which has been recorded in many fossil sites along Europe during lower to upper Miocene (Daams *et al.*, 1999; Oliver & Peláez-Campomanes, 2013).

4. CONCLUSIONS

2D geometric morphometric analysis has revealed as a tool to quantify the mandibular shape of *C. aff. aureus* and *M. minor*; and has let us to establish morphological differences among these species and determine a morphological pattern for each species. We could determine the regions that gather the greatest amount of variation: condylar and angular processes and lower masseter. These regions are fundamental to explain the biomechanical behaviour of the mandibles. Due to this fact, for the first time, a biomechanical analysis has been performed in fossil cricetids mandibles by the measurements of different ratios based on the length of these key structures. The results showed that *Megacricetodon minor* and *Cricetodon aff. aureus* present significant differences in most of the

values of the mechanical advantages and potentials of their mandibles and therefore they should develop different forces and speeds biting. The robust mandibular pattern that defines *C. aff. aureus* favours slower closure of the mandible but stronger biting forces of the molar region. This, together with its molar pattern could be indicating an herbivore diet. The narrow mandibular pattern that defines *M. minor* favours faster closure of the mandible and weaker biting forces of the molar region. These characteristics and the bunodont pattern of its molar could be compatible with an omnivore diet with faunivore preferences. These mechanical characteristics could indicate different diets of these species. However, further studies (increasing the sample with extant rodents with a defined diet, adding other related species in other fossil sites) are required in order to establish more concrete results.

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