First functional morphology comparison between two Miocene cricetid mandibles

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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 cricetids 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 estudiaba 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*

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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; Balutanás 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 (Heizmann & 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                  |
|--------------------------------|-----------------------------------|
| *Megacricetodon minor*         | 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         |
| *Cricetodon* aff. *aureus*     | 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, 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

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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                 |
| Lm13| 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                                                  |
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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.

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: radian(90º)-radian(angle A or B). Finally, the $MP_{Mo} = MA_{Mo} \times \cosine(FA-A)$ and $MP_{In} = MA_{In} \times \cosine(FA-B)$ (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...
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_T/Mo | MA_Mt/In | MA_Mt/Mo | MP_T/In | MP_T/Mo |
|----------|---------------|---------|---------|----------|----------|---------|---------|
| 3493     | C. aff. aureus| 0.229   | 0.532   | 0.356    | 0.827    | 0.120   | 0.185   |
| 3498     | M. minor      | 0.269   | 0.536   | 0.413    | 0.825    | 0.121   | 0.177   |
| 3516     | M. minor      | 0.275   | 0.565   | 0.415    | 0.853    | 0.138   | 0.188   |
| 3528     | M. minor      | 0.293   | 0.550   | 0.430    | 0.806    | 0.139   | 0.194   |
| 3539     | M. minor      | 0.259   | 0.549   | 0.384    | 0.815    | 0.172   | 0.233   |
| 3546     | M. minor      | 0.266   | 0.531   | 0.390    | 0.780    | 0.145   | 0.206   |
| 3555     | M. minor      | 0.251   | 0.575   | 0.358    | 0.822    | 0.145   | 0.199   |
| 8060     | C. aff. aureus| 0.158   | 0.609   | 0.253    | 0.973    | 0.084   | 0.133   |
| 8062     | C. aff. aureus| 0.237   | 0.584   | 0.385    | 0.949    | 0.099   | 0.163   |
| 8063     | M. minor      | 0.197   | 0.617   | 0.312    | 0.982    | 0.101   | 0.157   |
| 8067     | M. minor      | 0.238   | 0.609   | 0.385    | 0.986    | 0.089   | 0.144   |
| 8068     | M. minor      | 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 cricetids 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...
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 bunolophodont molars and som 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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