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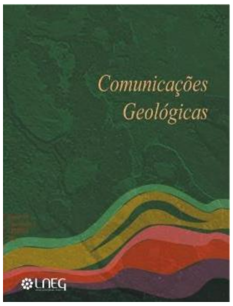
Geometric morphometrics applied to molars of Pleistocene *Bos* and *Bison* of Europe

Morfometria geométrica aplicada aos molares de Pleistoceno *Bos* e *Bison* da Europa



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Abstract: *Bos* e *Bison* (Bovinae, Mammalia) são mamíferos aparentados de grande porte, abundantes nas associações fossiliferas do Pleistocénico. A determinação dos elementos osteológicos destes bovinos é tradicionalmente baseada em diferenças morfológicas, contudo, novos estudos moleculares sugerem a sinonímia de ambos os géneros. Na sequência dos recentes avanços nos métodos de classificação morfológica, implementámos uma abordagem de morfometria geométrica bidimensional para analisar a superfície oclusal dos molares de *Bos* e *Bison*, e posteriormente, de espécies de bisontes extintas. Aplicámos esta metodologia em fotografias de molares superiores e inferiores utilizando os nossos novos protocolos para digitalizar a morfologia. A digitalização dos *landmarks* e *semi-landmarks* foi realizada com o software Viewbox 4 e a análise estatística com os softwares Morphologika2 2.5 e MophoJ. Os nossos resultados apresentam uma sobreposição na distribuição dos principais aspectos relativos à forma dos molares, sem qualquer diferenciação entre taxas. Isto poderá dever-se ao pequeno tamanho da amostra, e/ou às diferentes fases de desgaste.

Keywords: *Bison*, *Bos*, Morfologia, Dentes molariformes, Quaternário

Resumo: *Bos* and bison *Bison* (Bovinae, Mammalia) are closely related large mammals abundant in Pleistocene fossil assemblages. The determination of osteological elements of these bovines is traditionally based on morphological differences, but new molecular studies suggest the synonymy of both genera. Following recent advances in morphological classifying methods we implemented a two-dimensional geometric morphometric approach to analyse the occlusal surface of molars in *Bos* and *Bison*, and secondly on extinct bison species. We have applied this methodology in photographs of upper and lower molars using our new templates proposals to digitise the morphology. The digitalisation of the landmarks and semilandmarks was carried out with Viewbox 4 software and the statistical analysis with Morphologika2 2.5 and MophoJ softwares. Our results show an overlapping distribution regarding the main aspects of shape of the molars, with no discrimination between taxa. This can be due to the small sample size, and/or the different wear stages.

Palavras-chave: *Bison*, *Bos*, Morphology, Cheek teeth, Quaternary.

1. Introduction

The relationship of bison (*Bison*) with oxen (*Bos*) is controversial and dates back from decades ago. Throughout the years several studies were carried out to establish and delve into the phylogenetic relationship between both genera (Hernández-Fernández and Vrba, 2005; Nijman *et al.*, 2008; Hassanin *et al.*, 2013). Despite the molecular results suggesting the synonymy of Bos and Bison, the incongruence with morphological analysis keeps the scientific community divided between accepting the synonymy or defend each genus identity (Ghassemi-khademi *et al.*, 2021). Morphological distinctions between oxen and bison are established in horn cores, skull, upper and lower third molars, metapods and phalanges (López González *et al.*, 1999; Sala *et al.*, 2010; Galindo-Pellicena *et al.*, 2019).

Two-dimensional geometric morphometric (2DGM) is a precise methodology to compare morphologies. This approach analyses morphological differences between elements (*e.g.* teeth) through coordinates on homologous structures, which allows comparing different specimens by reducing the distance between these structures (Klingenberg, 2015). Previous studies on the dentition of bovids applying 2DGM show favourable results discriminating molars at different taxonomic levels (Brophy *et al.*, 2019; Cucchi *et al.*, 2019).

To test the morphological differences between oxen and bison and contribute to the debate we propose 2DGM to compare molars of all wear stages of living and extinct *Bos* and *Bison* species. Secondly, we will assess 2DGM as a complementary method to classical systematic palaeontology in extinct bison.

2. Material and Methods

2.1. Material

The present study focuses on the analysis of upper and lower molars of *Bos* and *Bison*. Within each genus we studied the following species of *Bos*: *B. taurus*, *B. sauveli*, *B. gaurus* and *B. oldowayensis*; and *Bison*: *Bi. bison*, *Bi. bonasus*, *Bi. priscus*, *Bi. menneri*, *Bi. degiulii*, *Bi. schoetensacki*, *Bi. voigtstedtensis* and *Bi.*

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palaeosinensis. We considered both subgenus of *Bison*: *Bison* and *Eobison*, the latter only represented by *Eobison* sp. and *Bi. degiulii*, although recent studies question the position of this species (Kostopoulos *et al.*, 2018). We included living and fossil specimens gathered from bibliography (Skinner and Kaisen, 1947; Kostopoulos, 1997; Sher, 1997; Martínez-Navarro *et al.*, 2007, 2012; France, 2009; Marra *et al.*, 2014; Bojar *et al.*, 2015; Bona and Sala, 2016; Suraprasit *et al.*, 2016; Made *et al.*, 2017; Tong *et al.*, 2017; Van Asperen and Kahlke, 2017; Kostopoulos *et al.*, 2018), online resources (www.animaldiversity.org, www.morphobank.org) and contemporary and fossil collections from the Department of Palaeobiology from the National Museum of Natural Sciences (CSIC). Living species are the standard dataset. The teeth represent almost all wear stages of the dentition, from slightly worn to heavily worn teeth. We did not include unworn teeth since we needed the dentine-enamel limit for the template (see 2.2. 2D Geometric morphometric).

The original material was photographed with a Canon EOS70D camera, with a 0.39m/1.3ft EFS 18-135mm Macro objective in a perpendicular angle to the occlusal plane. This standardizes the perspective to avoid interfering in the statistical analysis, although bibliographical photographs were not normalised. Throughout the manuscript, M^x indicates upper molar and M_x lower molar.

Our sample consists of 128 molars. M^1, M^3 and M_1 are represented by 19 specimens each, M^2 by 26, M_2 by 22 and M_3 by 23. The M^3 and M_3 are the ones with more taxonomic disparity whilst the M^2 is the most abundant molar.

2.2. 2D Geometric morphometric

Our study concerns the shape of the occlusal surface of the molars and required the design of three templates (Fig. 1): one for the upper molars, one for the M_1 and M_2 and the last one for the M3. There are 15 landmarks for the upper molars, M1 and M2, 155 semilandmarks for the upper molars and 136 semilandmarks for the lower molars. For the M_3 there are 20 landmarks and 154 semilandmarks. We followed the protocol of Cucchi *et al*. (2019) for the development of the templates: landmarks represent the maximum curvature of each structure in the dentine-enamel contact. Unlike these authors, we included the fossas since they are often useful for the diagnosis (Kostopoulos, 1997; Tong *et al.*, 2017). Semilandmarks were slided with the bending energy method (Bookstein, 1996; Gunz *et al.*, 2005). All pictures were scaled as part of our own protocol. We used the Viewbox 4.0.1.7 software (dHAL software, Kifissia, Greece) for the digitalization of the landmarks following the protocols of Bastir *et al*. (2019).

2.3. Statistical analysis

For the statistical analysis we used Morphologika2 2.5 and MorphoJ 1.05d softwares (O'Higgins and Jones, 2006; Klingenberg, 2011). We performed a Generalized Procrustes Analysis (GPA), which removes size, position, orientation and comparing the shape of the molars and a Principal Component Analysis (PCA) to describe the tooth shape. Both GPA and PCA analyses were performed for each molar. We also performed a Discriminant Function Analysis (DFA) to compare both genera. This last analysis included a Permutation test of 1000 repetitions and included all pairs of groups.

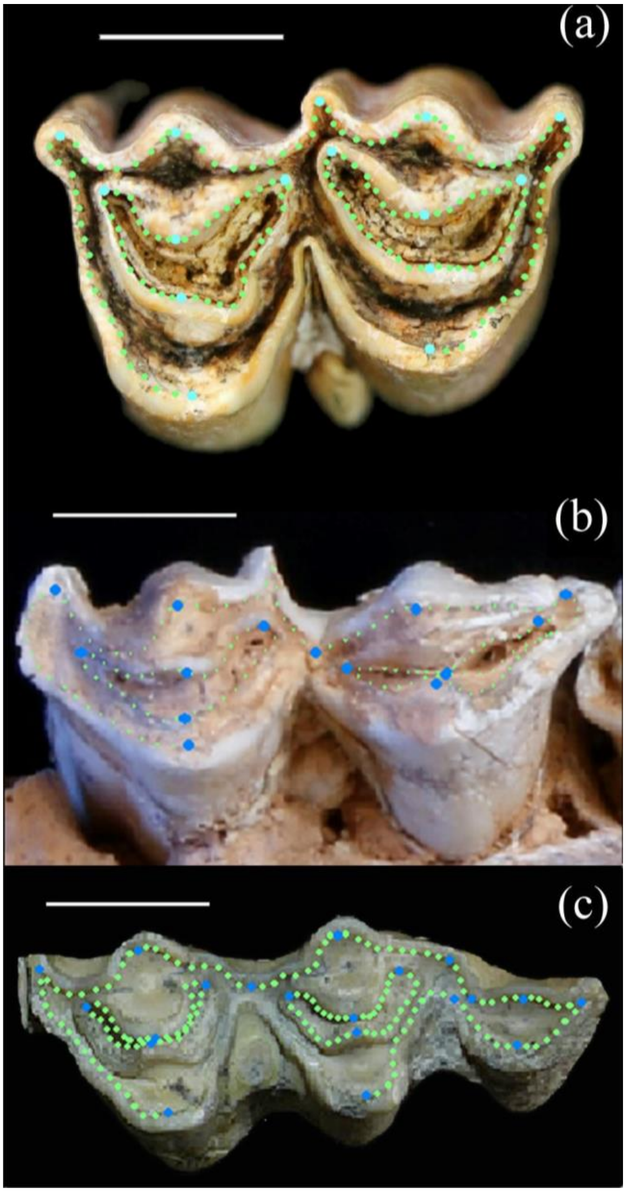

Figure 1. Templates for the two-dimensional geometric-morphometrics analysis: (a) upper molar, (b) lower first and second molars, (c) lower third molar. Bigger, blue/dark points indicate landmarks and smaller, green/light points semilandmarks. All the scale bars are 1 cm.

Figura 1. Modelos para a análise de morfometria geométrica bidimensional: (a) molar superior, (b) primeiro e segundo molares inferiores, (c) terceiro molar inferior. Pontos maiores, azuis/escuros indicam pontos de referência e pontos semilancos mais pequenos, verdes/claros. Todas as escalas são de 1 cm.

3. Results

The distribution of the data on the PCA plot answers to the different shape of the occlusal surface. The first and second principal components (PC1 and PC2) represent the length or antero-posterior diameter (DAP) and the width or transverse diameter (DT):in upper molars PC1 is DT while in lower molars PC1 is DAP. Together with the third principal component (PC3), which represents the change in size or orientation of the intermediate or posterior lobe compared to the anterior lobe, and the stylids orientation in M_3, the first three components explain by themselves 64.3% of the shape variability. We considered other PCs but neither of them reflected an arrangement closer to the taxonomic criteria. Table 1 summarises the variability of the first three components for each molar and the number of components that collect 90% of this variability.

Table 1. Results of the Principal Component Analysis (PCA) and the Discriminant Function Analysis (DFA) for each molar. The first column has the upper molars (M^x) and lower molars (M_x), the second to fourth columns represent the variability (%) of the first three principal component. The next column indicates the number of principal components needed to explain the 90% of variability from each sample and the final column represents the *p* value obtained for each molar with the DFA.

Tabela 1. Resultados da Análise da Componente Principal (PCA) e da Análise da Função Discriminatória (DFA) para cada molar. A primeira coluna tem os molares superiores (M^x) e inferiores (M_x), a segunda a quarta colunas representam a variabilidade (%) dos três primeiros componentes principais. A coluna seguinte indica o número de componentes principais necessários para explicar os 90% de variabilidade de cada amostra e a coluna final representa o valor de *p* obtido para cada molar com o DFA.

	PC1	PC2	PC3	90% Cum. Variab.	*p* value
M^1	50.045	12.818	9.646	7	0.9979
M^2	41.097	12.525	8.233	11	0.9940
M^3	46.247	9.714	7.544	10	0.9986
M_1	38.087	20.253	8.196	9	0.9994
M_2	31.651	17.348	10.443	10	0.9982
M_3	30.649	18.063	13.243	9	0.9987

In Figure 2 the plots display the morphology variability along PC1 and PC2 for each molar. The DAP component always arranges the data from longer to shorter teeth, whilst the DT component arranges it from wider to narrower. Although showing an overlap, in M^3 *Bos* arranges with a quadrangular-shape tendency whereas *Bison* has a more rectangular-shape tendency.

We also performed a PCA on living and extinct specimens separately and repeated the analysis of the complete dataset without extreme wear stages (slightly worn and heavily worn) for each molar, obtaining a similar arrangement of the data. We noticed that even the specimens of the same species were widely distributed along the components instead of grouped together. The DFA shows a $p \geq 0.99$ in every molar (Tab. 1), supporting the lack of significant differences in our data regarding the occlusal surface of oxen and bison. This is also appreciable in Table 2 with the classification matrix. Our results led us to assess our sample and the procedure followed before continuing with more analyses.

4. Discussion

As mentioned above, the data does not follow a taxonomical criterion. The variables explaining such distribution are DT and DAP for both upper and lower molars. This is coherent with molar's shape: upper molars are similar in length and lower molars are similar in width. Regarding PC3, the proportions of the lobes in a single tooth varies with wearing in both upper and lower molars similarly, same as stylids orientation. These PCs relate with attrition: in less worn teeth DAP values are greater, DT lower and stylids are more pronounced and oriented to the centre axis of the tooth. On the contrary, in more worn teeth DAP reduces with wearing, DT acquires greater values and stylids are less pronounced and more parallel to the tooth transverse axis.

The variance expressed by the first three components of the PCA does not reach the minimum percentage (70%) for a good representation of variability (Jollife and Cadima, 2016). Together with the similar arrangement of the data on the remaining PCs and the DFA analysis results, we decided to focus on PC1-PC3. The PCA plot (Fig. 2) suggests some potential for the M^3, which needs to be evaluated with a larger sample. This is consistent with the use of M^3 and M_3 as the most diagnostic teeth (López González *et al.*, 1999; Stampfli, 1963 in Sala *et al.*, 2010).

In systematic palaeontology the determination of fossil molars comes from DAP, DT and lobes proportions measurements. Yet our study is inconsistent with this but with the wearing stages of each molar. When looking to the distribution of the species (Fig. 2) the data also shows overlapping.

Although Sten (2004) mentions that wearing affects the occlusal surface shape changing it throughout the life of an individual, previous studies reflected phylogenetic signals on the M^2, M^3 and M_3 of cattle (Cucchi *et al.*, 2019) with negligible effect of wearing on the taxonomic determination. It is important to consider that they only analysed heavily worn teeth (*i.e.* only one wear stage). Similarly, Brophy *et al.* (2019) published good results on the occlusal surface of teeth with an elliptical Fourier analysis. However, this method requires a closed shape and would prevent us from comparing different wear stages, since wearing leads to the presence of an entostyle or ectostylid in the occlusal surface and the fossas could not be collected.

The protocol here applied allows comparing different wear stages at the same time, although our results could not assist the discrimination of *Bos* and *Bison*. Future applications focused on ecomorphology, or wear estimating purposes, may show profitable results. Dividing the sample on different wear stages may provide a better alternative to analyse the teeth and reduce the wearing influence on the classification of specimens, as already demonstrated by Cucchi *et al*. (2019).

Our work presents some limitations like a small and heterogeneous sample. It is also important to consider the different wearing stages analysed influence the shape of the occlusal surface morphology through an individual life and interferes with the taxonomic relationships.

To avoid wearing from interfering with shape analysis we propose two alternatives: analyse a sample representing only one wear stage and enlarge the sample. Both alternatives could be successful, with the former promising better results as stated in other studies. Regarding the 2DGM procedure, most of the photographs gathered were not taken or published with morphometrics purposes, which entails the lack of quality needed to digitise the landmarks and adds the difference in perspective as a variability factor.

Our results meet the expectations of Sher (1997) and Sorbelli *et al*. (2021), who claim the difficulties of teeth occlusal surface as a diagnostic element in low sample size. At present we are developing new studies on bovid teeth morphology as a diagnostic element by implementing a three-dimensional geometric morphometrics approach. We also contemplate a three/four wear stages classification of teeth to analyse the specimens on each taxonomic rank, as well as new material including more living specimens for the control dataset. We recommend taking the photographs personally to ensure a good quality and equal perspective to eliminate these as a variability

5. Conclusion

The present study proposes 2DGM as a new approach to analyse the morphological differences on molars of *Bos* and *Bison*. The results show that both genera are similar regarding the occlusal surface of molars, which also happens at species level. In larger samples the M^3 may stand a good element for determination

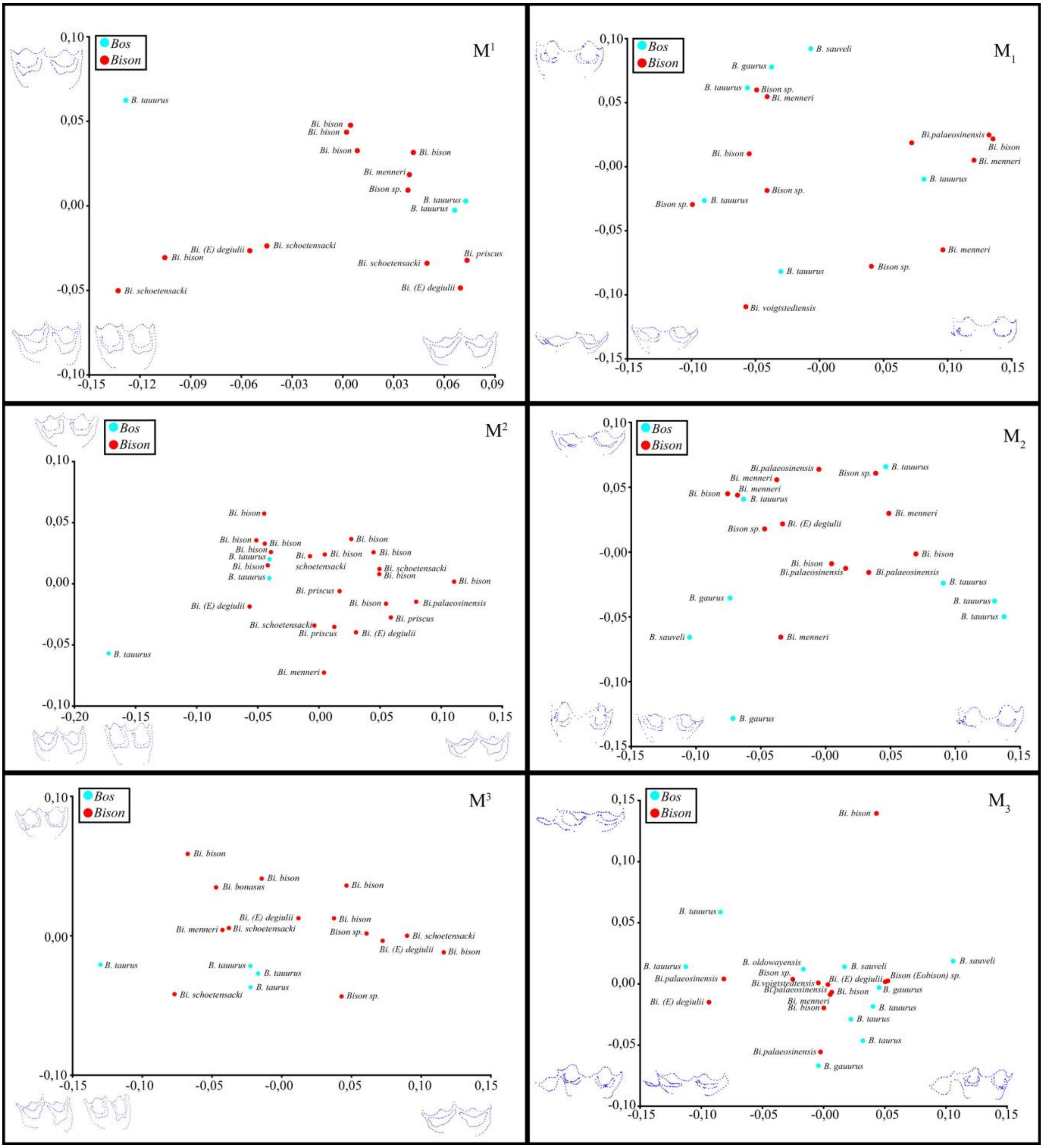

Figure 2. Principal Component Analysis performed on upper (M^x) and lower (M$_x$) molars. Blue/light dots: *Bos*; Red/dark dots: *Bison*. Ellipses were calculated for the mean of each genus with a confidence of 0.95. x axis is the first component (PC1) and y axis the second component (PC2). Molar wireframes are for the PC1 (above the axis except for M^2 and M^3) and PC2. The percent of explained variance of PC1 and PC2 for each molar is indicated on Table 1

Figura 2. Análise de Componentes Principais realizada em molares superiores (M^x) e inferiores (M$_x$). Pontos azuis/claros: *Bos*; pontos vermelhos/escuros: *Bison*. As elipses foram calculadas para a média de cada género com uma confiança de 0,95. O eixo x é a primeira componente (PC1) e o eixo y a segunda componente (PC2). O wireframe dos molares são para o PC1 (acima do eixo, excepto para M^2 e M^3) e PC2. A percentagem de variância explicada de PC1 e PC2 para cada molar é indicada na Tabela 2

purposes. From these results, we conclude that the wearing of the teeth highly influences the molars shape. More studies are ahead before resolving the *Bos*-*Bison* debate applying geometric morphometrics, as well as its implementation for determination purposes.

Table 2. Classification matrix obtained from the Discriminant Function Analysis (DFA) and Cross-validation (CR) for each molar.

Tabela 2. Matriz de classificação obtida a partir da Análise da Função Discriminatória (DFA) e Validação Cruzada (CR) para cada molar.

		M^1		M^2		M^3		M_1		M_2		M_3	
		Bison	*Bos*	*Bison*	*Bos*	*Bison*	*Bos*	*Bison*	*Bos*	*Bison*	*Bos*	*Bison*	*Bos*
DFA	*Bison*	11	0	20	0	12	0	11	1	12	1	11	1
	Bos	2	3	1	3	2	4	1	5	1	7	1	9
CR	*Bison*	12	2	19	2	11	2	9	3	10	3	7	4
	Bos	1	1	2	1	3	2	3	3	3	5	5	6

We suggest alternatives to improve the results when applying two-dimensional geometric morphometrics on bovid molars, which may be helpful to alleviate the *Bos-Bison* debate.

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