Research Article

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

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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,
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

| 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 Carrascal2| Chalcolithic| 0                 | 5                    | 5               |
| Total             |            | 12                 | 25                   | 37              |
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 (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).

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                   |
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
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...
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 & Corrucchini, 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

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References

Agostini, G., Holt Brigitte, M., & Relethford John, H. (2018). Bone functional adaptation does not erasne neutral evolutionary information. *American Journal of Physical Anthropology*, 166(3), 708–729. doi: 10.1002/ajpa.23460.

Amano, H., Kikuchi, T., Morita, O., Suzuki, H., Ponce de Leon, M. S., & Oghara, N. (2015). Virtual reconstruction of the Neanderthal Amud 1 cranium. *American Journal of Physical Anthropology*, 158(2), 185–197. doi: 10.1002/ajpa.22777.

Araújo, A. C. (2003). The emergence of muge Mesolithic shell Middens in Central Portugal and the effects of dietary consistency on craniofacial and occlusal development in the rat. *Anthropologischer Anzeiger*, 72(2), 129–140.

Beecher, R. M., & Corruccini, R. S. (1981). Effects of dietary consistency on craniofacial and occlusal development in the rat. *The Angle Orthodontist*, 51(1), 61–69. doi: 10.1043/0003-3219(1981)051<0061:EODCOC>2.0.CO;2.

Benazzi, S., Bookstein, F. L., Strait, D. S., & Weber, G. W. (2011). A new OHS reconstruction with an assessment of its uncertainty. *Journal of Human Evolution*, 61(1), 75–88. doi: 10.1016/j.jhevol.2011.02.005.

Bicho, N., Cascalheira, J., Marreiros, J., Gonçalves, C., Pereira, T., & Dias, R. (2013). Chronology of the Mesolithic occupation of the Muge valley, central Portugal: The case of Cabeço da Amoreira. *Quaternary International*, 308–309, 130–139. doi: 10.1016/j.quaint.2012.10.049.

Bicho, N., Umbelino, C., Detry, C., & Pereira, T. (2010). The emergence of muge Mesolithic shell Middens in Central Portugal and the 8200 cal yr BP Cold Event. *The Journal of Island and Coastal Archaeology*, 5(1), 86–104. doi: 10.1080/15564891003638184.

Bouvier, M., & Hylander, W. L. (1984). The effect of dietary consistency on gross and histologic morphology in the craniofacial Region of Young Rats. *American Journal of Anatomy*, 170(1), 117–126. doi: 10.1002/aja.1001700109.
Godinho, R. M., Meiklejohn, C., von Cramon-Taubadel, N., & Pinhasi, R. (2014). Cranio-metric analysis of European Upper Palaeolithic and Mesolithic samples supports discontinuity at the Last Glacial Maximum. *Nature Communications*, 5, 4094. doi: 10.1038/ncomms5094.

Buck, T. J., & Vidarsdottir, U. S. (2004). A proposed method for the identification of race in sub-adult skeletons: A geometric morphometric analysis of mandibular morphology. *Journal of Forensic Science*, 49(6), JFS2004074-JFS2004076.

Calce, S. E., Kurki, H. K., Weston, D. A., & Gould, L. (2018). The relationship of age, activity, and body size on osteoarthritis in weight-bearing skeletal regions. *International Journal of Paleopathology*, 22, 45–53. doi: 10.1016/j.ijpp.2018.04.001.

Cardini, A., & Elton, S. (2007). Sample size and sampling error in geometric morphometric studies of size and shape. *Zoomorphology*, 126(2), 121–134. doi: 10.1007/s00435-007-0036-2.

Cardini, A., Seetah, K., & Barker, G. (2015). How many specimens do I need? Sampling error in geometric morphometrics: Testing the sensitivity of means and variances in simple randomized selection experiments. *Zoomorphology*, 134(2), 149–163. doi: 10.1007/s00435-015-0253-z.

Chattah, N. L.-T., & Smith, P. (2006). Variation in occlusal dental wear of two Chalcolithic populations in the southern Levant. *American Journal of Physical Anthropology*, 130(4), 471–479. doi: 10.1002/ajpa.20388.

Cohen, M. N. (1989). *Health and the rise of civilization*. New Haven: Yale University Press.

Cunha, E., & Umbelino, C. (2001). Mesolithic people from Portugal: An approach to Sado osteological series. *Anthropologie*, 39(2/3), 125–132.

Currey, J. D. (2006). *Bones, structure and mechanics*. New Jersey: Princeton University Press.

Fedorov, A., Beicheli, R., Kalpathy-Cramer, J., Finet, J., Filion-Robin, J.-C., Pujol, S., ... Kikinis, R. (2012). 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging*, 30(9), 1323–1341. doi: 10.1016/j.mri.2012.05.001.

Filipe, V., Godinho, R. M., Granja, R., Ribeiro, A., & Valera, A. (2013). Bronze age funerary spaces in Outeiro Alto 2 (Brinches, Serpa, Portugal): The hypogea cemetery. *Zephyrus*, 71, 107–129.

Galland, M., Van Gerven, D. P., Von Cramon-Taubadel, N., & Pinhasi, R. (2016). 11,000 years of craniofacial and mandibular variation in Lower Nubia. *Scientific Reports*, 6, 31040. doi: 10.1038/srep31040. http://www.nature.com/articles/srep31040.

Godinho, R. M., Filton, L. C., Toró-Ibáche, V., Stringer, C. B., Lacruz, R. S., Bromage, T. G., & O’Higgins, P. (2018). The biting performance of *Homo sapiens* and *Homo heidelbergensis*. *Journal of Human Evolution*, 118, 56–71. doi: 10.1016/j.jhevol.2018.02.010.

Godinho, R. M., & Gonçalves, C. (2020). Antropologia Virtual: Novas metodologias para a análise morfológica e funcional. In J. M. Arnaud, C. Neves, & A. Martins (Eds.), *Actas do III Congresso da Associação dos Arqueólogos Portugueses* (pp. 311–323). Lisboa: Associação dos Arqueólogos Portugueses e CITCEM.

Godinho, R. M., Gonçalves, D., & Valera, A. C. (2019). The preburning condition of Chalcolithic cremated human remains from the Perdigões enclosures (Portugal). *International Journal of Osteoarchaeology*, 29(5), 706–717. doi: 10.1002/oa.2768.

Godinho, R. M., & O’Higgins, P. (2017). Virtual reconstruction of cranial remains: The *H. heidelbergensis*, Kabwe 1 fossil. In D. Errickson & T. Thompson (Eds.), *Human remains – Another dimension: The application of 3D imaging in funerary context* (pp. 135–147). London: Elsevier.

Godinho, R. M., & O’Higgins, P. (2018). The biomechanical significance of the frontal sinus in Kabwe 1 (*Homo heidelbergensis*). *Journal of Human Evolution*, 114, 141–153. doi: 10.1016/j.jhevol.2017.10.007.

Godinho, R. M., O’Higgins, P., & Gonçalves, C. (2020). Assessing the reliability of virtual reconstruction of mandibles. *American Journal of Physical Anthropology*, 172(4), 723–734. doi: 10.1002/ajpa.24095.

Godinho, R. M., Santos, A. L., & Valera, A. C. (2020). A lunate-triquetral coalition from a commingled funerary context from the Chalcolithic Perdigões ditched enclosures of Portugal. *Anthropologischer Anzeiger*, 77(1), 83–88. doi: 10.1127/anthranz/2019/0935.

Godinho, R. M., Spikins, P., & O’Higgins, P. (2018). Supraorbital morphology and social dynamics in human evolution. *Nature Ecology & Evolution*, 2(6), 956–961. doi: 10.1038/s41559-018-0528-0.

Gonçalves, C. (2009). *Modelos preditivos em SIG na localização de sitios arqueológicos de cronologia mesolítica no Vale do Tejo*. (Master thesis). Faro: Universidade De Algarve.

Gonçalves, C., Cascalheira, J., & Bicho, N. (2014). Shellmiddens as landmarks: Visibility studies on the Mesolithic of the Muge valley (Portugal). *Journal of Anthropological Archaeology*, 36, 130–139. doi: 10.1016/j.jaa.2014.09.011.

Griffin, R. C., & Donlon, D. (2009). Patterns in dental enamel hypoplasia by sex and age at death in two archaeological populations. *Archives of Oral Biology*, 54, S93–S100. doi: 10.1016/j.archoralb.2008.09.012.

Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G. W., & Bookstein, F. L. (2009). Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution*, 57(1), 48–62. doi: 10.1016/j.jhevol.2009.04.004.

Haak, W., Lazaridis, I., Patterson, N., Rohland, N., Mallick, S., Llamas, B., ... Reich, D. (2015). Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature*, 522(7555), 207–211. doi: 10.1038/nature14317.

He, T. L., & Killaridis, S. (2003). Effects of masticatory muscle function on craniofacial morphology in growing ferrets (Mustela putorius furo). *European Journal of Oral Sciences*, 111(6), 510–517. doi: 10.1111/j.0909-8836.2003.00080.x.
Henderson, C. (2013). Subsistence strategy changes: The evidence of ensetheal changes. HOMO, 64(6), 491–508. doi: 10.1016/j.homo.2013.08.002.

Holt, B. M. (2003). Mobility in Upper Paleolithic and Mesolithic Europe: Evidence from the lower limb. American Journal of Physical Anthropology, 122(3), 200–215. doi: 10.1002/ajpa.10256.

Jackes, M., & Lubell, D. (1999). Human biological variability in the Portuguese Mesolithic. Arqueologia, 24, 25–42.

Judek, S., Gross, T. S., & Zemnicke, R. F. (1997). Strain gradients correlate with sites of exercise-induced bone-forming surfaces in the adult skeleton. Journal of Bone and Mineral Research, 12(10), 1737–1745. doi: 10.1001/jbmr.1997.12.10.1737.

Judek, S., Lei, X., Han, D., & Rubin, C. (2007). Low-magnitude mechanical signals that stimulate bone formation in the ovariectomized rat are dependent on the applied frequency but not on the strain magnitude. Journal of Biomechanics, 40(6), 1333–1339. doi: 10.1016/j.jbiomech.2006.05.014.

Judek, S., & Rubin, C. T. (2010). Is bone formation induced by high-frequency mechanical signals modulated by muscle activity? Journal of Musculoskeletal & Neuronal Interactions, 10(1), 3–11.

Katz, D. C., Grote, M. N., & Weaver, T. D. (2017). Changes in human skull morphology across the agricultural transition are consistent with softer diets in preindustrial farming groups. Proceedings of the National Academy of Sciences. doi: 10.1073/pnas.1702586114.

Kiliaridis, S., Engstroem, C., & Thilander, B. (2011). The relationship between masticatory function and craniofacial morphology. A cephalometric longitudinal analysis in the growing rat fed a soft diet. European Journal of Orthodontics, 7(4), 273–283.

Klingenberg, C. P. (2011). MorphoJ: An integrated software package for geometric morphometrics. Molecular Ecology Resources, 11(2), 353–357. doi: 10.1111/j.1755-0998.2010.02924.x.

Lanyon, L. E. (1984). Functional strain as a determinant for bone remodeling. Calcified Tissue International, 36(1), 556–561. doi: 10.1007/bf02406134.

Lanyon, L. E., & Rubin, C. T. (1984). Static vs Dynamic Loads as an Influence on Bone Remodeling. Journal of Biomechanics, 17(12), 897–905. doi: 10.1016/0021-9290(84)90003-4.

Larsen, C. S. (1997). Bioarchaeology: Interpreting behavior from the human skeleton. Cambridge: Cambridge University Press.

Larsen, C. S. (2006). The agricultural revolution as environmental catastrophe: Implications for health and lifestyle in the Holocene. Quaternary International, 150(1), 12–20. doi: 10.1016/j.quaint.2006.01.004.

López-Onaíndia, D., Gibaja, J. F., & Subirá, M. E. (2019). Heirs of the Glacial Maximum: Dental morphology suggests Mesolithic human groups along the Iberian Peninsula shared the same biological origins. Archaeological and Anthropological Sciences, 11(10), 5499–5512. doi: 10.1007/s12520-019-00877-6.

Lukacs, J. R. (1989). Dental paleopathology: Methods for reconstructing health status and dietary patterns in prehistory. In M. Y. Içan & K. A. R. Kennedy (Eds.), Reconstructing Life from the Skeleton (pp. 261–286). New York: Alan R. Liss.

Macintosh, A. T., Pinhasi, R., & Stock, J. T. (2014). Lower limb skeletal biomechanics track long-term decline in mobility across ~6150 years of agriculture in Central Europe. Journal of Archaeological Science, 52, 376–390. doi: 10.1016/j.jas.2014.09.001.

Martins, H., Oms, F. X., Pereira, L., Pike, A. W., Rowseell, K., & Zilhão, J. (2015). Radiocarbon dating the beginning of the Neolithic in Iberia: New results, new problems. Journal of Mediterranean Archaeology, 28(1), 105–131.

May, H., Sellé-Tunis, T., Pokhojaev, A., Peled, N., & Sarig, R. (2018). Changes in mandible characteristics during the terminal Pleistocene to Holocene Levant and their association with dietary habits. Journal of Archaeological Science: Reports, 22, 413–419. doi: 10.1016/j.jasrep.2018.03.020.

Menegaz, R. A., & Ravosa, M. J. (2017). Ontogenetic and functional modularity in the rodent mandible. Zoology, 124, 61–72. doi: 10.1016/j.zool.2017.05.009.

Menegaz, R. A., Sublett, S. V., Figueroa, S. D., Hoffman, T. J., & Ravosa, M. J. (2009). Phenotypic Plasticity and Function of the Hard Palate in Growing Rabbits. The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology, 292(2), 277–284. doi: 10.1002/ar.20840.

Miguel, L., & Simão, P. (2017). Minimização de Impactes sobre o Património Cultural decorrentes da execução dos Blocos de Rega de Pias (Fase de Obra) – Relatório dos Trabalhos Arqueológicos Monte da Guarita 2(2017). Retrieved from Lisboa. https://biblioteca.edca.pt/BiblioNET/Upload/PDF5/M03608.pdf.

Mosley, J. R., & Lanyon, L. E. (1998). Strain rate as a controlling influence on adaptive modeling in response to dynamic loading of the ulna in growing male rats. Bone, 23(4), 313–318. doi: 10.1016/S8756-3282(98)00113-6.

Mosley, J. R., March, B. M., Lynch, J., & Lanyon, L. E. (1997). Strain magnitude related changes in whole bone architecture in growing rats. Bone, 20(3), 191–198. doi: 10.1016/S8756-3282(96)00385-7.

Mountier, A., Correia, M., Rivera, F., Crivellaro, F., Power, R., Jeffery, J., & Mirazón Lahr, M. (2018). Who were the Nataruk people? Mandibular morphology among late Pleistocene and early Holocene fisher-forager populations of West Turkana (Kenya). Journal of Human Evolution, 127, 235–253. doi: 10.1016/j.jhevol.2018.04.013.

Neezer, R., Ackermann, R. R., & Gain, J. (2009). Comparing the accuracy and precision of three techniques used for estimating missing landmarks when reconstructing fossil hominin crania. American Journal of Physical Anthropology, 140(1), 1–18. doi: 10.1002/aja.21023.

Nyström, K. C., & Malcom, C. M. (2010). Sex-specific phenotypic variability and social organization in the Chiribaya of Southern Peru. Latin American Antiquity, 21(4), 375–397. doi: 10.1163/1045-6635.21.4.375.

O’Higgins, P. (2000). The study of morphological variation in the hominin fossil record: Biology, landmarks and geometry. Journal of Anatomy, 197, 103–120. doi: 10.1046/j.1469-7580.2000.19710103.x.
O’Higgins, P., Fitton, L. C., & Godinho, R. M. (2019). Geometric morphometrics and finite elements analysis: Assessing the functional implications of differences in craniofacial form in the hominin fossil record. Journal of Archaeological Science, 101, 159–168. doi: 10.1016/j.jas.2017.09.011.

Oladle, I., Mallick, S., Patterson, N., Rohland, N., Villalba-Mouco, V., Silva, M., & Reich, D. (2019). The genomic history of the Iberian Peninsula over the past 8000 years. Science (New York, N.Y.), 363(6432), 1230. doi: 10.1126/science.aav4040.

Olalde, I., Schroeder, H., Sandoval-Velasco, M., Vinner, L., Lobón, I., Ramirez, O., & Lalueza-Fox, C. (2015). A Common genetic origin for early farmers from Mediterranean cardial and central European LBK Cultures. Molecular Biology and Evolution, 32(12), 3132–3142. doi: 10.1093/molbev/msv181.

Peyròt-Stjerna, R. (2020). Chronology of the burial activity of the last hunter-gatherers in the Southwestern Iberian Peninsula. Portugal. Radiocarbon, 63, 1–35. doi: 10.1017/RDC.2020.100.

Pokhojaev, A., Avni, H., Sella-Tunis, T., Sarig, R., & May, H. (2019). Changes in human mandibular shape during the Terminal Pleistocene-Holocene Levant. Scientific Reports, 9(1), 8799. doi: 10.1038/s41598-019-45279-9.

Ravosa, M. J., Kunwar, R., Stock, S. R., & Stack, M. S. (2007). Pushing the limit: Masticatory stress and adaptive plasticity in mammalian craniomandibular joints. Journal of Experimental Biology, 210(4), 628–641. doi: 10.1242/jeb.02683.

Ravosa, M. J., Lopez, E. K., Menegaz, R. A., Stock, S. R., Stack, M. S., & Hamrick, M. W. (2008a). Adaptive plasticity in the mammalian masticatory complex: You are what, and how, you eat. In C. Vinyard, M. J. Ravosa, & C. Wall (Eds.), Primate craniofacial function and biology (pp. 293–328). Boston: Springer US.

Ravosa, M. J., López, E. K., Menegaz, R. A., Stock, S. R., Stack, M. S., & Hamrick, M. W. (2008b). Using “Mighty Mouse” to understand masticatory plasticity: Myostatin-deficient mice and musculoskeletal function. Integrative and Comparative Biology, 48(3), 345–359. doi: 10.1093/icb/icn050.

Ruff, C. B., Holt, B., Niskanen, M., Sladek, K., Berner, M., Garofalo, E., & Whitley, E. (2015). Gradual decline in mobility with the adoption of food production in Europe. Proceedings of the National Academy of Sciences, 112(23), 7147.

Senck, S., Bookstein, F. L., Benazzi, S., Kastner, J., & Weber, G. W. (2015). Virtual reconstruction of modern and fossil Hominoid Crania: Consequences of reference sample choice. The Anatomical Record, 298(5), 827–841. doi: 10.1002/ar.23104.

Smith, B. H. (1984). Patterns of molar wear in hunter–gatherers and agriculturalists. American Journal of Physical Anthropology, 63(1), 39–56. doi: 10.1002/ajpa.1330630107.

Stock, J. T., & Pinhasi, R. (2011). Introduction: Changing paradigms in our understanding of the transition to agriculture: Human bioarchaeology, behaviour and adaptation. In Human bioarchaeology of the transition to agriculture (pp. 1–13). Chichester: John Wiley & Sons, Ltd. doi: 10.1002/9780470670170.ch1.

Stojanowski, C. M., & Schillaci, M. A. (2006). Phenotypic approaches for understanding patterns of intracemetery biological variation. Yearbook of Physical Anthropology, 53(43), 69–88. doi: 10.1002/ajpa.20517.

Turner, C. H. (1998). Three rules for bone adaptation to mechanical stimuli. Bone, 23(5), 399–407. doi: 10.1016/S8756-3282(98)00118-5.

Umbelino, C. (2006). Outros sabores do passado: As análises de oligoelementos e de isótopos estáveis na reconstituição da dieta das comunidades humanas do Mesolítico Final e do Neolítico Final-Calcolítico do território português. Coimbra: University of Coimbra.

Umbelino, C., Gonçalves, C., Figueiredo, O., Pereira, T., Cascalheiro, J., & Marreiros, J. (2015). Life in the Muge shell middens: Inferences from the new skeletons recovered from Cabeço da Amoreira. In N. Bicho, C. Detry, T. Price, & E. Cunha (Eds.), Muge 150th: The 150th anniversary of the discovery of Mesolithic Shellmiddens (Vol. 1, pp. 209–224). Cambridge: Cambridge Scholars Publishing.

Valera, A. C., Santos, H., Figueiredo, M., & Granja, R. (2014). Contextos funerários na periferia do Porto Torrão: Cardim 6 e Carrascal 2. In A. C. Santos, F. T. Regala, & M. Martinho (Eds.), 4 Colóquio de Arqueologia do Alqueva (pp. 83–95). Évora: EDIA/DRCALen.

Villalba-Mouco, V., de Loosdreicht, M. S., Posth, C., Mora, R., Martínez-Moreno, J., Rojo-Guerra, M., & Haak, W. (2019). Survival of Late Pleistocene Hunter-Gatherer Ancestry in the Iberian Peninsula. Current Biology, 29(7), 1169–1177.e1167. doi: 10.1016/j.cub.2019.02.006.

Villotte, S., Castex, D., Couallier, V., Dutour, O., Knüsel, C. J., & Henry-Gambier, D. (2010). Enthesopathies as occupational stress markers: Evidence from the upper limb. American Journal of Physical Anthropology, 142(2), 224–234. doi: 10.1002/ajpa.21217.

Villotte, S., Churchill, S. E., Dutour, O. J., & Henry-Gambier, D. (2010). Subsistence activities and the sexual division of labor in the European Upper Paleolithic and Mesolithic: Evidence from upper limb enthesopathies. Journal of Human Evolution, 59(1), 35–43. doi: 10.1016/j.jhevol.2010.02.001.

von Cramon-Taubadel, N. (2011). Global human mandibular variation reflects differences in agricultural and hunter-gatherer subsistence strategies. Proceedings of the National Academy of Sciences, 108(49), 19546–19551. doi: 10.1073/pnas.1103050108.

Zelditch, M. L., Swiderski, D. L., Sheets, H. D., & Fink, W. L. (2012). Geometric Morphometrics for biologists: A primer. New York: Elsevier.

Zilhão, J. (2000). From the Mesolithic to the Neolithic in the Iberian Peninsula. In T. Price (Ed.), Europe’s first farmers (pp. 144–182). Cambridge: Cambridge University Press.

Zilhão, J. (2001). Radiocarbon evidence for maritime pioneer colonization at the origins of farming in west Mediterranean Europe. Proceedings of the National Academy of Sciences, 98(24), 14180–14185. doi: 10.1073/pnas.241522898.
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 |
|------------|--------------|-------|
| From discriminant function | Chalcolithic (non-population specific) | Chalcolithic (population specific) | 11 |
| Chalcolithic (non-population specific) | 11 | 0 | 11 |
| Chalcolithic (population specific) | 2 | 9 | 11 |
| From cross-validation | Chalcolithic (non-population specific) | 5 | 6 | 11 |
| Chalcolithic (population specific) | 6 | 5 | 11 |

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 | Total |
|------------|--------------|-------|
| From discriminant function | Chalcolithic (non-population specific) | Mesolithic (non-population specific) | Total |
| Chalcolithic (non-population specific) | 11 | 0 | 11 |
| Mesolithic (non-population specific) | 0 | 26 | 26 |
| From cross-validation | Chalcolithic (non-population specific) | 8 | 3 | 11 |
| Mesolithic (non-population specific) | 2 | 24 | 26 |
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                                      |
|-----------------------------------|--------------------------------------------------|
|                                   | Chalcolithic (non-population specific) | Mesolithic (population specific) | Total |
| 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                                      |
|-----------------------------------|--------------------------------------------------|
|                                   | Chalcolithic (population specific) | Mesolithic (non-population specific) | Total |
| 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                                      |
|-----------------------------------|--------------------------------------------------|
|                                   | Chalcolithic (population specific) | Mesolithic (population specific) | Total |
| 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                                      |
|-----------------------------------|--------------------------------------------------|
|                                   | Mesolithic (non-population specific) | Mesolithic (population specific) | Total |
| 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.