



# New Methods for Old Questions: The Use of Elliptic Fourier Analysis for the Formal Study of Palaeolithic Art

Miguel García-Bustos<sup>1</sup> · Paula García Bustos<sup>2</sup> · Olivia Rivero<sup>1</sup>

Accepted: 17 May 2024  
© The Author(s) 2024

## Abstract

One of the main objectives of Palaeolithic art researchers is to study and systematise the form of artistic representations. Some methodologies include the analysis of qualitative variables, linear measurements or the use of geometric morphometry with landmarks. However, these techniques depend to a large extent on the subjectivity of the researcher, which often leads to biased results. To overcome this issue, we present an application of geometric morphometry using Elliptic Fourier Analysis (EFA), together with multivariate statistics and hypothesis testing, for the first time to the study of form in prehistoric art. In order to explain its use, the “duck-bill” convention of pre-Magdalenian horses, often used as a chronological and geographical marker, has been used as a case study. This formalism is described disparately in the literature, so the main objective is to use EFA to determine whether it is possible to characterise this type of convention according to the definitions given by certain authors. The results indicate a possible classification of the heads of these animals. Through this taxonomic proposal, it has been possible to verify the great diversity of forms in which the authors classify the duck-bill horses and, therefore, to demonstrate that this peculiar form can be considered neither a conventionalism nor a chronological/regional marker. In conclusion, the methodology based on EFA combined with multivariate statistics for the objective study of form in prehistoric art is effective and opens a new avenue of analysis in the art of prehistoric societies.

**Keywords** Geometric morphometrics · Multivariate analysis · Pre-Magdalenian art · Conventionalism · Duck-bill horse

---

✉ Miguel García-Bustos  
miguelgarbus@usal.es

<sup>1</sup> Dpto. de Prehistoria, Hª Antigua y Arqueología, Facultad de Geografía e Historia, Universidad de Salamanca, C. Cervantes, 37002 Salamanca, Spain

<sup>2</sup> Departament d’Història I Arqueologia, Facultat de Geografia i Història, Universitat de Barcelona, C. de Montalegre, 6-8, 08001, Barcelona, Spain

## Introduction

Since the discovery of European Palaeolithic art in the nineteenth century, one of the main objectives has been the description and formal study of the figures. The results obtained have usually influenced the chronological ascription of the motifs, as well as the interpretation of the art from a symbolic and cultural point of view, especially with regard to the notion and evolution of “style” (Breuil, 1952; Graziosi, 1956, 1973; Jordá, 1964; Leroi-Gourhan, 1965). The authors who approached this analysis established the basic guidelines for the study of these Palaeolithic graphic manifestations based on three pillars that supported the concept and meaning of “form” and “style” (Palacio-Pérez, 2017). First, the linear and progressive evolution from a simple form to a more complex one. Second, the importance of technical and formal innovations as the main driving force for progress. And third, the positive correlation between greater naturalism and greater artistic skill. These criteria were used as true axioms, applying style as a fundamental factor of spatial and temporal discrimination (Domingo & Fiore, 2014). Likewise, variables such as conventionalisms, proportion, type of perspective or type of animation were used as indirect dating methods in the manner of fossil directors.

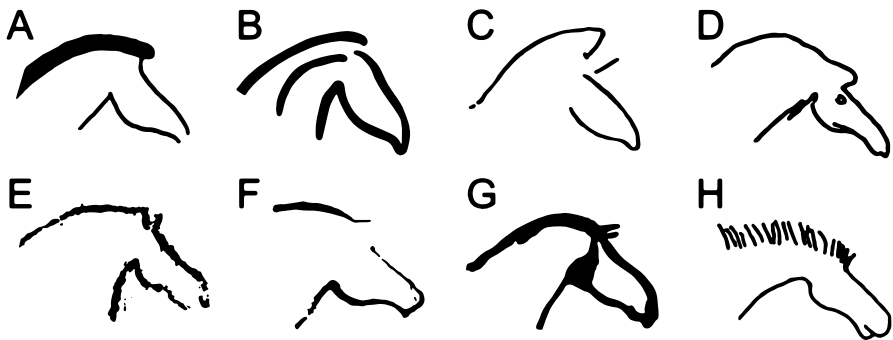
Today, traditional chronostylistic frames, of which those of Breuil (1952) and Leroi-Gourhan (1965) are the most widely used, have been overcome by the revolution in direct dating of Palaeolithic art and the discovery of Chauvet (Clottes et al., 1995; Lorblanchet & Bahn, 1993; Quiles et al., 2016). In addition to this, it should be noted that Palaeolithic art shows tendencies that go beyond the search for realism. Thus, schematic representations do not imply, as was thought in early research, “backwardness” or “antiquity” (Apellániz, 2004), as in the case of ibex in frontal view or the Gonnërsdorf-type venuses of the Upper Magdalenian. Currently, the main interest in the analysis of form is the attempt to assess regional connections rather than chronological periods (e.g. Fano & Rivero, 2007; Fuentes et al., 2019; García-Diez et al., 2015; González Sainz, 2007; Honoré et al., 2019; Petrognani, 2015; Rivero, 2010; Sauvet et al., 2014), although they still rely on traditional variables such as perspective, animation, anatomical details, proportion, outline or conventions of representation (e.g. Hernando, 2013, 2014; Petrognani, 2009; Rivero, 2020; Ruiz-Redondo, 2014).

If one animal has been most important in the attempt to systematise and study form, it is undoubtedly the horse, the most numerous figurative representation in Palaeolithic art (García-Bustos, 2021; García-Bustos & Rivero, 2023; Groenen, 2007; Sauvet, 2018, 2019). Analyses of qualitative variables have been applied to this motif, focusing on the outline and the presence or absence of anatomical details such as the mane, eyes or ears. On the one hand, studies such as those by Corchón et al. (2013), Corchón and Rivero (2010), Huard (2010), Petrognani (2009), Petrognani and Sauvet (2012), Pigeaud (2004) and Villaverde (1994) stand out, applied to specific cases such as La Griega, Las Caldas, Gargas, Lascaux, Gabillou, Mayenne-Sciences and Parpalló, respectively, determining specific graphic morphotypes for certain sites or periods. But also others, such as

those carried out by Buisson et al., (1996a, 1996b), Pigeaud (2005), Sauvet and Rivero (2016), Schmid (1984), Rivero and Sauvet (2014) and Tosello (2003), who propose global studies of form use this animal as an example.

Additionally, the measurements and proportions of equids have been the subject of various analyses with the aim of comparing the horses that lived in Palaeolithic times with their hypothetical representatives today (Bernáldez-Sánchez & García-Viñas, 2019; Bourdelle, 1958) and thus determining the species (Bourdelle, 1938; Capitan et al., 1924; Madariaga de la Campa, 1969; Prat, 1986). This metric methodology has also been used to calculate the homogeneity of a graphic set (Huard, 2007), to characterise the style, authorship and chronology (Apellániz, 1990; Apellániz & Calvo, 1999; Lión, 1971; Pigeaud, 1997, 2000, 2007) or to seek an explanation for the deformity of the outlines of equid representations (Rouzaud et al., 1992).

However, there are two fundamental problems with all these studies. Either they are based on qualitative variables whose definition is not always entirely objective, or they present large numbers of proportions or measurements that make it difficult to generalise the results. This paper introduces a new methodology based on geometric morphometrics to analyse variation in the form of Palaeolithic parietal and portable art, an innovative proposal aimed at overcoming the prevailing chronostylistic criteria, many of which are based on subjective considerations. In order to demonstrate its application, the analysis of a paradigmatic example in the formal study of equid figures called the “duck-billed” muzzle has been chosen as a case study.



**Fig. 1** Examples of duck-bill horses. At a glance, it is possible to observe the great variability with which experts categorise this type of formalism (the orientation of the tracings has been modified). **A** Pair non Pair (Delluc & Delluc, 1992). **B** Chauvet (Tosello & Fritz, 2004). **C** La Griega (Corchón, 1997). **D** Ardales (Cantalejo et al., 2006). **E** Mayenne-Sciences (Pigeaud, 2004). **F** Parpalló (Villaverde, 1994). **G** La Pileta (Breuil et al., 1915). **H** Gargas (Barrière, 1976)

## Materials and Methods

### A Case Study: The “Duck-Bill” Conventionalism

The conventionalism known as a “duck-bill” is a particular way of describing the beak-like muzzle of equine depictions (Fig. 1). The term was coined in theory by Breuil (Capitan et al., 1910) for the first time, although it does not actually appear in the aforementioned work. The lack or loss of an initial definition, as already indicated by Hernando (2013), has led to the proliferation of a variety of definitions, with important differences between authors. As a result, there is currently a lack of consensus on the definition of this graphic convention that generates as many proposals as authors who write about it, and they sometimes differ significantly (Table 1).

The importance of this stereotyped form lies in its use as a chronological and territorial marker. In principle, the “duck-bill” was regarded as an artistic resource typical of the Mediterranean Solutrean (Fortea, 1978) on the basis of the Solutrean chronology of plaquettes at Parpalló (Villaverde, 1994). The same chronology is attributed to the representation of a “duck-bill” equid at La Pileta, assuming that the figure is coeval with the aurochs dated to  $20,130 \pm 350$  BP (Sanchidrián et al. 2001). Another case is Cosquer, where most of the figurative representations (including horses with this formalism) are usually ascribed to its Solutrean phase, although there are some problems derived from direct dating that make it difficult to clearly ascribe them to the Solutrean or Gravettian (Clottes et al., 2005). We now know that this conventionalism might date back to the Aurignacian, although the few examples that can prove it, such as Bouil-Bleu, are found in poorly characterised contexts

**Table 1** Different authors’ definitions of the “duck-bill” conventionalism. All definitions have been translated except the one proposed by M. Lorblanchet

Author	Definition
Moure et al (1991:56)	“Head of elongated profile, with a rounded, downward pointing muzzle and a rather pronounced jaw line.”
Villaverde (1994: 354)	“A markedly convex silhouette at the start, with a tendency to taper—one might say rather sharply—towards the nose, giving rise to a certain, rather attenuated concavity, which helps to emphasise the duck-billed shape.”
Sanchidrián (1994: 174)	“A very sinuous jaw ending in a rectilinear muzzle that gives the figure a clearly flat appearance [...] with an arched maxillary-inferior outline [...] giving a sensation of a globular protome.”
Pigeaud (2005: 247)	“The rounding of the ganache and the hollowing of the trough are accentuated, so that the tip of the nose protrudes and appears flattened, like the mitre of a duck’s beak.”
Lorblanchet (2007: 215)	“An elongated and fine head, whose extremity is curved downward like that of a duck bill: the lips are well developed and droop down.”
Petrognani (2015: 228)	“Accentuated convexity of the jaw, pronounced ganache with more or less pronounced return of the tip of the muzzle: translation of a sinuosity passing from the concavity of the muzzle to the convexity of the tip of the nose and which may end in a point [...] or in a very rounded manner [...]”

(Sauvet et al., 2013). What does seem more certain is its use during the Gravettian period, although again we find no directly dated figures. The most cited example is at Mayenne-Sciences where one of the horses with an open muzzle was dated to  $24,220 \pm 850$  and  $24,900 \pm 360$  BP (Pigeaud et al., 2003). This chronology has then been extended to the rest of the cave figures, including duck-bill equids. Chauvet, Ardales and Croze-à-Gontran are other caves that house potential Gravettian representations with this type of conventionalism (Hernando, 2014; Sauvet et al., 2013).

As for its geographical distribution, it is found in practically all the territories of western Europe: from the south of Spain (Ardales, La Pileta), to the north and north-east of France (Mayenne-Sciences, Margot, Gorges), via the centre of the Iberian Peninsula (La Griega), the Cantabrian region in Spain (La Pasiaga, Askondo), the Pyrenees (Gargas), the Quercy (Roucadour), the Dordogne (La Croze-à-Gontran, Pair-non-Pair) and the Ardèche (Chauvet, Cosquer) (Petrognani, 2015) as well as in the open-air art of Siega Verde and Foz Côa. This is, therefore, a characteristic example of the extensive geographical and chronological extension of a particular type of representation in Palaeolithic art, a key to determining the existence of contacts, albeit indirect ones, over long distances of more than 1200 km.

As we have tried to show, despite its relevance, the inaccuracy and lack of consensus in the determination of this convention is evident, so the present study aims to precisely define this formalism on the basis of a comprehensive study of the complete outline of the horses' heads. To this end, 287 representations covering five regions have been analysed in order to determine whether or not this type of formal convention exists and whether it is a determining factor in characterising a chronological period or a specific region.

## GMM in Archaeology and Rock Art

Geometric Morphometric Methods (GMM) can be defined as “the scientific description of biological or medical shape variation and shape change” (Bookstein, 1996), “a class of multivariate methods for measuring and analyzing the shapes of objects” using Cartesian coordinates (Polly, 2018: 1) or “the analysis of size and shape derived numerically from landmarks (topographically corresponding points) on biological/ nonbiological organisms”, where the shape can be either the whole object or a specific part of it (Seetah, 2014: 3033).

This method, initiated in the 1980s and called traditional morphometry or multivariate morphometry for application in the field of biology (Adams et al., 2004), consists of taking linear measurements (measures, angles or proportions) with the aim of applying multivariate statistical analyses (Rohlf, 1999; Marcus, 1990; Reyment, 1991; Rohlf & Marcus, 1993; Zelditch et al., 2012). Two sources of information are used in geometric morphometrics: biological homology (biological elements of structures of individuals) and geometric localisation (2D or 3D spatial configuration of biological structures of specimens) (Klingenberg and Monteiro, 2005). Once the data are obtained, a Generalized Procrustes Analysis (GPA) or Procrustes overlay is performed to eliminate errors due to translation, rotation and scale of the samples taken.

Although the main field where this type of methodology has been applied is biology, it is now used in other disciplines such as archaeology. The main examples of its application in the latter discipline come from taphonomic studies for the recognition of cut marks (Maté-González et al., 2015), carnivore tooth marks (Arriaza et al., 2017, 2023; Yravedra et al., 2017a, 2017b) or trampling marks for their characterisation (Courtenay et al., 2019, 2020), thus facilitating the identification and determination of different bone modifications. Likewise, it has also allowed the differentiation in the use of different flint and quartzite materials through experimentation (Maté-González et al., 2018), even developing specific software for their detection (Palomeque-González et al., 2017).




The field of archaeobotany has applied this method for the examination of the remains of plant species (Portillo et al., 2020), such as vine seeds (Terral et al., 2010), date palm (*Phoenix dactylifera* L.) (Terral et al., 2012), cherry (*Prunus avium* L.) pits (Burger et al., 2011) or olive (*Olea europaea* L.) pits (Newton et al., 2014), including studies based on seed experiments before and after carbonisation (Charles et al., 2015) in the case of barley (Ros et al., 2014) and wheat (Bonhomme et al., 2017).

With regard to material culture such as lithic, bone, metallurgical or ceramic industries, GMM provides information such as the chronology or functional character of the site where these artefacts are found (Martínez-Carrillo et al., 2010). This method has been incorporated in recent studies to compare lithic or ceramic assemblages from the same site (Hashemi et al., 2021; Wang & Marwick, 2020), examine taxonomic variability (Matzig et al., 2021; Méndez-Quintas, 2022; Serwatka, 2015; Vestergaard & Hoggard, 2019), analyse the diachronic evolution of artefacts (Cortell-Nicolau et al., 2020; Hoggard et al., 2019; Loftus, 2022) or better understand the manufacturing design, level of standardisation, degree of specialisation and possible uses for which they were employed (Birch & Martínón-Torres, 2019; Chacón et al., 2016; Timbrell et al., 2022).

In reference to rock art, studies that have applied GMM have been limited and recent. This methodology has been applied to the analysis of dimorphism in Palaeolithic hands, based on experimentation (Nelson et al., 2017), in the study of late Holocene camelids from the Quebrada de Humahuaca (Charlin & Llosas, 2016) and the recognition of camelid morphological variability in southern Pozuelos (Puna de Jujuy, Argentina). But also in the identification of extinct fauna in Arnhem Land rock art (Cobden et al., 2017) or the comparison of representations between Leang Tumpuseng and Sulawesi rock art (Hayes and van den Bergh, 2018).

At the moment, the most common method for applying GMM in rock art is the landmark technique. This is a study that calculates the variation of the samples taken through a series of invariable points that act as anatomical references. These points, known as landmarks, are processed by means of Procrustes Analysis, which is necessary to be able to incorporate all the samples in the same Cartesian space. The latter allows the application of a series of multivariate statistical analyses to reduce variability and classify the samples into different groups. However, the use of this methodology has certain drawbacks and disadvantages (Table 2). The most notorious is the subjectivity in planning and choosing landmarks. By definition, these points must be placed at locations that are continuously replicated in the sample for

**Table 2** Comparison of quantitative methods used for the study of form in rock art

	<b>Linear measurements</b>	<b>Landmarks</b>	<b>Fourier</b>
			
<b>Measurement</b>	Based on longitudinal lines of the shape	Pre-selection of anatomical parts	Based on the Fourier transform of the whole contour
<b>Accuracy</b>	It depends on the accuracy of the archaeologist	It depends on the location of points and their quantity	It depends on the number of harmonies selected
	It analyses the variation of the area that has been measured	It analyses the variation of selected points	It identifies the variation in all its contours
<b>Subjectivity</b>	It depends on the location and number of measurements taken into account by the archaeologist	It depends on the location and number of anatomical references taken into account by the archaeologist	It depends on the number of harmonies chosen, although it is an easily controllable method
<b>Optimising time</b>	It is necessary to perform all measurements on each sample used in the study	It is necessary to use tracings or photographs and to place landmarks in each of samples.	The use of tracings is necessary but the contour can be extracted automatically by means of a function
<b>Use of complex shapes</b>	High level of difficulty in defining measurement locations of the form	High level of difficulty in defining key points of the form	Less difficulty by taking into account the whole contour of shape

use in the comparison. Unlike in the biological domain, in the archaeological field, their selection might depend on the researcher and the type of sample. Also, the level of complexity of the figures to be analysed can produce certain biases in the precision of the analysis, especially if they are shapes with a high level of curves.

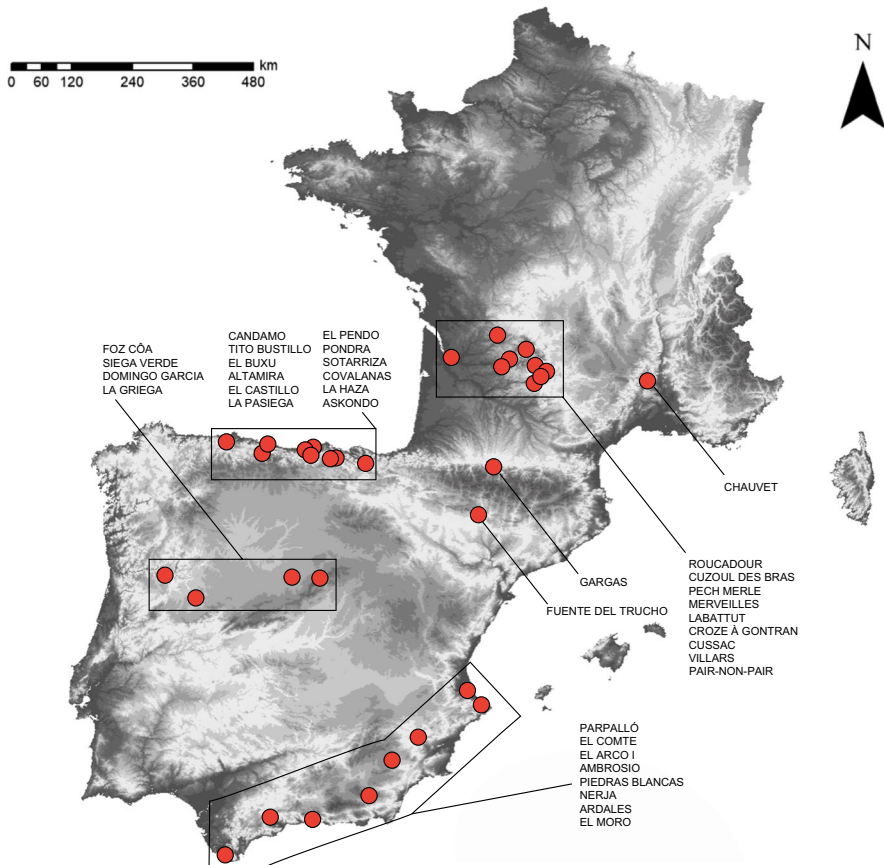
In an attempt to overcome this important limitation, this article presents an application of Elliptic Fourier Analysis (EFA) on representations from Franco-Cantabrian Palaeolithic art. This technique is based on Fourier transforms, a mathematical tool by means of which it is possible to quantitatively decompose a geometric figure into functions known as harmonics (Bonhomme et al., 2014; Caple et al., 2017; Crampton, 1995; Kuhl & Giardina, 1982). The outline of the figure is expressed in a set of coordinates (x, y) in a 2D plane that can be mathematically processed to calculate the four Fourier coefficients (a, b, c, d), a and b for the x-coordinate and c and d for the y-coordinate (Giardina & Kuhl, 1977). Ultimately, from these coefficients (four for each harmony retained), it is possible to define the variability in the shape of a set of samples through a series of statistical analyses.

This methodology has certain advantages over the use of landmarks, bearing in mind that the samples must still be capable of being compared by means of reproducible geometric characteristics (Cardillo, 2010; Crampton, 1995). Firstly, it is a method in which the continuous function of the figure to be studied is taken into account and not only key points that the researcher deliberately considers significant for discretising the shape. Secondly, it involves a greater optimisation of time. By using landmarks, the researcher must plan which common points should unite his samples and proceed to incorporate them for the subsequent analytical study. However, with EFA, the contour as a whole is taken into account, and it is the subsequent analysis that specifies which areas produce the most variability. Finally, with EFA, a continuous and smoother representation of the sample is achieved as opposed to the

greater rigidity and possible fragmentation of the landmark. In conclusion, with this methodology, we obtain a greater ability to apprehend morphological variation and fewer limitations when interpreting the factors that cause it (Table 2).

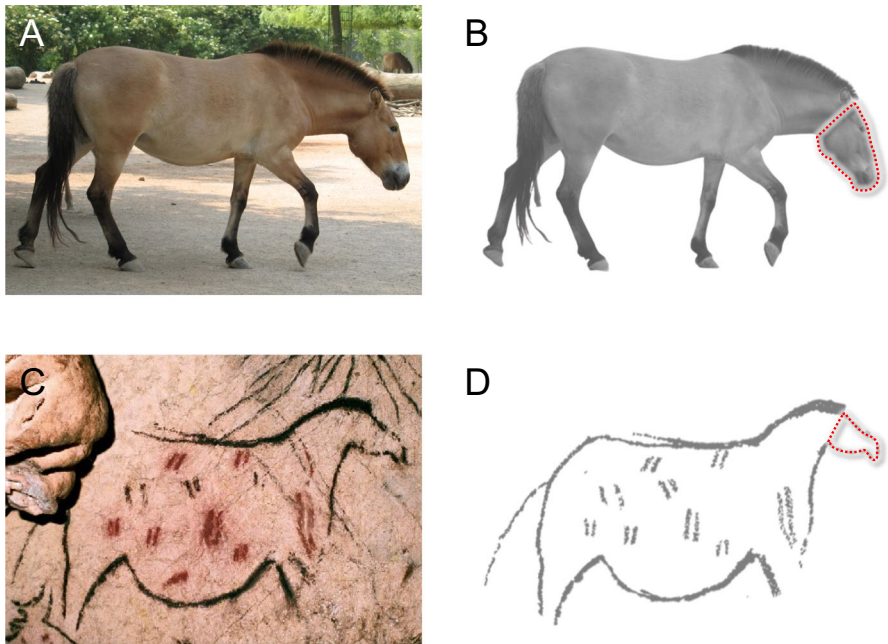
## Tracing Digitalisation

For the study of equid heads, sites with cave or portable art from before 14,500 BP were sampled. A total of 287 graphic units were collected (257 rock art and 30 portable), of which 237 came from sites in the Iberian Peninsula and 50 from France (Fig. 2). Only the head has been taken as a sample because the conventionalism only appears and refers to this anatomical part, so the rest of the body has not been considered (Fig. 3). Those samples with an outline that is open in lines whose continuation is predictable, such as frontonasal straight lines, have been included in the study. On the other hand, samples with an open outline where it is not possible to



**Fig. 2** Sites whose Palaeolithic art is part of the created corpus

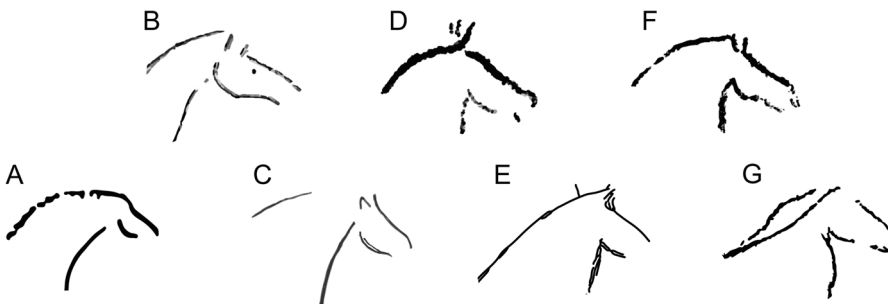




**Fig. 3** Anatomical delimitation of the head in the tracings made on the art samples taken. **A, B** Theoretical delimitation of the head taken from a real horse (Modified photograph by Lars Schmitt/ CC-BY-2.5). **C, D** Delimitation of the head tracing on a rock art sample (Photograph by J. Sanchidrián and tracing by H. Breuil)

reproduce the continuation of the line, such as the muzzle or the mandible, were not taken into account (Fig. 4).

Once the final corpus had been compiled, the next step was to trace the head of each sample taken. To do this, Illustrator software was used, as meticulously as possible when tracing the outline of the animal by hand. We have used both



**Fig. 4** Examples of horses discarded in the study. **A** Pech Merle (Lorblanchet, 2010). **B** La Griega (Corchón, 1997). **C** Roucadour (Lorblanchet, 2010). **D** Las Chimeneas (Echegaray, 1974). **E** Parpalló (Villaverde, 1994). **F** Mayenne-Sciences (Pigeaud, 2004). **G** SiegaVerde (Alcolea & Balbín, 2006)

bibliographical resources and photographs of the art sites we are investigating to obtain these tracings.

The contours were then processed to obtain the morphometric variables using the freely available software R (R Core Team, 2022), which allows the use of customisable code through a large number of predefined packages. We used the “Momocs” package, which specialises in the study of outlines using EFA (Bonhomme et al., 2014). As indicated in the introduction section, the use of landmarks to study shapes in archaeology has certain disadvantages. For this reason, this technique, which includes the complete outline, has been used for the first time to study Palaeolithic rock art.

Once all the traces have been included in R, it is necessary to run a Procrustes analysis, a step in which the proposal and part of the code of Smith and Kriebel (2018) has been used. In this way, all the outlines could be homogeneously oriented, scaled and rotated, thus eliminating the bias that these conditioning factors could cause and definitively preparing the samples for statistical analysis. After having described each contour as a list of coordinates ( $x, y$ ), four reference points were positioned to align all the samples and apply the aforementioned Procrustes analysis. In this section, it was also important to choose the number of harmonics to be used in the statistical tests. This is an important step since the number of harmonics selected must be manageable for the researcher but at the same time sufficient to retain the optimum information to ensure reliable results. As a sine wave describing a shape breaks down into harmonics, the harmonics lose power and convey less and less information. To assess this process, we have examined a cumulative power graph represented in boxplots.

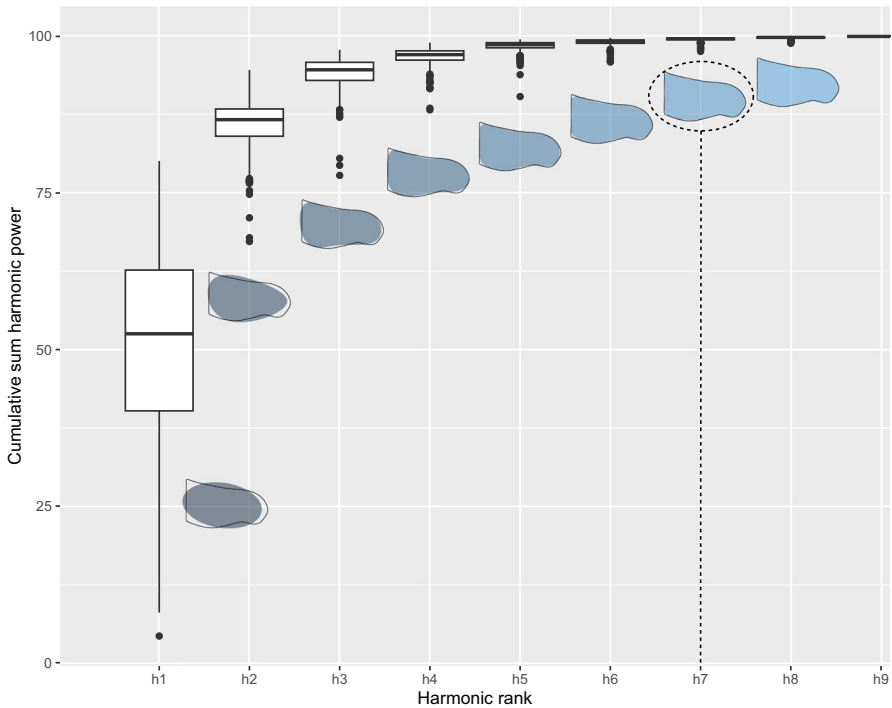
## Statistical Analysis

To examine the shape variability, a Principal Component Analysis (PCA) was performed on Fourier coefficients, a dimensional reduction technique that facilitates the possible interpretation of the data (López-Roldán & Fachelli, 2015). We also applied a cluster analysis to the total set of principal component scores using the Euclidean distance and the Ward method as a grouping system (López-Roldán & Fachelli, 2015). The Euclidean distance, the type of distance most used with quantitative variables, is the shortest line that joins two samples in the graphic space created. The Ward method is used to create groups that are as homogeneous as possible, to minimise internal variance. In summary, the multivariate analyses were applied to identify the most objective commonalities between the analysed samples.

The clusters created are then analysed in greater depth using three other techniques; some also included through different functions in the Momocs package. First, a grid deformation map through isolines (*tps\_iso*) and a graph of the differences between the average shapes (*coo\_ruban*) as it has been used in other works (e.g. Jeanty et al., 2024). These functions are a first approximation to locate intuitively and visually the parts of the outline that a priori contribute most to creating the mean shapes of equine heads.

Next, an attempt was made to test more objectively for significant differences between the clusters. To do this, the PC scores were used as the data to be analysed, testing whether they follow a normal distribution in order to choose the most appropriate test. In addition, a linear discriminant analysis (LDA) was used to validate the results of the cluster analysis and evaluate its effectiveness. In this way, it will be possible to determine whether the samples forming each of the four groups can be well distinguished from the samples of the rest (Cortell-Nicolau et al., 2020; Matzig et al., 2021; Timbrell et al., 2022).

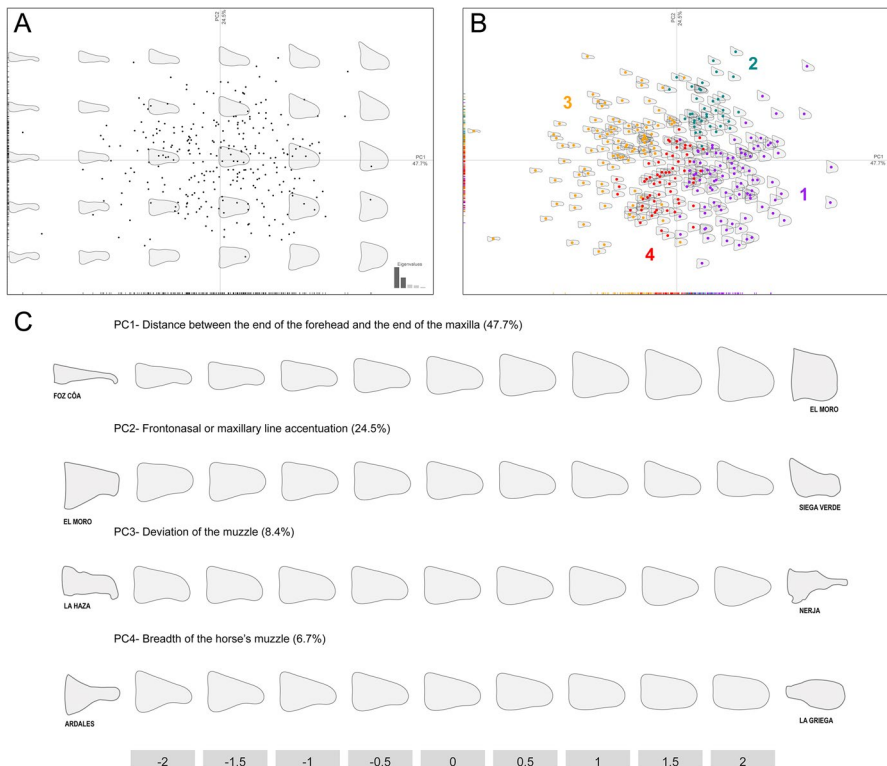
Finally, following the work and methodology of Wang and Marwick (2020), the coefficient of variation (CV) was used to analyse the degree of standardisation of the samples according to certain variables such as the geographical region, the type of deposit, the technique used or the groups created by the cluster analysis (Eerkens & Bettinger, 2001; Krishnamoorthy & Lee, 2014). For this purpose, the first four principal components have been used as variables of the shape of the samples (Hoogard et al. 2019, Loftus, 2022). These principal components have also been normalised between 0 and 1 to be as informative as possible. A low CV means a high degree of standardisation and vice versa. To compare whether there are significant differences in the CVs of the variables, the Modified Signed-Likelihood Ratio (MSLR) test and the asymptotic test were used (Wang & Marwick, 2020; Loftus, 2022).



**Fig. 5** Cumulative power of harmonics. As can be seen, as they increase, the information they provide is reduced increasingly. From seven harmonics, it is possible to retain 99% of the outline

## Results

For the application of this methodology, we have chosen to extract up to seven harmonics, enough to retain more than 99% of the information with which to analyse the outline of the pre-Magdalenian horses (Fig. 5). With this number of harmonics, a PCA has been created obtaining 28 components in total, which is the result of multiplying the seven retained harmonics by the four Fourier coefficients. The first component explains 47.7% and the second component 24.5%, giving a total inertia of 72.2% (Fig. 6A and 6C). In an attempt to complement the analytical study, the third and fourth components have also been consulted, although their impact on the graphic distribution accounts for only 8.4% and 6.7%, respectively.

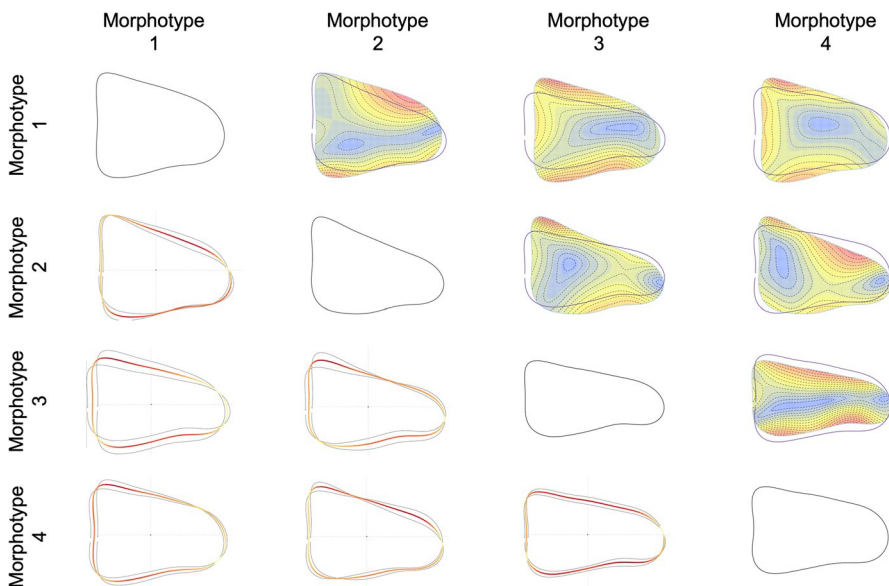


**Fig. 6** Graphic summary of the results of the multivariate analysis. **A** PCA of the first two dimensions (72.2%) created on the coefficients in the Fourier matrix. **B** Cluster analysis applied to the PCA with Euclidean distance and Ward method, which divides the corpus into four possible groups. **C** Forms created as a function of the first four components that explain the variation in the outline in the order of the largest percentage contribution. First component: vertical length of the back of the head. Second component: accentuation of the frontonasal or maxillary line. Third component: deviation of the muzzle. Fourth component: muzzle breadth. The samples that most contribute to the creation of these forms are shown at the end of each component line

The first component explains the variation according to the opening of the back part of the animal's head. The second component emphasises the accentuation with which the frontonasal or maxillary line is marked in exclusion of each other. The third component explains the variation in the deviation of the muzzle, from a downward to a more upright orientation. Finally, the fourth component indicates the width of the muzzle from narrower to more rounded, globular head shape. This technique reveals the first aspect to take into account: the main differences in the samples are related more to the shape of the head in posterior anatomical areas (transition to the neck, final frontonasal line and maxillary line) than with the type of outline with which the animal's muzzle was represented.

Through a cluster analysis applied on the principal component scores, it has been possible to classify the head shape of the pre-Magdalenian equids into four groups (Fig. 6B). The first and third groups, which are the most numerous, can be divided along the Y-axis. Similarly, the second and fourth clusters can be divided along the X-axis. In this way, the epicentres of distribution of each cluster are marked in each quadrant. Throughout this clusters, it has been possible to extract four average shapes (hereafter "morphotypes").

The first model is characterised by a rather oblique frontonasal and maxillary line, with a broad muzzle. The second morphotype in comparison is represented by a less pronounced jaw drawn along the entire lower line of the head, resulting in a narrow muzzle. In contrast to the latter, the third morphotype has a less oblique frontonasal line, with a more pronounced jaw towards the end of the head and an even narrower muzzle. The last model arises from a combination of the



**Fig. 7** Comparison of the average shapes by means of a grid deformation map using isolines (for the whole head) and a graph of the differences between the average shapes (for the contour). A warmer colour, such as red, indicates more marked deformations

**Table 3** Summary statistics for the PERMANOVA test

	Df	Sums Of Sqs	Mean Sqs	F. Model	R2	<i>p</i> -value
Ward	3	1.3020	0.43401	74.147	0.44009	<0.0001
Residuals	283	1.6565	0.00585	-	0.55991	-
Total	286	2.9585	-	-	1.00000	-

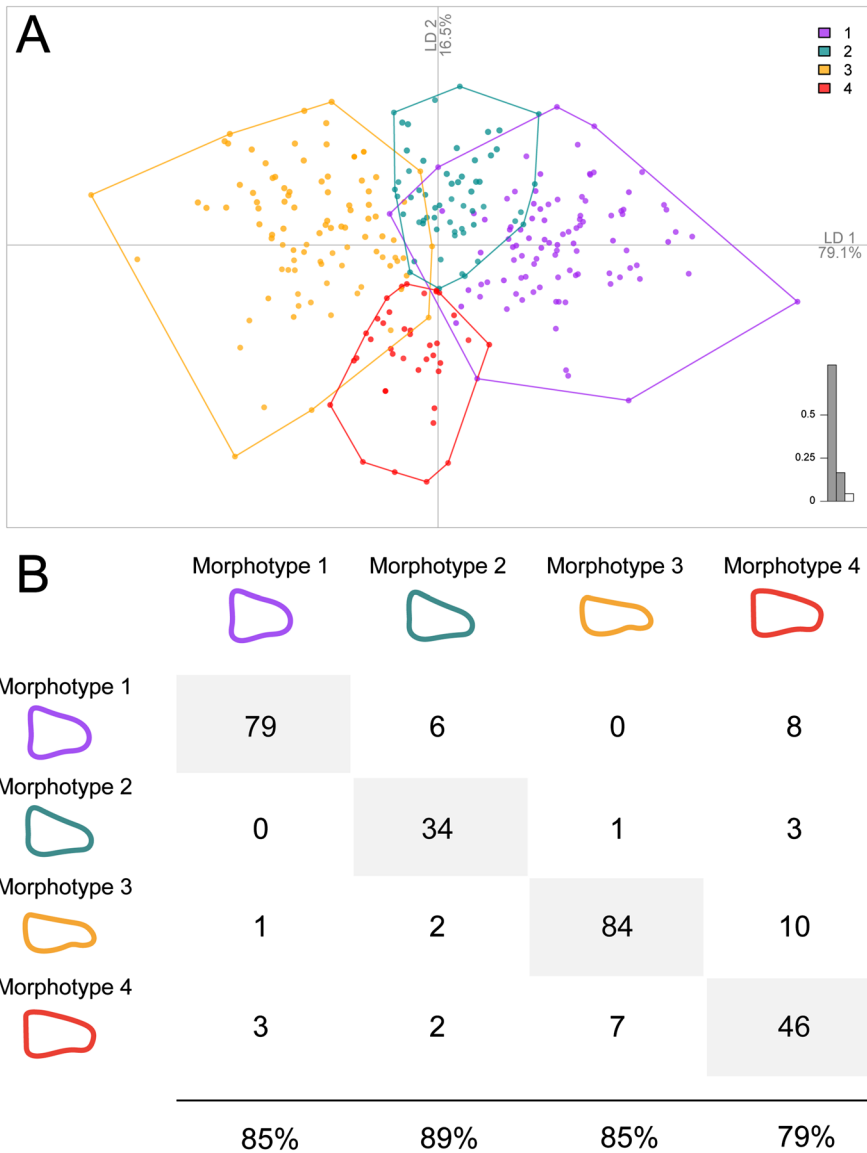
**Table 4** Summary statistics for the pairwise PERMANOVA test

Pairs	Df	Sums Of Sqs	F. Model	R2	<i>p</i> -value	<i>p</i> -adjusted
1–2	1	0.234	49.411	0.277	<0.05	<0.0006
1–3	1	1.012	145.846	0.436	<0.05	<0.0006
1–4	1	0.258	52.284	0.26	<0.05	<0.0006
2–3	1	0.411	59.833	0.309	<0.05	<0.0006
2–4	1	0.258	70.212	0.428	<0.05	<0.0006
3–4	1	0.193	28.424	0.156	<0.05	<0.0006

frontonasal line and the jaw of this third morphotype, but slightly more oblique, and a muzzle with a wider opening. The four models found have an unequal percentage of occurrence, with the third head type standing out above the rest (34.1%), followed by the first (32.4%), the fourth (20.2%) and the second (13.2%) (Fig. 7).

To determine whether these results are statistically relevant, *i.e.* whether the groups are objectively different, a comparison of samples test was applied. To do this, we determined whether the principal components followed a normal distribution. First, it has been observed through a Q-Q plot (Fig. S1-S2) that the data fit well to the normal distribution. However, the Kolmogorov–Smirnov test (with Lilliefors correction) shows that not all principal components follow a normal distribution (Table S1). Therefore, the data have been treated with a non-parametric method to be as rigorous as possible. As has been done in other studies (Falcucci & Piresani, 2022; Matzig et al., 2021; Radinović & Kajtez, 2021; Rossini et al., 2022), we used a Permutational Multivariate Analysis of Variance (PERMANOVA) on the 28 principal components and a *p*-value estimated on 10,000 permutations. A pairwise PERMANOVA using Euclidean distance and with Bonferroni-corrected *p*-value was also used to find significant differences.

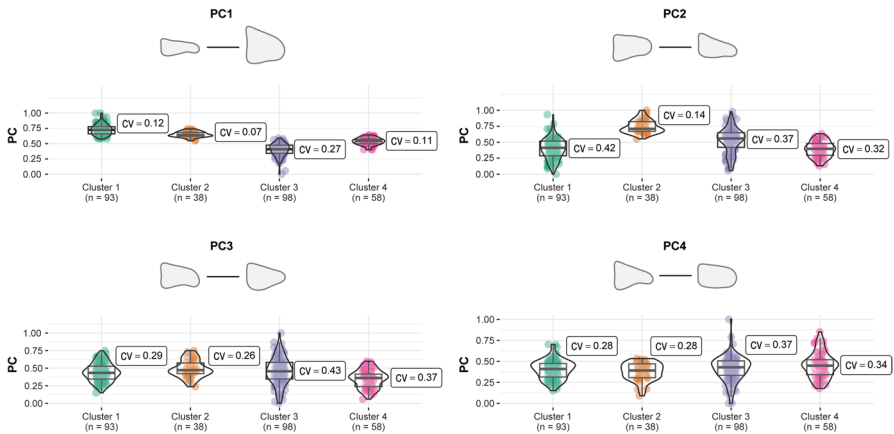
The PERMANOVA results indicate that there are significant morphological differences between the four groups (Table 3), as well as in all cases of the pairwise comparison with a *p*-value <0.05 (Table 4). To corroborate this results, an LDA was then applied, a test that returns a formula with which the program tries to correctly classify the samples into their respective morphotypes. For the first morphotype, it correctly classified 85%, for the second 89%, for the third 85% and the fourth 79% (Fig. 8). Although there are sample transfers from one group to another, especially in the fourth case, in the form of a global computation, the validation of the models using this last methodology returns an 84.7% accuracy rate (243/287). All this



**Fig. 8** LDA of the samples taken. **A** Graph showing the classification of the samples into their respective groups. **B** Table showing the percentage of success for each morphotype, giving an overall result of 84.7% success in the classification

indicates that the use of this morphometric technique is effective and can be used for future formal studies in rock art.

As for the study of these morphotypes, we finally believe that it is important to assess the intra-group variability, *i.e.* whether each group has very different samples. Although the PCA graph can give us a clue as to the level of homogeneity of



**Fig. 9** Violin plot showing the distribution of PC scores normalised from 0 to 1 as a function of the groups formed by the cluster analysis. The coefficient of variation (CV) is shown next to each distribution

the shape according to the dispersion of each group, thanks to the CV applied to the first four components, we can observe two important aspects (Fig. 9). Firstly, morphotype no. 2 is the one with the least intra-group variation, with a CV always below the rest and in almost all cases with significant differences (Table S2-S3). On the other hand, a greater variability is observed in the morphotype 3, which, except for PC2, is the most variable group of all. From this, it can be inferred that it groups formally more disparate samples than in the other cases. At the geographical level, certain aspects of these formal models should be highlighted.

The CVs indicate little standardisation depending on the type of site (Fig. S3), although it increases in the case of outdoor art motifs for the first component (26%) and the fourth (29%), being statistically significant in the latter case (Table S4). This is reflected in a formal tendency that they share in open-air sites: broad head and round snout, similar to what is illustrated in morphotype 1. Precisely, if we study the proportion in which the morphotypes appear according to the type of site, we can observe that the first morphotype is over-represented in open-air sites in the

**Table 5** Proportions of the four morphotypes by archaeological site type. Red indicates the significant proportion above the expected and in blue the significant proportion below

Deposit	Morph. 1	%	Morph. 2	%	Morph. 3	%	Morph. 4	%
Open-air	40/98	40.8%	13/98	13.2%	25/98	25.5%	20/98	20.4%
Cave	53/189	28%	25/189	13.2%	73/189	38.7%	38/189	20.1%
p-value		97.15%		0.8%		97.36%		4.78%



west of the Iberian Peninsula ( $p$ -value=97.1%). In this sense, only three sites (Foz Côa, Siega Verde and Domingo García) account for around 40% of this first model, with the Portuguese site standing out with 22.4%. Furthermore, compared to open-air sites, the representation of morphotype no. 3 is more common in caves ( $p$ -value=97.4%), as can be seen in a nucleus of samples taken from Ardales, Roucadour, Parpalló, La Griega and Gargas, among others (Table 5).

These results may indicate a relationship between the type of site and one of the styles with which the horse was represented. However, we must not forget that there is a diversity of head types in both types of sites and these “preferences” must be taken only as trends.

Another similar analysis has made use of macro-geographical zones defined based on a geographic division and the distance between site clusters: the Mediterranean coast, the interior of the Iberian Peninsula, the Cantabrian region, the Dordogne, the Pyrenees and the Ardèche. Before presenting the results, something fundamental must be considered. In this work, we have used as many samples as possible, but these samples are very limited in archaeology and, particularly, in Palaeolithic art. For this reason, there may be regions where it has not been possible to collect a high number of samples, which could lead to biased results of which we are fully aware. Nevertheless, we have carried out this regional analysis as a first exploratory study that can be improved over time.

Excluding both the Ardèche and the Pyrenees because of their low representativeness, in general, we find a poor standardisation in all regions, although the Cantabrian region is particularly noteworthy, with 25 - 30% between the four components. Likewise, we also found no significant differences comparing the CVs between the regions (Table S5-S6). From this, it can be inferred that the equine head is represented in a variety of forms within the same region.

However, we can observe whether there is an over- or under-representation of a type of morphotype according to the region. Comparison using the Z-score test considered the proportion of each morphotype with its overall proportion in each territory. The results indicate that the first three head types are over- or under-represented in three different areas. Starting with those with the lowest numbers, the Mediterranean coast and Aquitaine show a small number of morphotype no. 2 ( $p$ -value=97.3%) and morphotype no. 1 ( $p$ -value=96.9%), respectively. In contrast, the areas where there is a higher number than expected are the Cantabrian region with the first morphotype ( $p$ -value=97.7%) and Aquitaine with the third morphotype ( $p$ -value=96.2%) (Table 6).

In short, this study shows it is possible to analyse form in Palaeolithic art and to establish more objective classifications than those currently proposed. Through this analysis, it can be shown that the greatest variability in the shape of the head of pre-Magdalenian equids lies in two variables: the vertical length of the back of the head and the pronunciation of the jaw or the end of the forehead. Although the angle and breadth of the muzzle are factors to be considered, their contribution to creating significantly different groups is very small. As we can see, there are significant results if we take into account the type of site and the geographical area. From a territorial point of view, we can only speak in terms of preference and not exclusivity of a model, since the representation of one form or another does not eliminate the

**Table 6** Proportions of the four morphotypes in each region. A significant proportion above the expected percentage is indicated in red and a significant proportion below in blue. The Ardèche and the Pyrenees region have not been included because of their small number and the possibility of distorting the result

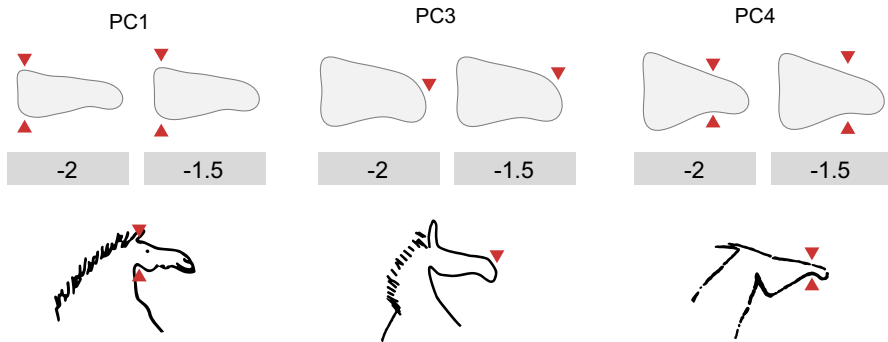
Region	Morph. 1	%	Morph. 2	%	Morph. 3	%	Morph. 4	%
South-East	21/74	28.4%	3/74	4.1%	31/74	41.9%	19/74	25.7%
Inner Iberia	43/119	36.1%	23/119	19.3%	32/119	26.9%	21/119	17.6%
Cantabrian	22/44	50%	4/44	9.1%	12/44	27.3%	6/44	13.6%
Aquitain	4/30	13.3%	3/30	10%	16/30	53.3%	7/30	23.3%
Global	93/287	32.4%	38/287	13.2%	98/287	34.1%	58/287	20.2%

possibility of finding other types of heads. In addition, the shape and the style of this anatomical segment do not allow us to delimit cultural areas. We could hypothesise that the artist's preference for depicting one type of head could also respond to chronological variables which, however, cannot be detected in the absence of direct dating of the motifs. Ultimately, a possible classification of this anatomical part is presented, which can be used for cataloguing purposes and can be improved as more specimens are added.

## Discussion: The “Duck-Bill” Muzzle Conventionalism Through EFA

Palaeolithic art is characterised by thematic, technical and formal homogeneity. However, it was not until the Middle Magdalenian that this reached its zenith. During the Pre-Magdalenian period, the conventions of representation followed less strict norms than those observed from the Middle Magdalenian onwards (Petrognani, 2015; Sauvet, 2014). This resulted in a greater variety of art forms that gradually diminished and became restricted from generation to generation through mechanisms such as apprenticeship (Rivero, 2010, 2016). Although conventionalisms are factors that fossilise form, it is possible that they are sometimes simply attempts by the archaeologist to systematise and organise the accumulated information used to interpret form and style in a more objective way. To further explore this aspect, we analysed the morphotypes from the previous analysis to determine if the “duck-bill” convention, as defined in the literature, is discernible. This will help establish if it can still be used as a fossil director of the pre-Magdalenian phase in both portable and parietal art or we should use it with more caution.

The aspect that most closely resembles what authors refer to as the duck-bill in our study is reflected in the first, third and fourth principal components beyond a standard deviation of  $-1.5$  (Fig. 10). These three components precisely explain the



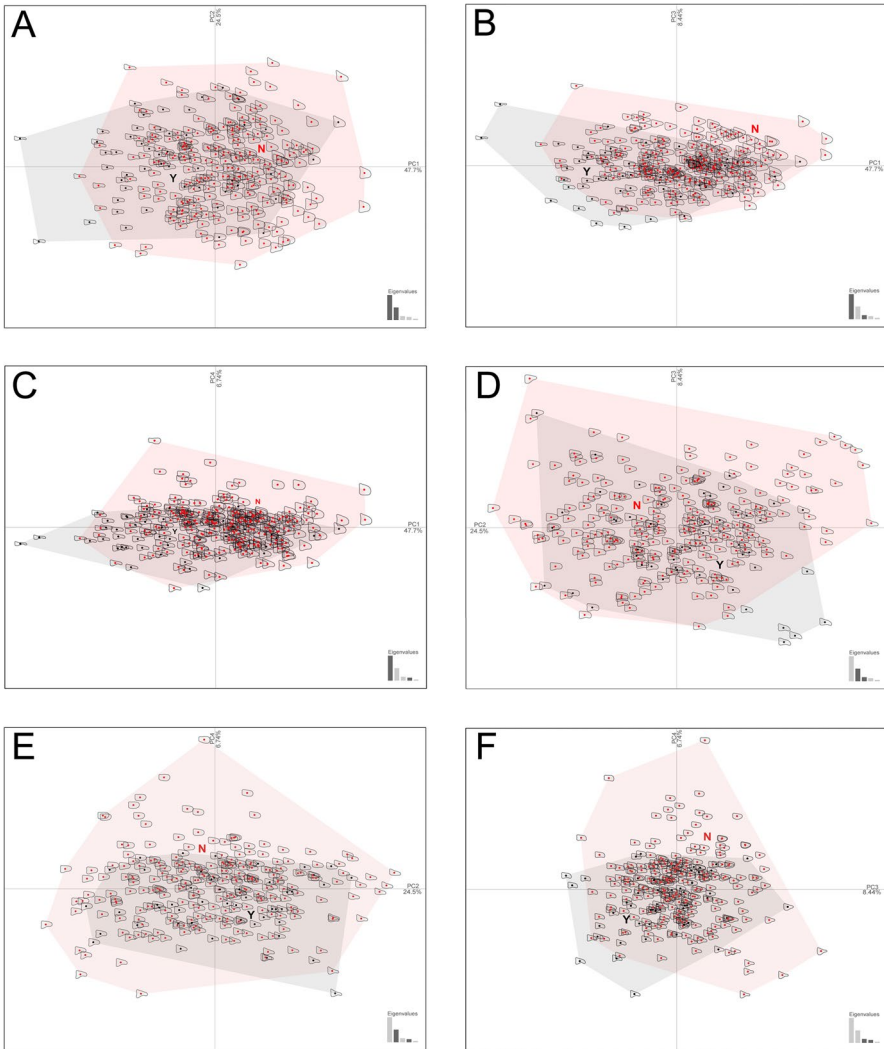
**Fig. 10** Diagram of the morphological features of a “duck-billed” conventionalism according to some of the researchers’ definitions. Above, the shape that explains the PCA. Below, an archaeological example that has been documented as a duck-billed horse. From right to left: Ardales (Cantalejo et al., 2006), Gargas (Barrière, 1976) and Cussac (Feruglio et al., 2019)

variation of the average form with some of the features of this convention according to some authors (Moure et al., 1991; Villaverde, 1994): a short distance between the end of the frontonasal and maxillary, the muzzle directed downwards, and a narrowing between the lip and the jaw. However, this does not prove its characterisation as conventionality. Only when a large group of samples sharing these anatomical traits can be isolated or grouped together can the existence of such formalism be discussed.

In the principal component analysis, samples described by the authors as having a duck-bill have been identified. As shown in Fig. 11, samples with this convention in all four factorial dimensions typically extend along the X-axis, always overlapping with the group of samples that do not have a duck bill, indicating the enormous morphological variability of this type of formality. This is the case, even taking into account the first, third and fourth components (Fig. 11B, 11C and 11F), which, as mentioned above, are in principle the most similar forms to those defined by the authors. If it were a formal norm, all samples would have to be constrained and clustered in a particular place in the factor space, which is not the case. The difficulty of defining the duck-bill as a conventionalism is also demonstrated by the LDA, which only identifies 59% of the samples with a duck-bill.

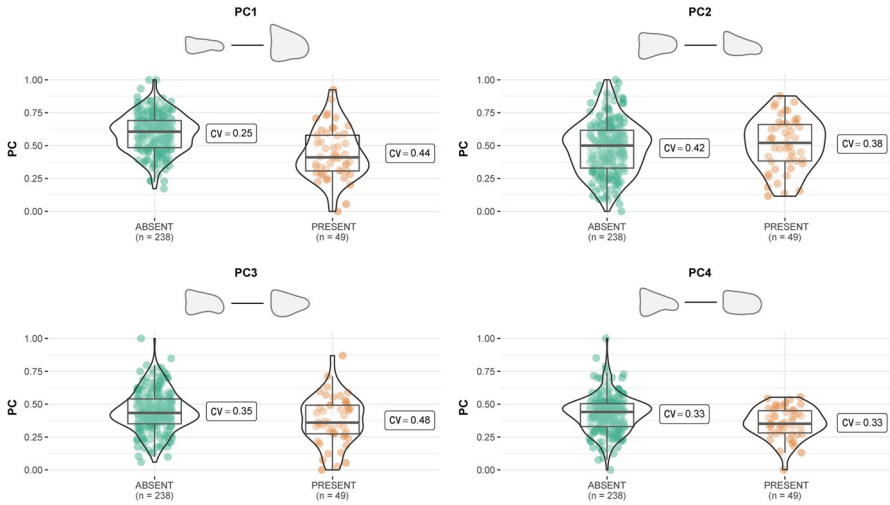
All this leads us to consider the morphological inaccuracy when cataloguing representations with this type of muzzle. A conclusion also reached by Hernando (2013) who, using a homogeneity index with qualitative variables, points out that the samples referred to by various authors as duck-bills actually display marked anatomical dissimilarity.

The results of this homogeneity index are also reflected in our study from other points of view. Firstly, if we look at the calculated CV (Fig. 12), the samples that present the conventionalism have a low degree of standardisation (48–33%) in the first four components. The difference in standardisation between samples that show the conventionalism and those that do not is significantly different only in PC1 and PC3, where the CV of the samples with “duck bill” is also higher (44%



**Fig. 11** PCA of the pairwise combination of the first four components as a function of the presence (black colour) and absence (red colour) of the duck-bill formalism in the samples taken. In all cases, both groups appear widely overlapped, showing the lack of difference between the sets if we take the presence or absence of this formalism. **A** Components 1–2. **B** Components 1–3. **C** Components 1–4. **D** Components 2–3. **E** Components 2–4. **F** Components 3–4

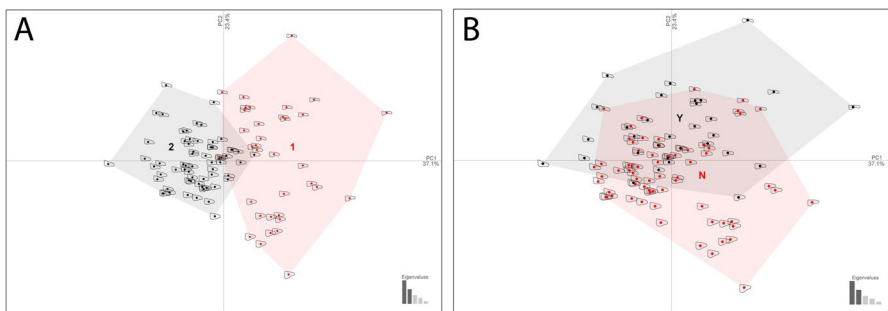
and 48% respectively) (Table S7). And secondly, as can be seen in Table 7, in the four morphotypes detected, there are at least three samples that present this type of conventionalism, other proof of the variability of this formalism. However, the number found in morphotype no. 3 is particularly noteworthy. A Z-score test applied for each pair indicates that the percentage of duck-bill morphotype 3 is statistically significant ( $p$ -value < 0.05).



**Fig. 12** Violin plot showing the distribution of PC scores normalised from 0 to 1 depending on the absence or presence of the “duck-bill” conventionalism. The coefficient of variation (CV) is shown next to each distribution

**Table 7** Proportions of the presence and absence of the duck-bill conventionalism in the four morphotypes

Duck-bill	Morph. 1	%	Morph. 2	%	Morph. 3	%	Morph. 4	%
Yes	9/93	9.7%	3/38	7.9%	33/98	33.7%	4/58	6.9%
No	84/93	90.3%	35/38	92.1%	65/98	66.3%	54/58	93.1%



**Fig. 13** Division by means of different criteria of the samples that make up morphotype no. 3. **A** Division on the basis of cluster analysis, which seeks to create as homogeneous sets as possible. **B** Division according to the presence (black) or absence (red) of the duck-bill convention in the samples

Trying to go deeper into the possibility of discerning the characteristics that may distinguish the “duck-bill” muzzle, the same method has been replicated but only on the samples that make up group three, where most of the samples with this

formalism are concentrated. The PCA and cluster analysis show the possibility of clearly distinguishing two subgroups separated by the second principal component (Fig. 13A). The first subgroup consists of 35 samples, of which 16 are duck-billed horses, while the second subgroup consists of 63 samples, of which 17 have such a conventionalism. The Z-score test indicates that the differences in this distribution are not significant ( $p$ -value > 0.05). If we disregard the partitioning of the cluster analysis (which seeks to create groups that are as different as possible) and instead differentiate two groups according to the presence or absence of duck-bill, it is even more complicated to distinguish graphically between the two sets (Fig. 13B). In this latter case, it would only be possible to discern some extreme cases, since most of the samples overlap with the group of cases without “duck-bill” head.

To sum up, the results that have been shown call into question the distinction of the duck-bill as a conventionalism on the basis of the definitions that can be found in the literature. In other words, we conclude that the way in which the conventionalism has been defined up to now is dependent on the interpretation of researchers, an aspect that other authors have already highlighted (Hernando, 2013; Villaverde, 2017).

Three arguments support that conclusion. First, it is a type of shape that is present in all the groups that multivariate analysis has differentiated. If we take into account that these techniques seek to create sets that are as different as possible, the characteristics of the duck-bill head are not significant in the morphological study and the subsequent partitioning of the cluster analysis. Besides, although most of the samples with a duck-bill muzzle are included in morphotype no. 3, they coexist with other types of muzzle that differ completely from this conventionalism. This corroborates the difficulty in defining this formalism, whose morphological characteristics are described by the authors in a subjective and widely variable way. Finally, as the CV shows it cannot be concluded that the two main variables with which a priori it is possible to distinguish the four morphotypes described (amplitude of the beginning of the neck and muzzle and the accentuation of the jaw or the frontonasal line) are determinant in the definition of the conventionalism. Nor if we consider the third and fourth components centred on the variation of the muzzle, considering its minimal impact on the differentiation and grouping of the samples.

All this leads to an important conclusion: it is not possible to consider the duck-bill as a type of equine head or conventionalism, but as a set of independent anatomical features that all horses could have. For this reason, it is impossible to isolate a general model representing the so-called duck-bill muzzle.

## Conclusion

The analysis of form has been an object of study since the discovery of prehistoric art. However, it is extremely difficult to approach its study from an objective point of view. Many analyses have tried to propose a research method based on linear measurements (e.g. Apellániz & Calvo, 1999; Lión, 1971; Pigeaud, 1997, 2000, 2007) or to characterise form depending on the description of qualitative variables (e.g. Corchón et al., 2013; Petrognani & Sauvet, 2012; Sauvet & Rivero,

2016; Tosello, 2003; Villaverde, 1994). Similarly, few attempts have been made to use geometric morphometry and the vast majority use the landmark technique, with all the disadvantages that this entails (e.g. Charlin & Llosas, 2016; Cobden et al., 2017; Nelson et al., 2017).

This paper opens the possibility of applying Elliptic Fourier Analysis (EFA) to rock art in general and Palaeolithic art in particular. This method is currently the only way of objectifying the study of form and offers advantages that cannot be achieved by the other techniques described above. However, it also has certain limitations, mainly the obligatory reproducibility of the part of the entity to be analysed or the need to have somewhat advanced notions in the creation of codes and statistics. Nevertheless, this study, focused on the head outline of pre-Magdalenian equids and on the duck-bill conventionalism, shows that this type of application can provide excellent results that enable both the proposal of new ideas and the correction of more traditional ones.

The complete study of the shape of the head of these animals has followed a methodological protocol that has already been applied to other types of archaeological remains such as pottery, lithics or seed remains. Its application has not only made it possible to study the variables that best explain the differences between the heads of the pre-Magdalenian equids or to propose a possible classification of the latter but also to address an important issue within the discipline, namely the need for rigour when using “conventionalisms” as a method of analysing figures.

Anatomical characteristics, which can be defined as a recurrent formal peculiarity, have been repeatedly used by researchers not only to analyse the style of figures but also to locate, geographically and above all chronologically, the documented graphic units that present the conventionalism. Of all these, the so-called “duck-bill” stands out, a trait that Palaeolithic horses display in their muzzles and that is usually dated to the pre-Magdalenian period. In principle, this is a formal peculiarity that is easy to recognise. However, the definitions of different authors do not converge in a single model, leading to a wide variety of forms that are regarded as a duck-bill muzzle.

From the morphometric analysis, we can conclude that this conventionalism is indeed highly variable and that it is not possible to define a single model to serve as a paradigm. In this situation, we should redefine what can be considered a duck-bill or stop using it as a chronological and spatial marker of the Palaeolithic representation under study.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10816-024-09656-7>.

**Acknowledgements** We would like to thank the two reviewers who have helped to improve this work with their advice and corrections.

**Funding** Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This work has been supported financially by the Consejería de Educación de la Junta de Castilla y León and the European Social Fund through a pre-doctoral researcher contract [ORDEN EDU/875/2021] and Proyecto PID2021-125166OB-I00 financiado por MCIN/ AEI/10.13039/501100011033/ y por FEDER Una manera de hacer Europa. PI: Olivia Rivero.

**Data Availability** The data and code supporting the conclusions of this study are available only upon request from the corresponding author, as restrictions apply as part of an ongoing doctoral thesis.

## Declarations

**Competing Interests** The authors declare no competing interests.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## References

- Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: Ten years of progress following the 'revolution.' *Italian Journal of Zoology*, *71*(1), 5–16. <https://doi.org/10.1080/1125000409356545>
- Alcolea, J. J., & Balbín, R. de (2006). *Arte paleolítico al aire libre. El yacimiento rupestre de Siega Verde, Salamanca*. Arqueología en Castilla y León, Memorias 47
- Apellániz, J. M. (1990). Modèle d'analyse d'une école dans l'iconographie mobilier paléolithique: l'école des graveurs de chevaux hypertrophiés de La Madeleine. In J. Clottes (dir.), *L'Art des objets au Paléolithique. Tome 2. Les voies de la recherche* (pp. 105–138). Ministère de la Culture et alii
- Apellániz, J. M. (2004). La interpretación del arte paleolítico mediante la hipótesis de la evolución de los estilos o mediante las de la forma y atribución de autoría. *Trabajos De Prehistoria*, *61*(1), 63–79.
- Apellániz, J. M., & Calvo, F. (1999). *La forma del arte paleolítico y la estadística. Análisis de la forma del arte figurativo paleolítico y su tratamiento estadístico*. Universidad de Deusto
- Arriaza, M. C., Aramendi, J., Courtenay, L. A., Maté-González, M. Á., Herranz-Rodrigo, D., González-Aguilera, D., & Yravedra, J. (2023). An evaluation of landmark-based methods to explore tooth score morphology: A case study on felids and hyenids. *Applied Sciences*, *13*(6), 3864. <https://doi.org/10.3390/app13063864>
- Arriaza, M. C., Yravedra, J., Domínguez-Rodrigo, M., Mate-González, M. A., Vargas, E. G., Palomeque-González, J. F., et al. (2017). On applications of micro-photogrammetry and geometric morphometrics to studies of tooth mark morphology: the modern Olduvai Carnivore Site (Tanzania). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *488*, 103–112. <https://doi.org/10.1016/j.palaeo.2017.01.036>
- Barrière, C. (1976). *L'art pariétal de la grotte de Gargas*. BAR International Series 14, British Archaeological Reports
- Bernaldez-Sánchez, E., & García-Viñas, E. (2019). The equids represented in cave art and current horses: A proposal to determine morphological differences and similarities. *Anthropozoologica*, *54*(1), 1–12. <https://doi.org/10.5252/anthropozoologica2019v54a1>
- Birch, T., & Martínón-Torres, M. (2019). Shape as a measure of weapon standardisation: From metric to geometric morphometric analysis of the Iron Age 'Havor' lance from Southern Scandinavia. *Journal of Archaeological Science*, *101*, 34–51. <https://doi.org/10.1016/j.jas.2018.11.002>
- Bonhomme, V., Picq, S., Gaucherel, & C., Claude, J. (2014). Momocs: Outline analysis using R. *Journal of Statistical Software*, *56*(13), 1–24. <https://doi.org/10.18637/jss.v056.i13>
- Bonhomme, V., Forster, E., Wallace, M., Stillman, E., Charles, M., & Jones, G. (2017). Identification of inter-and intra-species variation in cereal grains through geometric morphometric analysis, and its resilience under experimental charring. *Journal of Archaeological Science*, *86*, 60–67. <https://doi.org/10.1016/j.jas.2017.09.010>



- Bookstein, F. (1996). *Morphometrics. Math Horizons*, 3(3), 28–31. <https://doi.org/10.1080/10724117.1996.11974967>
- Bourdelle, E. (1938). Essai d'une étude morphologique des Equidés préhistoriques de France, d'après les gravures rupestres. *Mammalia*, 2, 1–11.
- Bourdelle, E. (1958). Essai de classification morphologique des Équides, préhistoriques et actuels. *Société D'études Et De Recherches Préhistoriques Et Institut Pratique De Préhistorique*, 8, 56–60.
- Breuil, H. (1952). *Quatre cents siècles d'art pariétal. Les cavernes ornées de l'âge du renne*. Centre d'études et de documentation préhistoriques
- Breuil, H., Obermaier, H., & Verner W. (1915). *La Pileta à Benaoján (Málaga) (Espagne)*. Institute de Paléontologie Humaine.
- Buisson, D., Fritz, C., Kandel, D., Pinçon, G., Sauvet, G., & Tosello, G. (1996a). Analyse formelle des contours découpés de têtes de chevaux: Implications archéologiques. In *Actes Du Congrès National Des Sociétés Historiques et Scientifiques 18*, (pp. 327–340)
- Buisson, D., Fritz, C., Kandel, D., Pinçon, G., Sauvet, G., & Tosello, G. (1996b). Les contours découpés de têtes de chevaux et leur contribution à la connaissance du Magdalénien moyen. *Antiquités Nationales*, 28, 99–128.
- Burger, P., Terral, J. F., Ruas, M. P., Ivorra, S., & Picq, S. (2011). Assessing past agrobiodiversity of *Prunus avium* L. (Rosaceae): A morphometric approach focussed on the stones from the archaeological site Hôtel-Dieu (16th century, Tours, France). *Vegetation History and Archaeobotany*, 20, 447–458. <https://doi.org/10.1007/s00334-011-0310-6>
- Cantalejo, P., Maura, R., Espejo, M. M., Ramos, J., Medianero, A., Aranda, A., & Durán, J. J. (2006). *La Cueva de Ardales: Arte prehistórico y ocupación en el Paleolítico Superior*. Centro de Ediciones de la Diputación de Málaga
- Capitan, L., Breuil, H., & Peyrony, D. (1910). *La Caverne de Font-De-Gaume aux Eyzies (Dordogne)*. Imprimerie Vve. A. Chêne
- Capitan, L., Breuil, H., & Peyrony, D. (1924). *Les Combarelles aux Eyzies (Dordogne)*. Masson et Cie
- Caple, J., Byrd, J., & Stephan, C. N. (2017). Elliptical Fourier analysis: Fundamentals, applications, and value for forensic anthropology. *International Journal of Legal Medicine*, 131(6), 1675–1690. <https://doi.org/10.1007/s00414-017-1555-0>
- Cardillo, M. (2010). Some applications of geometric morphometrics to archaeology. In A.M.T., Elewa (Ed.), *Morphometrics for nonmorphometricians* (pp. 325–341). Springer. [https://doi.org/10.1007/978-3-540-95853-6\\_15](https://doi.org/10.1007/978-3-540-95853-6_15)
- Chacón, M. G., Déroit, F., Coudenneau, A., & Moncel, M. H. (2016). Morphometric assessment of convergent tool technology and function during the Early Middle Palaeolithic: The case of Payre. *France. Plos One*, 11(5), e0155316. <https://doi.org/10.1371/journal.pone.0155316>
- Charles, M., Forster, E., Wallace, M., & Jones, G. (2015). "Nor ever lightning char thy grain"<sup>1</sup>: Establishing archaeologically relevant charring conditions and their effect on glume wheat grain morphology. *STAR: Science & Technology of Archaeological Research*, 1(1), 1–6. <https://doi.org/10.1179/2054892315Y.0000000008>
- Charlin, J., & Llosas, M. I. H. (2016). Morfometría geométrica y representaciones rupestres: explorando las aplicaciones de los métodos basados en landmarks. *Arqueología*, 22(1), 103–125.
- Clottes, J., Chauvet, J. M., Brunel-Deschamps, E., Hillaire, C., Dugas, J. P., Arnold, M., Cachier, H., Évin, J., Fortin, P., Oberlin, C., Tisnerat, N., & Valladas, H. (1995). Les peintures paléolithiques de la Grotte Chauvet-Pont d'Arc, à Vallon-Pont-d'Arc (Ardèche, France): Datations directes et indirectes par la méthode du radiocarbone. *Comptes-Rendus De L'académie Des Scien Ces, Series Iia*, 320, 1133–1140.
- Clottes, J., Courtain, J., & Vanrell, L. (2005). *Cosquer redécouvert*. SEUIL
- Cobden, R., Clarkson, C., Price, G. J., David, B., Geneste, J. M., Delannoy, J. J., et al. (2017). The identification of extinct megafauna in rock art using geometric morphometrics: A Genyornis newtoni painting in Arnhem Land, northern Australia? *Journal of Archaeological Science*, 87, 95–107. <https://doi.org/10.1016/j.jas.2017.09.013>
- Corchón, M. S. (Coord.) (1997). *La cueva de La Griega de Pedraza (Segovia)*. Memorias 16, Junta de Castilla y León
- Corchón, M. S., Hernando Álvarez, C., Rivero Vilá, O., Garate, D., & Ortega, P. (2013). La cueva de La Griega (Pedraza, Segovia, España) en la encrucijada ibérica: nuevos análisis del arte parietal paleolítico a través del análisis factorial de correspondencias. *Espacio Tiempo y Forma. Serie I, Prehistoria y Arqueología*, 1(5), 527–542.

- Corchón, M. S., & Rivero, O. (2010). Le morphotype du cheval dans l'art mobilier du Magdalénien moyen de la grotte de Las Caldas (Asturies, Espagne): analyse technique et formelle. In J. Clottes (Ed.), *L'art pléistocène dans le monde. Actes du Congrès IFRAO* (Issue 65, pp. 1427–1442). <https://doi.org/10.4000/palethnologie.4909>
- Cortell-Nicolau, A., García-Puchol, O., & Shennan, S. (2020). Cultural continuities and discontinuities at the Neolithic transition in Eastern Iberia: An analysis of the morphometry of geometric microliths. *Archaeological and Anthropological Sciences*, 12(11), 253. <https://doi.org/10.1007/s12520-020-01204-0>
- Courtenay, L. A., Herranz-Rodrigo, D., Huguet, R., Maté-González, M. Á., González-Aguilera, D., & Yravedra, J. (2020). Obtaining new resolutions in carnivore tooth pit morphological analyses: A methodological update for digital taphonomy. *PLoS ONE*, 15(10), e0240328. <https://doi.org/10.1371/journal.pone.0240328>
- Courtenay, L. A., Yravedra, J., Huguet, R., Ollé, A., Aramendi, J., Maté-González, M. Á., & González-Aguilera, D. (2019). New taphonomic advances in 3D digital microscopy: A morphological characterisation of trampling marks. *Quaternary International*, 517, 55–66. <https://doi.org/10.1016/j.quaint.2018.12.019>
- Crampton, J. S. (1995). Elliptic Fourier shape analysis of fossil bivalves: Some practical considerations. *Lethaia*, 28(2), 179–186. <https://doi.org/10.1111/j.1502-3931.1995.tb01611.x>
- Delluc, B., & Delluc, G. (1992). *L'art pariétal archaïque en Aquitaine*. CNRS.
- Domingo, I., & Fiore, D. (2014). Style: Its role in the archaeology of art. In C. Smith (Ed.), *Encyclopedia of Global Archaeology* (pp. 7104–7111). Springer. [https://doi.org/10.1007/978-1-4419-0465-2\\_1276](https://doi.org/10.1007/978-1-4419-0465-2_1276)
- Echegaray, G. (1974). *Pinturas y grabados de la cueva de Las Chimeneas: (Puente Viesgo, Santander)*. Instituto de Prehistoria y Arqueología.
- Eerkens, J. W., & Bettinger, R. L. (2001). Techniques for assessing standardization in artifact assemblages: Can we scale material variability? *American Antiquity*, 66(3), 493–504. <https://doi.org/10.2307/2694247>
- Falucci, A., & Peresani, M. (2022). The contribution of integrated 3D model analysis to Protoaurignacian stone tool design. *PLoS ONE*, 17(5), e0268539. <https://doi.org/10.1371/journal.pone.0268539>
- Fano, M. Á., & Rivero, O. (2007). El territorio y la movilidad de los cazadores del final del Paleolítico: algunas reflexiones metodológicas. In P. Arias (Ed.), *El Paleolítico Superior Cantábrico. Actas de la Primera Mesa Redonda. San Román de Candamo (Asturias)* (pp. 207–216). Universidad de Cantabria
- Feruglio, V., Bourdier, C., Delluc, M., Mora, P., Aujoulat, N., & Jaubert, J. (2019). Rock art, performance and Palaeolithic cognitive systems. The example of the Grand Panel palimpsest of Cussac Cave, Dordogne, France. *Journal of Anthropological Archaeology*, 56, 101104. <https://doi.org/10.1016/j.jaa.2019.101104>
- Fortea, J. (1978). Arte paleolítico en el Mediterráneo Español. *Trabajos De Prehistoria*, 35, 99–150.
- Fuentes, O., Lucas, C., & Robert, E. (2019). An approach to Palaeolithic networks: The question of symbolic territories and their interpretation through Magdalenian art. *Quaternary International*, 503, 233–247. <https://doi.org/10.1016/j.quaint.2017.12.017>
- García-Bustos, M. (2021). Los temas figurativos del arte rupestre paleolítico en la península ibérica: Estudio estadístico y modelos de distribución. *Iberografías. Revista De Estudios Ibéricos*, 17, 117–138.
- García-Bustos, M., & Rivero, O. (2023). Making a difference: Palaeolithic iconography as a trait of identity in the Iberian Peninsula. *Oxford Journal of Archaeology*, 42(4), 282–300. <https://doi.org/10.1111/ojoa.12281>
- García-Diez, M., Vigiola-Toña, I., Ochoa, B., Garrido, D., & Rodríguez-Asensio, A. (2015). Parietal graphic territories in the Magdalenian: An initial proposal based on La Covaciella Cave (Asturias, Spain). In H. Collado, & J. J. García Arranz (Eds.), *XIX International Rock Art Conference IFRAO 2015. Symbols in the Landscape: Rock Art and Its Context* (pp. 1297–1303)
- Giardina, C. R., & Kuhl, F. P. (1977). Accuracy of curve approximation by harmonically related vectors with elliptical loci. *Computer Graphics and Image Processing*, 6(3), 277–285.>
- González Sainz, C. (2007). Quelques particularités des centres pariétaux paléolithiques dans la région cantabrique. *Préhistoire, Art Et Sociétés: Bulletin De La Société Préhistorique De L'ariège*, 62, 19–36. [https://doi.org/10.1016/S0146-664X\(77\)80029-4](https://doi.org/10.1016/S0146-664X(77)80029-4)
- Graziosi, P. (1956). *L'arte dell'antica età della pietra*. Sansoni
- Graziosi, P. (1973). *L'arte Preistorica in Italia*. Sansoni.

- Groenen, M. (2007). Le cheval dans l'art pariétal du Paléolithique Supérieur. In P. Cattelain & N. Bozet (Eds.), *Sur la piste du cheval de la Préhistoire à l'Antiquité* (pp. 25–32). Editions du Centre d'Etudes et de Documentation Archéologiques.
- Hashemi, S. M., Nasab, H. V., Berillon, G., & Oryat, M. (2021). An investigation of the flake-based lithic tool morphology using 3D geometric morphometrics: A case study from the Mirak Paleolithic Site, Iran. *Journal of Archaeological Science: Reports*, 37, 102948. <https://doi.org/10.1016/j.jasrep.2021.102948>
- Hayes, S., & van den Bergh, G. (2018). Cave art, art and geometric morphometrics: Shape changes and the babirusa of Sulawesi. In S. O'Connor, D. Bulbeck, & J. Meyer (Eds.), *The archaeology of Sulawesi: Current research on the Pleistocene to the Historic Period* (pp. 43–59). ANU Press.
- Hernando, C. (2013). Ciervas “trilineales” y caballos en “bec de canard”: contextualizando conceptos y objetos en el arte paleolítico. *Revista Atlántica-Mediterránea de Prehistoria y Arqueología Social*, 15(1), 13–37. [https://doi.org/10.25267/Rev\\_atl-mediterr\\_prehist\\_arqueol\\_soc.2013.v15.02](https://doi.org/10.25267/Rev_atl-mediterr_prehist_arqueol_soc.2013.v15.02)
- Hernando, C. (2014). *La sociedad a través del arte: las tradiciones gráficas premagdalenenses en la Región Cantábrica* [Tesis doctoral, Universidad de Salamanca]
- Hoggard, C. S., McNabb, J., & Cole, J. N. (2019). The application of elliptic Fourier analysis in understanding biface shape and symmetry through the British Acheulean. *Journal of Paleolithic Archaeology*, 2, 115–133. <https://doi.org/10.1007/s41982-019-00024-6>
- Honoré, E., Lucas, C., Petrognani, S., & Robert, E. (2019). Discussing the relevance and scope of ‘symbolic territories’ for Prehistory. *Quaternary International*, 503, 189–190. <https://doi.org/10.1016/j.quaint.2019.03.004>
- Huard, O. (2007). Les équides des grottes des Combarelles (Les Eyzies-de Tayac, Dordogne, France): étude morphométrique. *PALEO*, 19, 337–340.
- Huard, O. (2010). La figuration du cheval dans l'art pariétal de Gargas (Aventignan, Hautes-Pyrénées): un ensemble homogène? In J. Clottes (Ed.), *L'art pléistocène dans le monde. Actes du Congrès IFRAO* (pp. 227–247)
- Jeanty, A., Ros, J., Mureau, C., Dham, C., Lecomte, C., Bonhomme, V., ... & Evin, A. (2024). Identification of archaeological barley grains using geometric morphometrics and experimental charring. *Journal of Archaeological Science*, 162, 105924. <https://doi.org/10.1016/j.jas.2023.105924>
- Jordá, F. (1964). Sobre técnicas, temas y etapas del arte paleolítico de la región cantábrica. *Zephyrus*, 15, 5–26.
- Klingenberg, C. P., & Monteiro, L. R. (2005). Distances and directions in multidimensional shape spaces: Implications for morphometric applications. *Systematic Biology*, 54(4), 678–688. <https://doi.org/10.1080/10635150590947258>
- Krishnamoorthy, K., & Lee, M. (2014). Improved tests for the equality of normal coefficients of variation. *Computational Statistics*, 29, 215–232. <https://doi.org/10.1007/s00180-013-0445-2>
- Kuhl, F. P., & Giardina, C. R. (1982). Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing*, 18(3), 236–258.
- Leroi-Gourhan, A. (1965). *Préhistoire de l'art occidental*. Lucien Mazenod
- Lión, R. (1971). *El caballo en el arte cántabro-aquitano. Estudio estilístico, hipométrico y faneróptico de las representaciones paleolíticas*. Patronato de las cuevas Prehistóricas de la Provincia de Santander.
- Loftus, J. F. (2022). Reexamining ceramic standardization during agricultural transition: A geometric morphometric investigation of initial–early Yayoi Earthenware. *Japan. Open Archaeology*, 8(1), 1249–1268. <https://doi.org/10.1515/opar-2022-0273>
- López-Roldán, P., & Fachelli, S. (2015). *Metodología de la Investigación Social Cuantitativa*. Universitat Autònoma de Barcelona.
- Lorblanchet, M. (2007). The horse in the Palaeolithic parietal art of the Quercy: Outline of a stylistic study. In P. Pettitt, P. Bahn, & S. Ripoll (Eds.), *Palaeolithic cave art at Creswell Crags in European context* (pp. 207–228). Oxford Academic. <https://doi.org/10.1093/oso/9780199299171.003.0016>
- Lorblanchet, M. (2010). *Art pariétal. Grottes ornées du Quercy*. Rouergue
- Lorblanchet, M., & Bahn, P. (1993). *Rock art studies: The Post-Styletic era or Where do we go from here?*. Oxbow Monograph
- Madariaga de la Campa, B. (1969). *Las pinturas rupestres de animales en la región franco-cantábrica. Notas para su estudio e identificación*. Institución Cultural de Cantabria
- Marcus, L. F. (1990). Traditional morphometrics. In F. J. Rohlf and F. L. Bookstein (Eds.), *Proceedings of the Michigan Morphometrics Workshop* (pp. 77–122). University of Michigan

- Martínez-Carrillo, A. L., Lucena, M. J., Fuertes, J. M., & Ruiz, A. (2010). Morphometric analysis applied to the archaeological pottery of the valley of Guadalquivir. In A. M. T. Elewa (Ed.), *Morphometrics for nonmorphometricians* (pp. 307–323). Springer. [https://doi.org/10.1007/978-3-540-95853-6\\_14](https://doi.org/10.1007/978-3-540-95853-6_14)
- Maté-González, M. Á., Yravedra, J., González-Aguilera, D., Palomeque-González, J. F., & Domínguez-Rodrigo, M. (2015). Micro-photogrammetric characterization of cut marks on bones. *Journal of Archaeological Science*, 62, 128–142. <https://doi.org/10.1016/j.jas.2015.08.006>
- Maté-González, M. Á., Yravedra, J., Martín-Perea, D. M., Palomeque-González, J., San-Juan-Blazquez, M., Estaca-Gómez, V., et al. (2018). Flint and quartzite: Distinguishing raw material through bone cut marks. *Archaeometry*, 60(3), 437–452. <https://doi.org/10.1111/arcim.12327>
- Matzig, D. N., Hussain, S. T., & Riede, F. (2021). Design space constraints and the cultural taxonomy of European Final Palaeolithic large tanged points: A comparison of typological, landmark-based and whole-outline geometric morphometric approaches. *Journal of Paleolithic Archaeology*, 4(4), 27. <https://doi.org/10.1007/s41982-021-00097-2>
- Méndez-Quintas, E. (2022). Testing the bordes method on handaxes: A geometric morphometric approach. *Journal of Archaeological Science: Reports*, 45, 103563. <https://doi.org/10.1016/j.jas-rep.2022.103563>
- Moure, A., González Sainz, C., & González Morales, M. (1991). *Las cuevas de Ramales de la Victoria (Cantabria)*. Universidad de Cantabria.
- Nelson, E., Hall, J., Randolph-Quinney, P., & Sinclair, A. (2017). Beyond size: The potential of a geometric morphometric analysis of shape and form for the assessment of sex in hand stencils in rock art. *Journal of Archaeological Science*, 78, 202–213. <https://doi.org/10.1016/j.jas.2016.11.001>
- Newton, C., Lorre, C., Sauvage, C., Ivorra, S., & Terral, J. F. (2014). On the origins and spread of *Olea europaea* L. (olive) domestication: Evidence for shape variation of olive stones at Ugarit, Late Bronze Age, Syria—A window on the Mediterranean Basin and on the westward diffusion of olive varieties. *Vegetation History and Archaeobotany*, 23, 567–575. <https://doi.org/10.1007/s00334-013-0412-4>
- Palacio-Pérez, E. (2017). *El arte paleolítico. Historia de una idea*. Nadir Ediciones
- Palomeque-González, J. F., Maté-González, M. Á., Yravedra, J., San Juan-Blazquez, M., Vargas, E. G., Martín-Perea, D. M., et al. (2017). Pandora: A new morphometric and statistical software for analysing and distinguishing cut marks on bones. *Journal of Archaeological Science: Reports*, 13, 60–66. <https://doi.org/10.1016/j.jasrep.2017.03.033>
- Petrognani, S. (2009). À propos du traitement stylistique du cheval et du bison dans l'art pariétal paléolithique anté-magdalénien franco-ibérique. *Préhistoire, Art et Sociétés. Bulletin De La Société Préhistorique Ariège-Pyrénées*, 64, 165–174.
- Petrognani, S. (2015). L'art pariétal "ancien": fonds commun et traditions symboliques. *Paéthnologie*, 7. <https://doi.org/10.4000/paéthnologie.830>
- Petrognani, S., & Sauvet, G. (2012). La parenté formelle des grottes de Lascaux et de Gabillou est-elle formellement établie? *Bulletin De La Societe Prehistorique Francaise*, 109(3), 441–455. <https://doi.org/10.3406/bspf.2012.14170>
- Pigeaud, R. (1997). Les proportions des chevaux figurés dans l'art pariétal paléolithique: Problème esthétique ou affaire de point de vue? *PALEO*, 9, 295–324.
- Pigeaud, R. (2000). L'image du cheval dans l'art quaternaire. *Ethnozootechnie*, 64, 3–28.
- Pigeaud, R. (2004). La Grotte ornée Mayenne-Sciences (Thorigné-en-Charnie, Mayenne). Un exemple d'art pariétal d'époque gravettienne en France septentrionale. *Gallia Préhistoire*, 46, 1–154.
- Pigeaud, R. (2005). À propos des représentations de chevaux de la grotte Mayenne-Sciences (Thorigné-en-Charnie, Mayenne). Singularités stylistiques et formes d'usage dans «l'art de la silhouette» anté-magdalénien. In J. Jaubert & M. Barbaza (Eds.), *Territoires, déplacements, mobilité, échanges pendant la Préhistoire. Terres et hommes du Sud* (pp. 233–263). Éditions du Comité des Travaux Historique et Scientifiques
- Pigeaud, R. (2007). Determining style in Palaeolithic cave art: A new method derived from horse images. *Antiquity*, 81(312), 409–422. <https://doi.org/10.1017/S0003598X00095272>
- Pigeaud, R., Valladas, H., Arnold, M., & Cachier, H. (2003). Deux dates carbone 14 en spectrométrie de masse par accélérateur (SMA) pour une représentation pariétale de la grotte ornée Mayenne-Sciences (Thorigné-en-Charnie, Mayenne): émergence d'un art gravettien en France septentrionale? *Comptes Rendus Palevol*, 2, 161–168. [https://doi.org/10.1016/S1631-0683\(03\)00014-9](https://doi.org/10.1016/S1631-0683(03)00014-9)
- Polly, P. D. (2018). Geometric morphometrics. In S. L. López-Varela (Ed.), *The encyclopedia of archaeological sciences* (pp. 1–5). John Wiley and Sons. <https://doi.org/10.1002/9781119188230.sasa0258>

- Portillo, M., Ball, T. B., Wallace, M., Murphy, C., Pérez-Díaz, S., Ruiz-Alonso, M., et al. (2020). Advances in morphometrics in archaeobotany. *Environmental Archaeology*, 25(2), 246–256. <https://doi.org/10.1080/14614103.2019.1569351>
- Prat, F. (1986). Le cheval dans l'art paléolithique et les données de la paléontologie. *Arqueologia Porto*, 3(14), 27–33.
- Quiles, A., Valladas, H., Bocherens, H., Delqué-Količ, E., Kaltnecker, E., van der Plicht, J., & Delannoy, J.-J. (2016). A high-precision chronological model for the decorated Upper Paleolithic cave of Chauvet-Pont d'arc, Ardeche, France. *Proceedings of the National Academy of Sciences of the United States of America*, 113(17), 4670–4675. <https://doi.org/10.1073/pnas.1523158113>
- R Core Team (2022). R: a language and environment for statistical computing. R foundation for statistical computing, Vienna. <http://www.r-project.org/>
- Radinović, M., & Kajtez, I. (2021). Outlining the knapping techniques: Assessment of the shape and regularity of prismatic blades using elliptic Fourier analysis. *Journal of Archaeological Science: Reports*, 38, 103079. <https://doi.org/10.1016/j.jasrep.2021.103079>
- Reyment, R. A. (1991). *Multidimensional palaeobiology*. Pergamon Press.
- Rivero, O. (2010). *La movilidad de los grupos humanos del Magdaleniense en la región cantábrica y los Pirineos: una visión a través del arte*. [Tesis doctoral, Universidad de Salamanca]
- Rivero, O., & Sauvet, G. (2014). Defining Magdalenian cultural groups in Franco-Cantabria by the formal analysis of portable artworks. *Antiquity*, 88(339), 64–80. <https://doi.org/10.1017/S0003598X00050225>
- Rivero, O. (2016). Master and apprentice: Evidence for learning in palaeolithic portable art. *Journal of Archaeological Science*, 75, 89–100. <https://doi.org/10.1016/j.jas.2016.09.008>
- Rivero, O. (2020). El arte prehistórico. In E. Álvarez-Fernández, A. Blanco, & O. Rivero (Eds.), *Prehistoria de la península ibérica* (pp. 211–323). Ediciones Universidad de Salamanca.
- Rohlf, F. (1999). Shape statistics: Procrustes superimpositions and tangent spaces. *Journal of Classification*, 16, 197–223. <https://doi.org/10.1007/s003579900054>
- Rohlf, F. J., & Marcus, L. F. (1993). A revolution in morphometrics. *Trends in Ecology and Evolution*, 8(4), 129–132. [https://doi.org/10.1016/0169-5347\(93\)90024-J](https://doi.org/10.1016/0169-5347(93)90024-J)
- Ros, J., Evin, A., Bouby, L., & Ruas, M. P. (2014). Geometric morphometric analysis of grain shape and the identification of two-rowed barley (*Hordeum vulgare* subsp. *distichum* L.) in southern France. *Journal of Archaeological Science*, 41, 568–575. <https://doi.org/10.1016/j.jas.2013.09.015>
- Rossini, M., Falcucci, A., Dominici, C., Ronchitelli, A., Tomasso, A., & Boschini, F. (2022). Analytical potential of 2D shape analysis to study Epigravettian lithic assemblages. In *IMEKO TC-4 International Conference on Metrology for Archaeology and Cultural Heritage* (pp. 52–56). MetroArchaeo
- Rouzaud, F., Rouzaud, J.-N., & Lemaire, E. (1992). La “Vision Polaire” ou la transcription graphique bidimensionnelle des volumes au Paléolithique supérieur. *PALEO*, 4(1), 195–215. <https://doi.org/10.3406/pal.1992.1203>
- Ruiz-Redondo, A. (2014). *Entre el Cantábrico y los Pirineos: El conjunto de Altxerri en el contexto de la actividad gráfica magdaleniense*. [Tesis doctoral, Universidad de Cantabria]
- Sanchidrián, J. L. (1994). *Arte Rupestre de la Cueva de Nerja*. Patronato de la Cueva de Nerja.
- Sanchidrián, J. L., Márquez Alcántara, A. M., Valladas, H., & Tisnerat, N. (2001). Direct datations for Andalusian rock art (Spain). *International Newsletter on Rock Art*, 29, 15–19.
- Sauvet, G. (2018). La superior posición jerárquica del caballo en la iconografía parietal paleolítica. *Nailos*, 5, 43–64. <https://nailos.org/index.php/nailos/article/view/105>.
- Sauvet, G. (2019). The hierarchy of animals in the Paleolithic iconography. *Journal of Archaeological Science: Reports*, 28, 102025. <https://doi.org/10.1016/j.jasrep.2019.102025>
- Sauvet, G., Fritz, C., Fortea, J., & Tosello, G. (2014). Fluctuations des échanges symboliques au Paléolithique supérieur en France et dans le nord de l'Espagne. In J. Jaubert, N. Fourment, & P. Depaepe (Eds.), *Transitions, ruptures et continuité en Préhistoire* (pp. 403–415). Société Préhistorique Française.
- Sauvet, G., Fritz, C., & Tosello, G. (2013). El arte paleolítico antiguo del norte de España en su contexto europeo. En M. Rasilla (Coord.), F. Javier Fortea Pérez. *Universitatis Ovetensis Magister. Estudios en Homenaje* (pp. 347–362). Universidad de Oviedo
- Sauvet, G., & Rivero, O. (2016). D'un support à l'autre: l'art pariétal à la lumière de l'art mobilier. *PALEO*, Numéro spécial, 133–147
- Schmid, E. (1984). Some anatomical observations on Palaeolithic depictions of horses. In H.-G. Bandi, W. Huber, M.-R. Sauter, & B. Sitter (Eds.), *La contribution de la zoologie et de l'ethologie à*

- L'interprétation de l'art des peuples chasseurs préhistoriques* (pp. 155–160). John Hopkins University Press.
- Seetah, T. K. (2014). Geometric morphometrics and environmental archaeology. In C. Smith (Ed.), *Encyclopedia of global archaeology* (pp. 3029–3036). Springer. [https://doi.org/10.1007/978-3-030-30018-0\\_2123](https://doi.org/10.1007/978-3-030-30018-0_2123)
- Serwatka, K. (2015). Shape variation of Middle Palaeolithic bifacial tools from southern Poland: A geometric morphometric approach to Keilmessergruppen handaxes and backed knives. *Lithics-the Journal of the Lithic Studies Society*, 35, 18–32.
- Smith, S. D., & Kriebel, R. (2018). Convergent evolution of floral shape tied to pollinator shifts in Iochrominae (Solanaceae). *Evolution*, 72(3), 688–697. <https://doi.org/10.1111/evo.13416>
- Terral, J. F., Newton, C., Ivorra, S., Gros-Balthazard, M., de Morais, C. T., Picq, S., et al. (2012). Insights into the historical biogeography of the date palm (*Phoenix dactylifera* L.) using geometric morphometry of modern and ancient seeds. *Journal of Biogeography*, 39(5), 929–941. <https://doi.org/10.1111/j.1365-2699.2011.02649.x>
- Terral, J. F., Tabard, E., Bouby, L., Ivorra, S., Pastor, T., Figueiral, I., et al. (2010). Evolution and history of grapevine (*Vitis vinifera*) under domestication: New morphometric perspectives to understand seed domestication syndrome and reveal origins of ancient European cultivars. *Annals of Botany*, 105(3), 443–455. <https://doi.org/10.1093/aob/mcp298>
- Timbrell, L., de la Pena, P., Way, A., Hoggard, C., Backwell, L., d'Errico, F., et al. (2022). Technological and geometric morphometric analysis of 'post-Howiesons Poort points' from Border Cave, KwaZulu-Natal. *South Africa. Quaternary Science Reviews*, 297, 107813. <https://doi.org/10.1016/j.quascirev.2022.107813>
- Tosello, G. (2003). *Pierres gravées du Périgord magdalénien. Art, symboles, territoires*. CNRS Editions
- Tosello, G., & Fritz, C. (2004). Grotte Chauvet-Pont d'Arc: approche structurelle et comparative du panneau des chevaux. In M. Lejeune (Ed.), *L'art Pariétal Paléolithique dans son Contexte Naturel. Actes du colloque 8.2. Congrès de l'UISPP* (pp. 69–86). Éraul
- Vestergaard, C., & Hoggard, C. S. (2019). Novel geometric morphometric (GMM) application to the study of Bronze Age Tutuli. *Danish Journal of Archaeology*, 8, 1–24. <https://doi.org/10.7146/dja.v8i0.112494>
- Villaverde, V. (1994). *Arte paleolítico de la Cova del Parpalló. Estudio de la colección de plaquetas y cantos grabados y pintados: Vol. I*. Diputació, Servei d'Investigació Prehistòrica
- Villaverde, V. (2017). El análisis de la forma en las representaciones zoomorfas paleolíticas. *Criterios y Aplicaciones. Kobie*, 16, 115–134.
- Wang, L. Y., & Marwick, B. (2020). Standardization of ceramic shape: A case study of Iron Age pottery from northeastern Taiwan. *Journal of Archaeological Science: Reports*, 33, 102554. <https://doi.org/10.1016/j.jasrep.2020.102554>
- Yravedra, J., García-Vargas, E., Maté-González, M. Á., Aramendi, J., Palomeque-González, J. F., & Vallés-Iriso, J. (2017a). The use of micro-photogrammetry and geometric morphometrics for identifying carnivore agency in bone assemblages. *Journal of Archaeological Science: Reports*, 14, 106–115. <https://doi.org/10.1016/j.jasrep.2017.05.043>
- Yravedra, J., Maté-González, M. Á., Palomeque-González, J. F., Aramendi, J., Estaca-Gómez, V., Blazquez, S. J., & Domínguez-Rodrigo, M. (2017b). A new approach to raw material use in the exploitation of animal carcasses at BK (Upper Bed II, Olduvai Gorge, Tanzania): A micro-photogrammetric and geometric morphometric analysis of fossil cut marks. *Boreas*, 46(4), 860–873. <https://doi.org/10.1111/bor.12224>
- Zelditch, M. L., Swiderski, D. L., & Sheets, H. D. (2012). *Geometric morphometrics for biologists: A primer*. Elsevier

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.