

Research Article

Ricardo Miguel Godinho*, Cláudia Umbelino, Célia Gonçalves

Mesolithic and Chalcolithic Mandibular Morphology: Using Geometric Morphometrics to Reconstruct Incomplete Specimens and Analyse Morphology

<https://doi.org/10.1515/opar-2022-0247>

received June 01, 2021; accepted June 01, 2022

Abstract: Human skeletal remains are routinely used to examine cultural and biological aspects of past populations. Yet, archaeological specimens are frequently fragmented/incomplete and so excluded from analyses. This leads to decreased sample sizes and to potentially biased results. Digital methods are now frequently used to restore/estimate the original morphology of fragmented/incomplete specimens. Such methods include 3D digitisation and Geometric Morphometrics (GM). The latter is also a solidly established method now to examine morphology. In this study, we use GM-based methods to estimate the original morphology of incomplete Mesolithic and Chalcolithic mandibles originating from present Portugal and perform ensuing morphological analyses. Because mandibular morphology is known to relate to population history and diet, we hypothesised the two samples would differ. Thirty-seven specimens (12 complete and 25 incomplete) were CT-scanned and landmarked. Originally complete specimens were used as reference to estimate the location of absent anatomical landmarks in incomplete specimens. As predicted, our results show shape differences between the two samples which are likely due to the compounded effect of contrasting population histories and diets.

Keywords: biological anthropology, virtual anthropology, skeletal morphology, population history, bone adaptation

1 Introduction

Human skeletal remains are used routinely to examine various cultural and palaeobiological aspects of past populations, including, e.g., funerary behaviour (Filipe, Godinho, Granja, Ribeiro, & Valera, 2013; Godinho,

Special Issue published in cooperation with Meso'2020 – Tenth International Conference on the Mesolithic in Europe, edited by Thomas Perrin, Benjamin Marquebielle, Sylvie Philibert, and Nicolas Valdeyron

* **Corresponding author: Ricardo Miguel Godinho**, Interdisciplinary Centre for Archaeology and Evolution of Human Behaviour (ICArHEB), University of Algarve, Faculdade das Ciências Humanas e Sociais, Universidade do Algarve, Campus Gambelas, 8005-139, Faro, Portugal, e-mail: ricardomiguelgodinho@gmail.com

Cláudia Umbelino: Interdisciplinary Centre for Archaeology and Evolution of Human Behaviour (ICArHEB), University of Algarve, Faculdade das Ciências Humanas e Sociais, Universidade do Algarve, Campus Gambelas, 8005-139, Faro, Portugal; Department of Life Sciences, Research Centre for Anthropology and Health, University of Coimbra, Coimbra, Portugal

Célia Gonçalves: Interdisciplinary Centre for Archaeology and Evolution of Human Behaviour (ICArHEB), University of Algarve, Faculdade das Ciências Humanas e Sociais, Universidade do Algarve, Campus Gambelas, 8005-139, Faro, Portugal

ORCID: Ricardo Miguel Godinho 0000-0003-0107-9577

Gonçalves, & Valera, 2019), diet (Galland, Van Gerven, Von Cramon-Taubadel, & Pinhasi, 2016; Pokhojaev, Avni, Sella-Tunis, Sarig, & May, 2019; von Cramon-Taubadel, 2011), occupation (Henderson, 2013; Villotte et al., 2010; Villotte, Churchill, Dutour, & Henry-Gambier, 2010), mobility (Holt, 2003; Macintosh, Pinhasi, & Stock, 2014; Ruff et al., 2015), biological distances (Brewster, Meiklejohn, von Cramon-Taubadel, & Pinhasi, 2014; Nystrom & Malcom, 2010; Stojanowski & Schillaci, 2006), and palaeopathology (Calce, Kurki, Weston, & Gould, 2018; Godinho, Santos, & Valera, 2020; Griffin & Donlon, 2009). Yet, archaeological specimens are frequently fragmented, incomplete, and/or distorted, and so are often excluded from analyses (Godinho & O’Higgins, 2017; Gunz, Mitteroecker, Neubauer, Weber, & Bookstein, 2009; O’Higgins, Fitton, & Godinho, 2019). This leads to reduced sample sizes and hence, potentially biased results when examining past populations (Cardini & Elton, 2007; Cardini, Seetah, & Barker, 2015). To overcome such limitations, researchers frequently reconstruct incomplete specimens by estimating the original location of missing regions and include those specimens in the analyses to increase sample size. While reconstruction has frequently been based on individual expertise and morphological visual assessment, it is now commonly based on digital methods that allow more objective and reproducible approaches (Amano et al., 2015; Bauer & Harvati, 2015; Benazzi, Bookstein, Strait, & Weber, 2011; Godinho & O’Higgins, 2017). Such methods include 3D digitisation and Geometric Morphometrics (GM), which allow geometric- and statistical-technique-based digital reconstructions that are fully reproducible and so overcome the subjectivity of previous reconstruction methods (Gunz et al., 2009; O’Higgins et al., 2019). Moreover, GM also enables complex morphological analyses and examination of how form relates to other underlying variables (O’Higgins, 2000; Zelditch, Swiderski, Sheets, & Fink, 2012).

Here we use GM to reconstruct incomplete Mesolithic and Chalcolithic mandibles (from present Portugal) to increase sample size. The Mesolithic specimens originate from several Muge (Cabeço da Amoreira, Cabeço da Arruda, Cova da Onça, and Moita do Sebastião) and Sado (Arapouco, Cabeço de Pez, and Vale de Romeiras) shell middens and the Chalcolithic specimens from 2 distinct archaeological sites (Monte da Guarita 2 and Monte do Carrascal 2; Table 1 and Figure 1). The generally contemporaneous Muge shell middens are located in the Tagus valley and form one of the most important Mesolithic contexts worldwide (Bicho et al., 2013; Bicho, Umbelino, Detry, & Pereira, 2010; Gonçalves, 2009; Gonçalves, Cascalheira, & Bicho, 2014). They were formed by early Holocene hunter–gatherers and over 300 individuals were buried therein (Cunha & Cardoso, 2001; Jackes & Lubell, 1999; Peyroteo-Stjerna, 2020; Umbelino et al., 2015). The Sado complex also includes multiple middens and is located ~100 km south of the Muge complex (Araújo, 2003; Cunha & Umbelino, 2001), and from which over 100 individuals (generally coeval with those from the Muge shell middens) were excavated (Cunha & Umbelino, 2001; Peyroteo-Stjerna, 2020; Umbelino, 2006). Monte da Guarita 2 is located in Alentejo and corresponds to a Chalcolithic collective underground tomb (hypogeum) from where several individuals were exhumed (Miguel & Simão, 2017). Monte do Carrascal 2 is an archaeological complex including several Chalcolithic collective hypogea from which several individuals were exhumed (Valera, Santos, Figueiredo, & Granja, 2014). After reconstruction of the samples, we further used GM to perform ensuing morphological analyses of the samples and examine if Mesolithic specimens are morphologically distinct from Chalcolithic mandibles. Because mandibular

Table 1: Inventory of complete and incomplete specimens (per site and chronology) used in this study

Site	Chronology	Complete specimens	Incomplete specimens	Total specimens
Arapouco	Mesolithic	1	1	2
Cabeço da Amoreira	Mesolithic	0	1	1
Cabeço da Arruda	Mesolithic	2	4	6
Cabeço de Pez	Mesolithic	0	1	1
Cova da Onça	Mesolithic	1	0	1
Moita do Sebastião	Mesolithic	5	8	13
Vale de Romeiras	Mesolithic	1	1	2
Monte da Guarita 2	Chalcolithic	2	4	6
Monte do Carrascal 2	Chalcolithic	0	5	5
Total		12	25	37

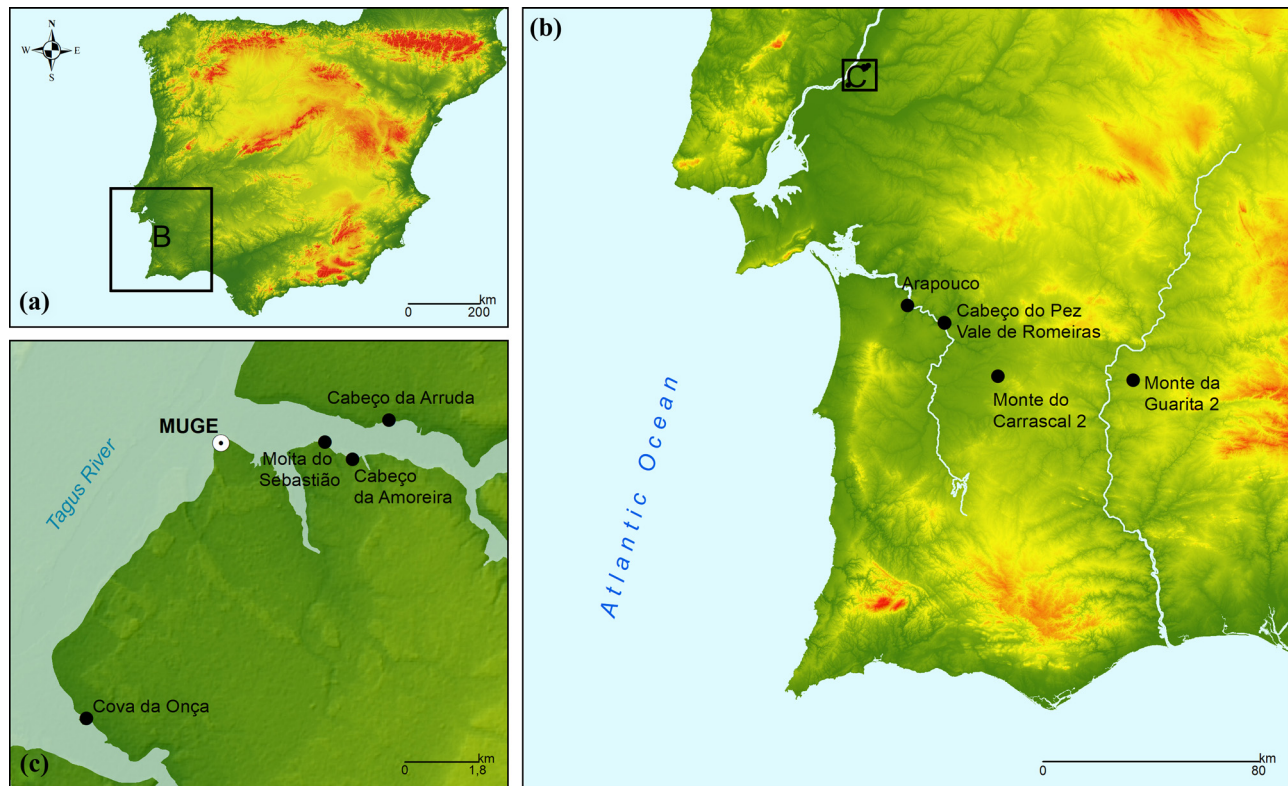


Figure 1: Location of the archaeological sites from which the specimens used in this study were recovered. (a) Overall location of sites within Iberia. (b) Cluster location of the Muge shell-middens and individual location of the remaining sites. (c) Individual location of each of the Muge sites.

morphology is impacted by population history (Buck & Vidarsdottir, 2004; Katz, Grote, & Weaver, 2017; Mounier *et al.*, 2018) and masticatory mechanics (Galland *et al.*, 2016; von Cramon-Taubadel, 2011), and based on previous research (given below), we hypothesised that specimens from these two periods are morphologically distinct.

Specifically, the Mesolithic hunter–gatherer mode of subsistence was replaced by Neolithic agro-pastoralism, which was introduced in Iberia in ~5500 cal. BC by populations originating in the Middle East (Martins *et al.*, 2015; Zilhão, 2000, 2001). This change in mode of subsistence is associated with marked genetic discontinuity between Iberian Mesolithic and Neolithic populations and substantial replacement of the former by the latter, despite some degree of population admixture (Haak *et al.*, 2015; Olalde *et al.*, 2015, 2019; Villalba-Mouco *et al.*, 2019). Moreover, bone adapts to various aspects of mechanical loading (Currey, 2006; Judex & Rubin, 2010; Judex, Gross, & Zernicke, 1997; Judex, Lei, Han, & Rubin, 2007; Lanyon & Rubin, 1984; Lanyon, 1984; Mosley & Lanyon, 1998; Mosley, March, Lynch, & Lanyon, 1997; Turner, 1998) and so several previous studies have demonstrated that the dietary changes that occurred in the Mesolithic – Neolithic transition impacted mandibular morphology (Galland *et al.*, 2016; Pokhojaev *et al.*, 2019; von Cramon-Taubadel, 2011). Thus, we hypothesise that Mesolithic and Chalcolithic mandibular morphology of the samples used in this study differ because it is impacted by both population history and diet.

2 Materials and Methods

This study is based on a total of 37 Mesolithic and Chalcolithic specimens originating from several sites located in the present Portugal (Table 1 and Figure 1).

All specimens were digitised using a Toshiba Astelion CT scanner (120 kV, voxel size $0.348 \times 0.348 \times 0.3$, revolution time 0.75 s, spiral pitch factor 0.94) at the Faculty of Veterinary Medicine of the University of

Lisbon. Segmentation ensued in 3D Slicer (Fedorov et al., 2012) using standard protocols described by Godinho and O’Higgins (2017, 2018), Godinho, Spikins, and O’Higgins (2018) and Godinho et al. (2018). Fragmented specimens were virtually pieced together (Godinho & Gonçalves, 2020). After this procedure, coordinates were extracted from a total of 21 anatomical landmarks (LMs; Table 2) from the most complete hemi-mandible of each specimen to capture mandibular morphology (Figure 2). The use of left hemi-mandibles was favoured. When specimens were incomplete, the location of the missing LMs was estimated using the thin plate spline (TPS) function of the Geomorph R package following the recommendations of Godinho, O’Higgins, and Gonçalves (2020). Specifically, excessively incomplete specimens were not reconstructed because reconstruction error may be larger than inter-individual differences and hence may lead to biased results. This led to the exclusion of specimens missing more than 5 LMs. Only 1 specimen with 5 missing LMs was included and incomplete specimens most often lacked 2 LMs (Table A1). Mesolithic specimens were used as reference to geometrically estimate the location of the missing landmarks in the incomplete Mesolithic specimens. The same procedure was applied to the Chalcolithic sample using complete Chalcolithic specimens. Thus, chronological specific references were used. This is because the use of inappropriate references (i.e., specimens with meaningful morphological differences due to, e.g., contrasting population history) leads to larger errors in the estimation of the location of missing anatomical regions (Gunz et al., 2009; Neeser, Ackermann, & Gain, 2009; Senck, Bookstein, Benazzi, Kastner, & Weber, 2015). Nevertheless, we tested if this population-specific reconstruction approach could be driving the hypothetical inter-population differences. To that end, a non-population specific reference was created using all complete specimens from both chronologies for ensuing reconstruction of incomplete specimens. Results from both reconstruction approaches were then compared using Principal Component Analysis (PCA) and Discriminant Function Analysis (DFA) (given below).

After estimation of the missing LMs, standard GM analysis ensued. The landmark coordinate datasets of all specimens were superimposed using Generalised Procrustes Analysis (GPA). GPA removes the effects of size, location, and orientation and produces shape variables that are used in shape analysis. Shape differences between samples were examined via the PCA and visualised using Thin Plate Splines (TPS) that depict shape differences along the selected PCs. The impact of reconstruction approach was examined by

Table 2: Mandibular landmarks used in this study

#	Landmark name	Landmark description
1	Gnathion	Midline of the inferior border of the mandible
2	Infradentale	Anterior alveolar ridge, between anterior incisors
3	Linguale	Genial tubercle: in case of a single tubercle, on its tip; in case of two, midpoint between them
4	Orale, mandible	Posterior alveolar ridge between the anterior incisors
5	Pogonion	Most anterior point of mandibular symphysis
6	C-P3	Anterior alveolar ridge between canine and first premolar
7	P4-M1	Anterior alveolar ridge between second premolar and first molar
8	M1-M2	Anterior alveolar ridge between first and second molar teeth
9	Mental foramen anterior	Anterior point of mental foramen
10	Ramus root	Anterior rim of the ramus (placed on the level of the alveolar ridge)
11	Gonion	A point on the projection of the bisection of the mandibular angle
12	Condyle, lateral	From a superior view, the lateral point on the condyle
13	Condyle, midpoint	From a superior view, a point in the centre of the condyle
14	Condyle, medial	From a superior view, the medial point on the condyle
15	Sigmoid Notch	The lowest point of the mandibular notch, with the mandible in the mandibular plane and in lateral view
16	Coronoid process	Tip of the coronoid process
17	Mandibular foramen, inferior	Most inferior point of the mandibular foramen
18	Alveolous, lingual posterior	From a superior view, the most posterior point on the lingual alveolar process
19	Condyle, anterior	A point on the antero-superior aspect of the mandibular notch (on the condyle)
20	Condyle, posterior	The centre of the condyle from a posterior view
21	Ramus, posterior	Posteriormost point of the ramus that is in line with the ramus root

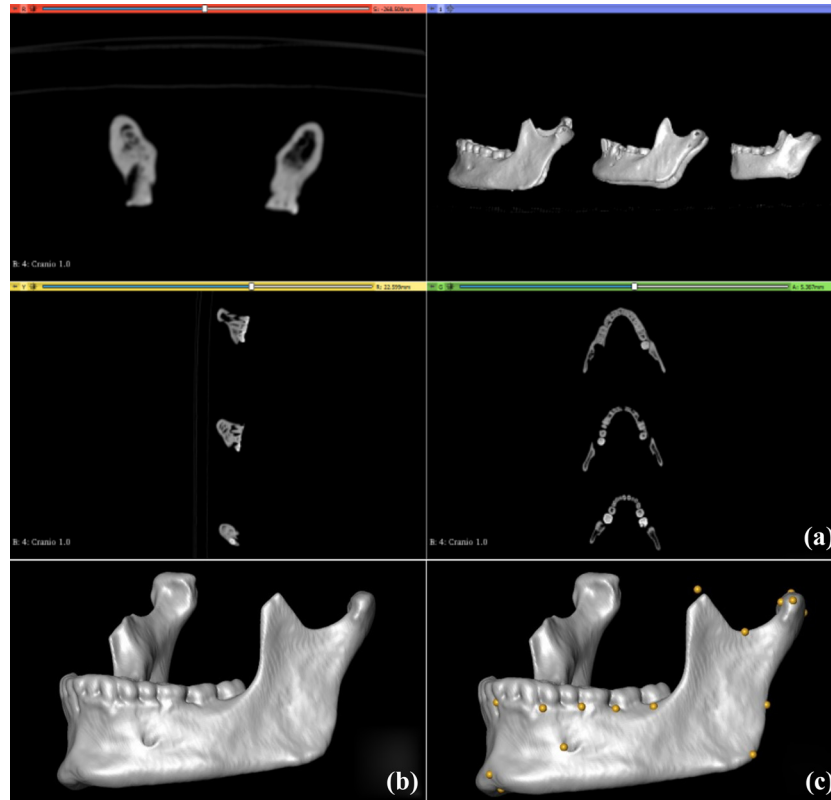


Figure 2: Visualisation of CT scan slices (a), ensued by rendering (b), and landmarking of individual specimens (c). Note that C shows the location of present and estimated missing (e.g., in the coronoid process) landmarks.

performing a PCA in which all specimens from the population-specific and non-population-specific reconstructions were included. DFA with 10,000 permutations and cross-validation scores was also used to examine the inter-population differences and was implemented using MorphoJ (Klingenberg, 2011). DFA was also used to examine the impact of population-specific vs non-population-specific reconstruction approaches (given above).

To examine if hypothetical morphological differences between Mesolithic and Chalcolithic samples are most likely related to population history or masticatory mechanics (given above), dental wear was also examined because it is related to the latter (Chattah & Smith, 2006; Smith, 1984). Wear magnitude was scored according to Smith (1984), averaged per individual and compared between the two samples using a boxplot and the Wilcoxon non-parametric statistical test.

3 Results

Digitisation and the use of GM-based reconstruction allowed estimating the original morphology of 25 originally incomplete specimens, thereby, increasing the sample size from 12 to 37 specimens.

Ensuing morphological analysis including all specimens shows limited overlap between the two samples (when plotting PC1 and 2, which explain ~34% of the total variance; Figure 3). This is because the Mesolithic sample clusters mostly along the positive values of PC2 and the Chalcolithic sample mostly clusters along the negative values. Morphologically, this corresponds to Chalcolithic specimens having, e.g., generally wider rami, taller coronoid processes, shorter mandibular symphyses, and more alveolar prognathism. Although there is overlap between the two samples in PC1, the most extreme positive specimens are Chalcolithic. Such specimens have, e.g., shorter mandibular symphyses, more flexure of the posterior border of the ramus and more anteriorly positioned coronoid processes. PCA comparison of full

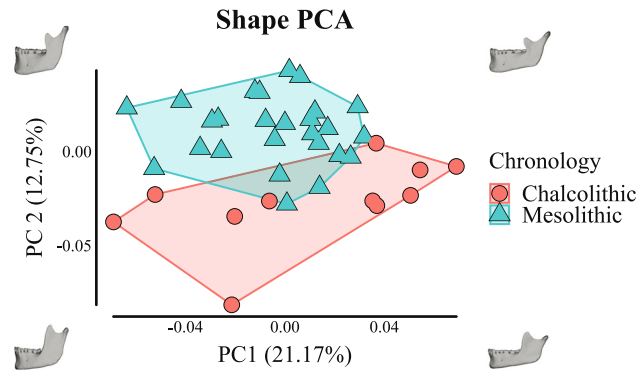


Figure 3: PCA of shape variation of Mesolithic hunter-gatherer and Chalcolithic agro-pastoralist mandibles.

samples including population- and non-population-specific reconstruction approaches show meaningful overlap between specimens and very little impact on the overlap between groups (Figure A1). DFA is unable to reliably discriminate between population- and non-population-specific reconstructions of the same populations, and discriminates similarly between Mesolithic and Chalcolithic specimens based on the two different reconstruction approaches (Tables A2–A7). This shows inter-population differences are not due to reconstruction approach.

DFA using 10,000 permutations shows significant inter-group differences (T -Square: $p < 0.0001$). Nevertheless, cross-validation results show misclassification of 4/11 Chalcolithic and 2/26 Mesolithic specimens (Table 3).

Dental wear magnitude is significantly heavier in the Mesolithic sample (Figure 4).

4 Discussion

The use of digital methods enabled the objective and reproducible reconstruction of 25 specimens that were originally incomplete. Thus, sample size was increased to a total of 37 specimens, which enabled further GM-based morphological analysis, a better representation of morphological variance, and hence more reliable results than if only the 12 originally complete specimens were included.

As expected, morphological analyses show shape differences between the Mesolithic and Chalcolithic samples. Our results also show negligible differences between population-specific and non-population-specific reconstructions. Thus, contrasting shapes between the two populations are not related to the reconstruction approach. Because mandibular morphology is known to relate to both population history (Buck & Vidarsdottir, 2004; Katz et al., 2017; Mounier et al., 2018) and masticatory mechanics (Galland et al., 2016; Katz et al., 2017; May, Sella-Tunis, Pokhojaev, Peled, & Sarig, 2018; Pokhojaev et al., 2019; von Cramon-Taubadel, 2011), these shape differences may relate to either of these two underlying factors.

Specifically, Iberian Mesolithic populations derived from previously existing Post-Glacial Upper Palaeolithic populations (Brewster et al., 2014; López-Onaindia, Gibaja, & Subirà, 2019). By no later than ~5500 cal. BC, populations originating in the Middle East reached the Iberian Peninsula and introduced

Table 3: Cross-validation scores of DFA (with 10,000 permutations)

True group	Allocated to		Total
	Chalcolithic	Mesolithic	
Chalcolithic	7	4	11
Mesolithic	2	24	26

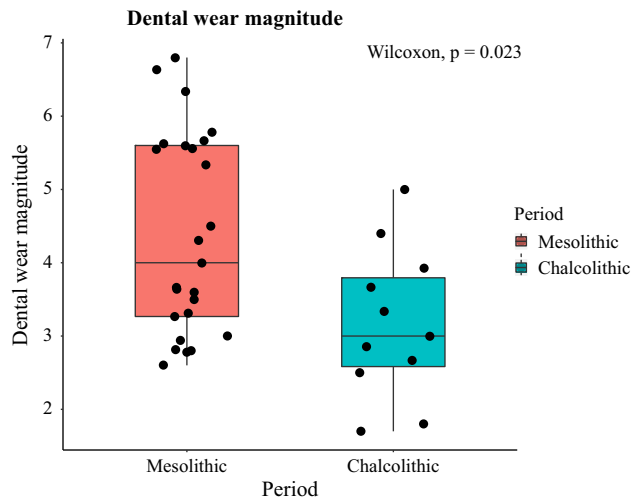


Figure 4: Dental wear magnitude (scored according to Smith, 1984) of the Mesolithic and Chalcolithic samples.

agriculture (Martins *et al.*, 2015; Zilhão, 2000, 2001). Ancient DNA studies show marked genetic discontinuity between Mesolithic hunter–gatherers and Neolithic agro-pastoralists, thus suggesting population replacement mainly in most European regions. However, such studies also show the presence of Mesolithic DNA in post-Mesolithic individuals and so at least some level of admixture exists between the local Mesolithic and the incoming Neolithic populations (Haak *et al.*, 2015; Olalde *et al.*, 2015, 2019; Villalba-Mouco *et al.*, 2019). Because mandibular morphology is known to relate to population history (Buck & Vidarsdottir, 2004; Katz *et al.*, 2017; Mounier *et al.*, 2018), our results showing shape differences between the two samples are to be expected and likely also related to population history.

Despite contrasts in mandibular shape being likely related to differences in population history in the samples, masticatory mechanics has also probably impacted mandibular morphology to some extent. The Mesolithic hunter–gatherer diet has been consistently said to be mechanically more demanding than the post-Mesolithic agro-pastoralist diet (Cohen, 1989; Larsen, 1997, 2006; Stock & Pinhasi, 2011). This is because the latter included more processed food items that made the overall diet softer and so less demanding (Cohen, 1989; Larsen, 1997, 2006; Stock & Pinhasi, 2011). Previous experimental studies using non-human mammal models have shown that differences in the material properties of diet impact skull morphology (Beecher & Corruccini, 1981; Bouvier & Hylander, 1984; He & Kiliaridis, 2003; Kiliaridis, Engström, & Thilander, 1985; Menegaz & Ravosa, 2017; Menegaz, Sublett, Figueroa, Hoffman, & Ravosa, 2009; Ravosa, Kunwar, Stock, & Stack, 2007; Ravosa *et al.*, 2008a,b), and so differences in skull form between hunter–gatherers and agro-pastoralists are frequently linked to differences in the masticatory demands due to dietary differences (Galland *et al.*, 2016; Katz *et al.*, 2017; May *et al.*, 2018; Pokhojaev *et al.*, 2019; von Cramon-Taubadel, 2011). Our results showing significantly heavier wear in Mesolithic specimens are consistent with previous studies (Larsen, 1997; Lukacs, 1989) and support the hypothesis that mandibular shape differences between the two samples are also related to differences in diet and therefore in masticatory demands. This is because dental wear is known to relate to the material properties of food, and so it is frequently used to examine differences in diet and food pre-processing (Chattah & Smith, 2006; Smith, 1984).

In summary, our results confirm our prediction that mandibular morphology differs between Mesolithic hunter–gatherers and Chalcolithic agro-pastoralists. This is probably due to the compounded effect of population history and masticatory mechanics. Although we are unable to discern which of these factors impacted morphology the most, previous research about limb skeletal morphology showed that differences in mechanical loading fail to erase the impact of population history in bone form (Agostini, Holt Brigitte, & Relethford John, 2018). This is consistent with previous studies showing that mandibular morphology is impacted more by population history than by masticatory mechanics (Katz *et al.*, 2017), and so the mandibular morphological differences detected in this study are most likely related to population history and, possibly, enhanced by contrasting masticatory demands.

Abbreviations

DFA	discriminant function analysis
GPA	generalised procrustes analysis
GM	geometric morphometric
LM	landmarks
PCA	principal component analysis
TPS	thin plate spline

Acknowledgments: Thanks to Dr Miguel Ramalho[†] and Dr José António Moita for granting access to the skeletal remains of Muge; António Valera and Era Arqueologia S.A. for providing access to the skeletal remains from Monte da Guarita 2; Sara Ramos for access to the skeletal remains from Monte do Carrascal 2; Prof. Sandra Jesus and Dr Óscar Gamboa for CT scanning at the Faculty of Veterinary Medicine of the University of Lisbon.

Funding information: RM Godinho was funded by Fundação para a Ciência e a Tecnologia (FCT; contract reference 2020.00499.CEECIND) and the European Regional Development Fund (FEDER) via the Programa Operacional CRESC Algarve 2020, of Portugal2020 (project ALG-01-0145-FEDER-29680), in the context of the MugePortal project (“Muge Shellmiddens Project: a new portal for the last hunter–gatherers of the Tagus Valley, Portugal (MugePortal);” project reference ALG-01-0145-FEDER-29680/PTDC/HAR-ARQ/29680/2017, funded by the Fundação para a Ciência e a Tecnologia (FCT)). C. Umbelino was funded by the Fundação para a Ciência e a Tecnologia (FCT, reference UIDB/00283/2020). C Gonçalves was funded by the Portuguese Foundation for Science and Technology (FCT; contract reference DL 57/2016/CP1361/CT0029). This research was also funded by the Archaeological Institute of America (The Archaeology of Portugal Fellowship).

Conflict of interest: The authors state no conflict of interest.

Data availability statement: The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Appendix

Table A1: Number of missing landmarks per specimen in the Mesolithic and Chalcolithic samples

Number of missing landmarks	Mesolithic	Chalcolithic	Total	%
0	10	2	12	32.43
1	4	1	5	13.51
2	6	3	9	24.32
3	3	2	5	13.51
4	3	2	5	13.51
5	0	1	1	2.70
Total	26	11	37	100.00

Table A2: DFA with cross-validation of the non-population-specific reconstructed Chalcolithic sample vs the population-specific reconstructed Chalcolithic sample (see details about reconstruction parameters in Materials and Methods)

True group	Allocated to		Total
	Chalcolithic (non-population specific)	Chalcolithic (population specific)	
From discriminant function			
Chalcolithic (non-population specific)			11
	11	0	
Chalcolithic (population specific)			11
	2	9	
From cross-validation			
Chalcolithic (non-population specific)			11
	5	6	
Chalcolithic (population specific)			11
	6	5	

Table A3: DFA with cross-validation of the non-population-specific reconstructed Chalcolithic sample vs the non-population-specific reconstructed Mesolithic sample (see details about reconstruction parameters in Materials and Methods)

True group	Allocated to		
	Chalcolithic (non-population specific)	Mesolithic (non-population specific)	Total
From discriminant function			
Chalcolithic (non-population specific)			11
	11	0	
Mesolithic (non-population specific)			26
	0	26	
From cross-validation			
Chalcolithic (non-population specific)			11
	8	3	
Mesolithic (non-population specific)			26
	2	24	

Table A4: DFA with cross-validation of the non-population-specific reconstructed Chalcolithic sample vs the population-specific reconstructed Mesolithic sample (see details about reconstruction parameters in Materials and Methods)

True group	Allocated to		Total
	Chalcolithic (non-population specific)	Mesolithic (population specific)	
From discriminant function			
Chalcolithic (non-population specific)	11	0	11
Mesolithic (population-specific)	0	26	26
From cross-validation			
Chalcolithic (non-population specific)	8	3	11
Mesolithic (population-specific)	1	25	26

Table A5: DFA with cross-validation of the population-specific reconstructed Chalcolithic sample vs the non-population-specific reconstructed Mesolithic sample (see details about reconstruction parameters in Materials and Methods)

True group	Allocated to		Total
	Chalcolithic (population specific)	Mesolithic (non-population specific)	
From discriminant function			
Chalcolithic (population specific)	11	0	11
Mesolithic (non-population specific)	0	26	26
From cross-validation			
Chalcolithic (population specific)	7	4	11
Mesolithic (non-population specific)	1	25	26

Table A6: DFA with cross-validation of the population-specific reconstructed Chalcolithic sample vs the population-specific reconstructed Mesolithic sample (see details about reconstruction parameters in Materials and methods)

True group	Allocated to		Total
	Chalcolithic (population specific)	Mesolithic (population specific)	
From discriminant function			
Chalcolithic (population specific)	11	0	11
Mesolithic (population specific)	0	26	26
From cross-validation			
Chalcolithic (population specific)	7	4	11
Mesolithic (population specific)	2	24	26

Table A7: DFA with cross-validation of the non-population-specific reconstructed Mesolithic sample vs the population-specific reconstructed Mesolithic sample (see details about reconstruction parameters in Materials and Methods)

True group	Allocated to		Total
	Mesolithic (non-population specific)	Mesolithic (population specific)	
From discriminant function			
Mesolithic (non-population specific)	22	4	26
Mesolithic (population specific)	6	20	26
From cross-validation			
Mesolithic (non-population specific)	7	19	26
Mesolithic (population specific)	17	9	26

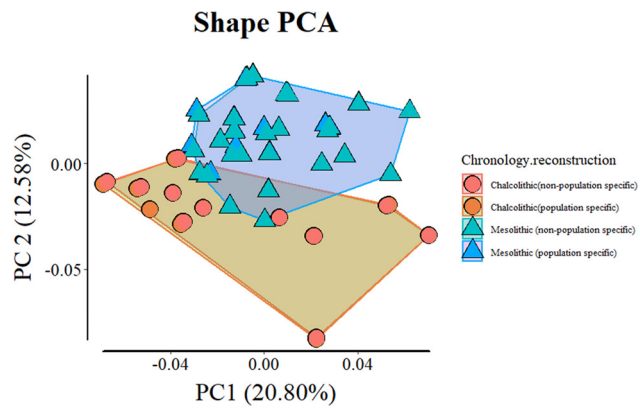


Figure A1: Shape PCA comparing population-specific and non-population-specific reconstruction of incomplete specimens. Note there is complete or almost complete overlap between specimens despite differences in reconstruction method.