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Non-metric dental analysis of human interactions around the Pyrenees during the Neolithic and their biological impact

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Abstract

Background: Interactions across the Pyreneans during the Middle-Neolithic (V-IV millennium BCE) have been described for a long time. Nevertheless, except for a few examples and attempts to describe it, the biological impact of these interactions on the human groups' make-up is not yet understood. The present work analyses the biological affinities of different groups from both sides of these mountains that represent the Populations of the Middle- and Late-Neolithic by means of the dental morphology.

Methods: We present novel dental morphological data of 221 individuals from 11 archaeological sites. These data have been analysed and compared to those from previously published 20 Iberian sites and one French site. Data were recovered following the ASUDAS protocol, and MMD biological measure was calculated between groups.

Results: Our results suggest that there were some differences between the analysed populations. These differences are observed at each side of the Pyrenees, but also across them. Concretely, the coastal groups across the mountains show more affinities between each other than the inland groups. In addition, the differences between groups decrease by the end of the Neolithic.

Conclusions: Therefore, our results indicate that the intense trade activities registered in the coastal area between both sides of the Pyrenees would have had the greatest biological impacts in the homogenisation of the groups. Although less intense, the across mountain network and coastal to mountain area trade networks to the south of Pyreneans, also influenced the biological make-up of the groups.

Key words: Exchange, dental morphology, biological affinities, Western Mediterranean, V-III millennium cal BCE

Introduction

Anatomical variations have been used to understand the biological impact of population interactions and migrations, to determine or to discriminate the geographic or biological origin of human populations, both ancient and modern, for a long time now (Howells, 1973; Berry, 1974; Milne et al., 1983; Rubini, 1996; Crubézy et al., 1999; Hanihara and Ishida, 2001a, 2001b, 2001c; Puişoru et al., 2006; Ricaut & Waelkens, 2008; Burnett et al., 2015). Concretely, in archaeological collections teeth are amongst the best-preserved osteological materials. This occurs mainly due to the hardness of the enamel, which is 96% mineral in composition (Simmer & Fincham, 1995; Nanci, 2008).

The study of dental morphology is based on the analysis of the phenotypic variation of teeth, by considering discrete traits such as cusps, tubercles, grooves and ridges from the crown and roots (Scott & Turner, 1997). These anatomical variations of teeth have increasingly been studied since the first quarter of the 20th century and applied to understand migration movements and origins of different human populations (Hrdlička, 1921; Gregory, 1922; Campbell, 1925; Shaw, 1931; Dahlberg, 1945, 1951; Pedersen, 1949). Since the 1990's a selection of traits identified by Turner and collaborators in their ASUDAS protocol (1991) has mainly been used to score variability in ancient populations of different periods and regions (Irish, 2006; Coppa et al. 2007; Desideri, 2011; Irish et al., 2017; López-Onaindia & Subirà, 2017; López-Onaindia et al., 2018, 2019). This protocol includes 36 standardised traits, chosen because of the lack of sexual dimorphism and because they are overall considered to be neutral to selection (Scott and Turner, 1997).

Although it has been determined that severe environmental stress during development might affect the expression of certain crown traits (Riga et al., 2014), the significant genetic inheritance in the expression of these discrete traits is consistent (Scott and Turner, 1997; Hlusko, 2016). This is further backed by the evidences that the heritability estimates for several traits in Australian twin studies are higher than 0.60 (Higgins, Hughes, James, & Townsend, 2009; Hughes & Townsend,

2011, 2013; Hughes, Townsend, & Bockmann, 2016), and in any case between 0.40-0.80 (Paul et al., 2020). Even, some syndromes characterised by strong genetic components show particular dental morphology manifestations that are inherited in the families (Skrinjaric et al., 2016). In addition, in recent years several studies have analysed the capability and reliability of dental non-metric traits for determining population dynamics and biological relationships between groups compared to genetic data. In this sense, the works by Hubbard and collaborators (2015) and Rathmann and Reyes-Centeno (2020) are worth mentioning. Comparing nine dental traits to 41 neutral nuclear STRs in several Kenyan populations, they were able to reconstruct a similar population history with both methods, thus validating the applicability of the dental traits as proxies for inferring biological distances between human populations (Hubbard et al., 2015). In addition, the work by Rathmann and Reyes-Centeno (2020) has confirmed this utility, but also remarked that there are certain sets of traits that are more useful and significant than other combinations. Nonetheless, although that as an analysis of population history this tool is reliable, it is not always as useful to predict ancestry at individual's level (Delgado et al., 2019).

The first Neolithic evidences in the Northwestern Mediterranean date from the middle of the 6th millennium cal BCE. The origin of these populations and the process known as Neolithisation has been debated throughout the last decades. These debates have been based on two different points of view for the interpretation of Neolithisation, the autoctonists and diffusionists, in the way to evaluate in combination the last Hunter-Gatherer communities from the Mesolithic and the first Farmers from the Neolithic (Vicent, 1997; Zilhao, 1997; Bernabeu, 2006; Binder & Perrin, 2014). Nevertheless, in the latest years, mixed proposals have also been suggested and encouraged by diverse data (Isern et al. 2014; Perrin et al. 2018). In the case of the Northeast of the Iberian Peninsula there is little information regarding the moment of transition, due to the relative scarceness of sites from the end of the 7th and beginnings of the 6th millennium cal BCE. This rare presence of remains might be related to a climatic cooling event around 8,200 BP and the abandonment of several territoires (Berger

& Guilaine, 2008; Morales & Oms, 2012), but further radiocarbon dating on Mesolithic materials must confirm this correlation.

Taking into account the archaeological data recovered to date, the Neolithisation in the Northwestern area of the Mediterranean can be linked to two events (García Martínez de Lagrán, 2015). The first of the events, after 5,800 cal BCE, is characterised by pottery with *Impressa-Ligur* style decoration (Bernabeu et al. 2011; Oms, 2014). These first Neolithic evidences are scarce, and related to an economy based on agriculture and livestock, dominated by herds of goats (*Capra hircus*) and emmer wheat (*Triticum disccocum*) crops. These archaeological sites are localised in zones near the Mediterranean sea; both in Southeast France, represented by the cases of Peito Signado and Pont de Roque-Haute (Briois & Manen, 2009; Guilaine et al., 2017), and in the East of the Iberian Peninsula with the sites of Guixeres de Vilobí and El Barranquet (Bernabéu et al., 2011; Oms et al., 2014).

The second event was related to the presence of Cardial decoration in the pottery, and is documented after 5,600-5,500 cal BCE (Guilaine et al., 2007; Oms et al., 2016). The sites that represent this moment are also found near the coastal and pre-coastal areas of the Northwest Mediterranean, and in isolated cases also in inland areas. At this time the economy was dominated by the culture of naked wheat (*Triticum aestivun/durum*) and barley (*Hordeum vulgare*), and by herds of ovicaprids (*Ovis* and *Capra*) (Saña, 2013), while the bovine and swine domestication was still of little importance.

The quantity of burials discovered in the Iberian Peninsula between the middle of the 6th and the middle of the 5th Millennium cal. BCE is fairly anecdotal (Bosch and Tarrús 1991; Blasco et al., 2005; Gonzalez et al. 2011; Oms et al. 2017). In the northeast of the peninsula, only around 10 sites with funerary structures of this period are known to date (García, 2007; García and Sesma, 2007; Pou

et al., 2010; López Quintana et al., 2015; Oms et al., 2016; 2017; Garcia-Sagastibeltza et al., 2020a; 2020b). Nevertheless, the situation changes if the focus moves towards the second half of the 5th Millennium cal BCE. It was then when a proliferation of funerary evidence becomes available, either in the form of necropolises or as isolated burials in different areas of Northwestern Mediterranean, and in the Northeast of the Peninsula (Martín 2009, Gibaja & Clop, 2012, Gibaja et al., 2016 a).

As regards to the funerary structures, between the end of the 5th and a long period during the 4th millennium cal BCE, two main burial groups can be identified in the Northeast of the Iberian Peninsula: burial pits dug in the soil, and sepulchres made of stone cists. The pit structures are usually found in areas near the coast, while the cysts are found in the inland and Pyreneans. These two groups equally exhibit certain variations concerning their morphology, size, and the employed constructive elements (Martín et al., 2016). At the same time, some of the burials were not made *ex profeso*, but by re-using different kinds of structures; we refer to the re-use of silos in which the wastes include one or several individuals or the re-use of mines as burial places, which is the case of the Prehistoric Mines of Can Tintorer/Gavà (Villalba, 1999; Bosch and Borrell, 2009). These kinds of funerary structures are also found in southern France from the beginning of the Middle Neolithic (Schmitt et al., 2017), which mainly comprises the Midi-Pyrénées, Languedoc and Provence-Alpes-Côte d'Azur areas.

Although there is some diversity on the funerary gestures, there are some common characteristics in both sides of the Pyreneans for the main defining structures of the mentioned cultures. In these "classic" structures, burials usually contain one or two individuals: either men, women, or child. Bodies were usually deposited in supine *de cubitus* with folded legs and arms in variable positions. Occasionally bodies are found fully stretched or in *lateral de cubitus*. Nevertheless, in both sides of the Pyreneans there were variations of these patterns. Certain graves exhibit bodies with no anatomical connection, or displaying only a partial connection, in unsual positions, as if they had

been thrown in the pit. Some graves contain multiple burials, where the bones from the primary burials were displaced towards the sides of the tomb or withdrawn from the tomb to make room for those buried later (Perrin et al., 2016; Alliès e et al., 2016; Martín et al., 2016; Schmitt & Michel, 2016; Gibaja et al., 2017; 2018; 2019).

Recent studies on funeral taphonomy have provided important information about certain aspects that help better understand these funerary behaviours. For example, today we know that these individuals were not simply deposited in the bottom of the funerary structure, but occasionally placed in the interior of the tomb within rigid boxes, probably wooden, or in bags (Alliès e et al., 2014).

During this period, there are evidences of exchange networks at different levels that connect both sides of the Pyrenees (Gibaja et al., 2016 b; Terradas et al., 2016). According to the evidence, these exchanges were stronger on an East-to-West direction than in the opposite sense (Gibaja et al., 2016 b; Terradas et al., 2016). In this context, researchers have found imported materials in the sepulchres from the Northeast of the Iberian Peninsula. Thes materials include Barrémo-Bédoulian Flint from Vaucluse (Provence) (Binder, 1998; Léa, 2004; Briois, 2005; Gassin et al., 2011; Gibaja et al., 2013), polished axes originated in the Alps (Léa, 2005; Vaquer et al., 2011; Pétrequin et al., 2012), and Obsidian blades and nuclei from Sardinia (Gibaja et al., 2013; Terradas et al., 2014). On the other hand, pieces made from Variscite exploited at Can Tintorer mines from Gava (Barcelona) appeared in Chasséen sites to the west of the Rhone (Terradas et al., 2016).

The relationship between these cultural changes with demographic changes and the biological composition of the involved populations has therefore been a subject of interest in different fields of physical anthropology (Schmitt, 2008; Alliès e, 2016; Le Luyer, 2016; Lopez-Onaindia and Subirà, 2017). In these latest years, the study of this subject from a paleogenetic perspective has added incredible amounts of information. From the first studies, focused on mitochondrial DNA (Hervella

et al., 2012; de la Rua et al., 2015; Szécsény-Nagi et al., 2017) to nuclear genome studies (Olalde et al., 2019; Villalba-Mouco et al., 2019; Rivollat et al., 2020), all of them indicate that the process was complicated and heterogeneous both geographically and diachronically. In this sense, it has been reported that the hunter-gatherer signal is preserved in the Neolithic group, but that the intensity of this signal varies amongst regions (Olalde et al., 2015, 2019; Szécsény-Nagi et al., 2017; Villalba-Mouco et al., 2019; Rivollat et al., 2020).

In addition, our previous results based on dental morphology suggest that there is a difference in the biological composition of the Neolithic groups from different regions of Northern Iberia (Subirà et al., 2016; López-Onaindia & Subirà, 2017; López-Onaindia et al., 2018). We have observed that these differences have both a microreographical (López-Onaindia et al., 2018) and cultural (López-Onaindia & Subirà, 2017; López-Onaindia et al., 2018) component. We specially were able to distinguish how the populations from the North East Ebro basin and the pre-pyrenean region differ from the coastal Mediterranean population in their biological composition (López-Onaindia & Subirà, 2017; López-Onaindia et al., 2018).

The aim of this work is to analyse the biological relationship amongst both Middle and Late Neolithic groups from both sides of the Pyreneans. This topic has scarcely been explored to date. In this work we aim to understand the effects on the populations of these geographic region of the demic migrations that affected the biological composition of the Iberian populations, the implications of the cultural similarities observed in both sides of the Pyreneans during the Neolithic and the effect of trade activities in the biological make up of these groups.

Materials and methods

This work presents novel data from 221 individuals and 3,977 human teeth from 11 southern French Neolithic and Chalcolithic sites (Table 1). In addition, these data have been used in combination to already published 20 Iberian sites and the French Les Crès site (255 individuals and their 3,661 teeth) (Schmitt, 2008; López-Onaindia & Subirà, 2017; López-Onaindia et al., 2018; Pascual et al., 2018; Subirà et al., 2016) (Supplementary Table S1). Thus, the whole corpus of this work includes dental morphological data from 31 Neolithic and Chalcolithic sites from the Northwest Mediterranean region (Figure 1).

The French samples belong both to the Middle- and Late-Neolithic, and almost the full extension (West-to-East) of the Southern part of the country. The Middle-Neolithic samples are grouped in three ensembles regarding their geographical and cultural characteristics: Middle-Neolithic from Languedoc-Midi Pyrénées; Middle-Neolithic from Provence-Alpes-Côte d'Azur; and Montbolò Neolithic (Supplementary Table S1).

The Middle-Neolithic from Languedoc-Midi Pyrénées is formed by the samples from, La Terrasse (La Vimona, Zac Agora), Narbons, Saint Gely-du-Fesc, et Le Crès. La Terrasse site is formed by hundreds of pits in the area of Tolouse, of which 20 were burials (Gandelin & Vaquer, 2008; Marlière et al. 2008). Narbons is located to the southeast of Montesquieu-de-Lauragais (Haute-Garonne) and provided six pit structures at the time of the archaeological intervention (Tchérémissinof et al., 2005). Four of these structures resulted to be sepulchres. Three are attributed to the Chasséen culture, and number 1020 is situated at the end of Middle Neolithic. The interventions in Saint Gely du Fesc were held in 1996 (Hérault), provided four burial pits in a concentrated area of less than $25m^2$, each of them containing a single individual (Schmitt et al., in press). Radiocarbon dates on each subject indicate that three belonged to the end of Middle Neolithic and one to the beginning of Middle Neolithic ("Néolithique moyen I" according to the French chronological system for the south of France). Le Crès site (Hérault) provided 190 negative structures, of which 31 were

burials that were excavated during 2000 and 2001 (Loison et al., 2004; Loison et Schmitt, 2009). 30 of these pits correspond to Chasséen burials and contained 49 individuals from this period. Moreover, compared to other sites this represented a wide variety of tomb typologies, from simple pits to proto-megalithic structures.

The Middle-Neolithic from Provence group includes the samples from Clos de Roque, Les Clavelles, Les Martins and Le Collet Redon. This last site is the sole collective burial of this group, located in La Couronne (Schmitt et al., 2018); the radiocarbon dates give a chronological interval situated between Middle and Late Neolithic. The burial provided a minimum number of 11 individuals in primary and secondary deposits. The tomb is installed in a quadrangular feature measuring 2.4 x 2.2 m. The walls of the pit are built with piled up stones. Les Martins is a site excavated in 1986 that produced two Middle-Neolithic burials (St. 6 and St. 8), consisting of individual burials in pits with a child and an adult male (d'Anna 1993; Van Willigen et al., 2014). In the case of Clos de Roque, 6 pits containing individual burials were discovered in 2011 (Remicourt et al., 2014; Schmitt et al., 2017 ; Olalde et al., 2018). From these six individuals, four belong to the beginning of the Middle-Neolithic (called "Néolithique moyen I" (St. 2209, 2215; 2205, 2224)).

Les Clavelles is an unpublished site. It provided a circular pit composed of two layers. 5 individuals were buried in this feature. An unpublished radiocarbon date on human bone indicates its belonging to the end of the 5th millennium cal BCE. The hypogeum of "les Crottes" was excavated in 1966. It is composed of 5 layers. Two of them are funerary collective deposits, level 2 and 5 (Courtin, 1974; Sauzade, 1983). The latest dates from the last quarter of the 4th millennium cal BCE.

The remains from the caves of Bélesta and Montou form the Montbolò group, in the Roussillon area. La Caune de Bélesta was excavated in 1983, when remains of a collective burial were identified together with many pieces of pottery (Claustre et al., 1993) that are attributed to the Montbolò culture.

Montou is located in Corbères-les-Cabanes (Eastern Pyrenees), and it represents a collective burial like Bélesta (Claustre & Ponsich, 2000; Valentin et al., 2003).

The last site analysed for the work is Grôtte Mykolas cave which was excavated in 2007 (Chancerel et al., 2007). This site is located to the North of Bugue (Aquitania) and its chronological affiliation corresponds to the Late-Neolithic age, the only French site from this period. According to the initial report an MNI of 9 individuals was calculated, but dental remains indicate that there were at least 12 inhumated individuals.

The analysis of the teeth was carried out following the Arizona State University's Dental Anthropology System (ASUDAS) (Turner et al. 1991) for scoring 35 non-metric dental traits. In individuals with full dentition, these 35 traits provide 121 variables for individual. Most traits are not just present or absent, but ranked in a scale of expression, and the level at which they are represented in each of the antimers of an individual may vary. For this reason, the antimere showing the highest level of expression, which is believed to be the one representing the trait's maximum potential for the individual and be genetically more reliable, is selected in each individual (Turner, 1985; Turner et al., 1991).

In order to identify correlations between traits, Kendall's Tau-b analysis was done on the ranked data (Irish, 2010) with IBM SPSS 20.00. A correlation was considered strong when the Tau-b value is superior to 0.5, and for it to be statistically significant we considered that the N must be >10 and the p value <0.05. This step is necessary to edit the database before calculating the biological distances, as one of the traits of the correlated pair was eliminated in order to avoid differential weighting of the underlying dimensions that might yield erroneous results (Sjøvold, 1977; Irish, 2010).

The ranked ASUDAS values were later dichotomised into presence or absence values, based on their reported morphological thresholds (Nichols, 1989) and according to standard procedure (Turner, 1985; 1987). From these dichotomised data, frequencies for the expression of traits were calculated for the different samples and groups.

Together with one of each pair of correlated traits, those traits that presented no frequency differences in the various samples were excluded from further analysis, because they were non-informative. The Mean Measure of Divergence (MMD) (Smith, 1972) was calculated between samples as an among-samples phenetic dissimilarity measure. The formula used to calculate the MMD contains Freeman and Tukey's angular transformation to correct for low or high trait frequencies and small sample sizes (Harris & Sjøvold, 2004). Nevertheless, each trait used must have been scored at least 10 times (including present and absent) in each sample. In order to determine if two samples are significantly different, the MMD has to be compared to its standard deviation (SD). Therefore, if MMD>2xSD, the null hypothesis of P1=P2 is rejected at the 0.025 level. In some cases, when the internal variability of a sample resulted greater to that between the two samples compared negative MMD values might result. These values are statistical artefacts, and therefore, they were set to 0 (Vargiu et al., 2009; Irish, 2010).

The matrices obtained with the MMD calculation were graphically represented in Multi-Dimensional Scaling (MDS) (Kruskal & Wish, 1978) using PAST software (Hammer et al. 2001). This representation is useful to obtain further information beyond if two samples are significantly different or not. The representations offer a stress value that indicates the accuracy with which the matrix has been represented. Usually, stress values <0.10 are considered excellent, while ≥0.15 are unacceptable (Borgatti, 1997). Moreover, Principal Component Analysis (PCA) were carried out based on the same traits used to calculate the MMD. These analyses usually provide complementary

information on which traits are more involved in the distribution observed on the MDS representations.

Due to the different conservation state and sample size of the collections included in this work, it was necessary to carry out a series of different analyses including different variables and samples at each of them to maximise the information. Two different sets of MMD calculations were carried out: one that included all the French and Iberian samples except for the Montbolò group, and was based on 10 traits. The other excluded some more French and Iberian samples, but included Italian samples (Coppa et al., 2007) in order to get a broader context on the relationships observed with the previous analysis.

The Montbolò samples were especially small, and after trait editing to avoid the non-informative and correlated variables, very few variables could be included in MMD calculation. For this reason, this group was compared with Fisher's exact test to the Iberian and French samples, for all those traits scoring more than 5 observations, to see which groups present less differences with it.

Results

The number of times a trait was scored in each group, the frequency for the presence of the traits and dichotomic breaking-point for each of them are shown in Table 2.

Some traits provided significant correlation values when analysed with Kendal's Tau-b. These traits were: *UM2 cusp5* was correlated to *UP4 m&d cusps* (Tau-b=0.716, N=25) and *UM3 cusp5* (Tau-b=0.642, N=19); on the other hand *UM1 Metacone* and *UM3 Carabelli's tubercle* were also correlated (Tau-b= 0.725, N=12).

The MMD analysis based on 10 variables that included both French and Iberian samples (Table 3), showed a complex scenario with significant differences among samples from each side of the Pyrenees, while there are no differences between some of the samples across the mountains. Those samples presenting significant differences at the 0.025 level are the Languedoc-Midi Pyrenees group and the Late Neolithic Mediterranean groups (Roaix, Cova del Pantà de Foix and Can Sadurní). On the other hand, those samples that presented no differences with any other sample were the Middle-Neolithic sample from Provence and Grôtte Mykolas.

When this matrix was represented (Figure 2) we obtained a MDS plot that provided a grouping of samples to the right end of the horizontal axis where two sites from the Iberian Peninsula with pit burials were registered (Los Cascajos, Early- and Middle-Neolithic from Navarre, and Bòbila Madurell) and a Chalcolithic cave from the Mediterranean coast of the same area (Cova del Pantà de Foix). On the other extreme we observe the Middle-Neolithic sample from Languedoc and Midi-Pyrénées area, and the rest of the samples appear in the centre between them. Therefore, the biggest differences are observed between Middle-Neolithic samples from both sides of the Pyreneans.

The PCA analysis for the same traits provides a similar representation to the MDS with the two first components (83.5% of the total variance explained): the Languedoc/Midi-Pyrénées sample was the most divergent from the rest, which was determined by higher frequencies of *LM1 cusp6* and *LM2 cusp 7* (Table 4). On the opposite side the Middle-Neolithic samples from Provence, Bòbila Madurell and Cascajos together with Cova del Pantà de Foix were characterised for having high frequencies for *LP4 cusp number* and relatively high presences of *Hypocone* in both UM1 and UM2.

When we excluded the smallest samples from the analysis (Grôtte Mykolas, Middle-Neolithic from Provence, and Cova del Pantà de Foix) and compared the other samples to Italian samples using 8 traits we obtained the matrix shown in Table 5. With the distance data, we observed that Italian

samples significantly differed from all Iberian and French samples. In the same sense, the French and Iberian samples differed between each other too. Nevertheless, these distance values were smaller than those any of both groups presented compared to the Italians.

The MDS representation of this matrix (Figure 3) shows the Italian Upper-Palaeolithic and Mesolithic sample appeared separated from all the other samples and the Italian Neolithic sample stands in the centre of the plot, while in the other corner French and Iberian samples appeared separated between them as well. From the Iberian and French samples those showing more affinities to the Italian Neolithic were Cascajos (Early- and Middle-Neolithic from Navarre), Bòbila Madurell (Middle-Neolithic from Catalonia) and Roaix (Late-Neolithic from Provence), while the Langedoc and Solsonian samples appeared farther.

When correlations between the main components in the PCA analysis and the variables were analysed (Table 6), we observed that the Italian groups present *UM2 cusp5* and *UM1 Carabelli's tubercle* in higher frequencies than Iberian and French groups, while the latter had overall more presence of *UI2 shovelling*, this differentiation occurs in the first component. The second component split the French and Iberian samples, although not in the same manner as the MDS. We observe the Languedoc and Solsonian Middle-Neolithic groups on one side and the other groups (Middle- and Late-Neolithic samples) on the other corner. In this sense, the most significant trait was the presence of *multiple lingual cusps in LP4*, which was most common in Late-Neolithic samples and the Middle-Neolithic samples of Bòbila Madurell and Los Cascajos.

The Montbolò sample did not show differences for most of the 18 analysed traits with the rest of samples when this was analysed by Fisher's exact test (Table 7). Moreover, when Bonferroni's correction was applied to the significance level ($p<0.0002777$), this sample only differed significantly in one trait from Los Cascajos sample: *LM1 Cusp5*.

Discussion

Although there are many cultural similarities between the two main Middle-Neolithic cultures from Catalonia and Mediterranean France (Sepulcres de Fossa Culture and Chasséen), our results indicate that in the biological background of the defined human groups there is some variance. This variance, thought, is not a simple divergence between French and Iberian samples. As it has previously been mentioned, many studies support a dual dispersion model for the Neolithic in the Northeastern area from the Mediterranean (Guilaine, 2003; Cruz-Berrocal, 2013).

In their recent work, Molist and collaborators (2016) analyse different material evidence between the Chasséen and the Sepulcres de Fossa cultures. This study suggests that although the affinities and the common elements between both cultures, each of them has singular elements related to the previous background in the territories. Nevertheless, they do also observe that the similarities between the two groups are greater than that each of them has with any other surrounding area. Moreover, both share common characteristics that can be interpreted as heritage from the Montbolò and Molinot cultures that spread through the eastern Pyrenees. Finally, as it has previously been mentioned, according to many evidence pieces, the exchange networks between these groups at both sides of the Pyrenees were strongly rooted (Gibaja et al., 2013; Terradas et al., 2014; 2016; Molist et al., 2016;).

Ancient DNA (aDNA) analyses of the region show that although there is an important new genetic composant in the Neolithic individuals from Southwestern Europe, there is a persistence of the Hunter-Gatherer component too (Villalba-Mouco et al., 2019; Brunel et al., 2020; Rivollat et al., 2020; Seguin-Orlando et al., 2021). Focusing in the Neolithic individuals from the Iberian Peninsula different studies show complex scenarios: while in some cases the Neolithic samples have signals similar to those from Eastern Mediterranean and LBK culture (Olalde et al., 2015), other studies show mixed signals in the different areas of the Iberian Peninsula (de la Rúa et al., 2015; Szécsény-Nagy

et al., 2017). Therefore, a mixed model would be the most accurate one explaining the current evidences. In this sense, some of our previous results evidence slight biological differences amongst some Iberian samples (López-Onaindia & Subirà, 2017; López-Onaindia et al., 2018). These works, in the same way as aDNA works remark, show that in the Northeast of the Iberian Peninsula there was biological variability during the Neolithic. These differences are observed sometimes related to funerary practices (López-Onaindia & Subirà, 2017), where the individuals buried in Megaliths significantly diverged from the rest of groups. Moreover, and still related to a different funerary structure represented by stone cists burials, we observed differences between mountain and coastal groups in the east of the Peninsula (López-Onaindia et al., 2018). In addition, a first exploration of the relationship between Iberian Hunter Gatherers and first farmers analysing dental morphology suggested that there were some affinities between them, suggesting a certain degree of continuity (López-Onaindia et al., 2019).

The present results show that, overall, those groups from coastal areas or valleys near the coast present differences with fewer groups than non-coastal samples. These differences of the inland groups are present at each side of the Pyreneans and between sides. Exchanges of materials and therefore potential population movements and mixtures are well recorded for the Neolithic in western Europe. The presence of raw materials like the Barrémo-Bédoulian flint (honey flint) from Vaucluse (Provence, France) in cist-like and pit burials from Northeastern Iberia and Southern France (Binder, 1998; Léa, 2004; Briois, 2005; Gibaja et al., 2010; Gassin et al., 2011); the presence of polished axes originated in the Alps in Iberian sites (Léa, 2005; Vaquer et al., 2011; Pétrequin et al., 2012); and the evidence of the trade of variscite from Gavà to the Rhone's valley (Terradas et al., 2016) are good examples for this trans-pyrenean trade. This trade seems especially intense throughout the coast compared to more mountainous regions (Terradas et al., 2011), which is further supported by the discovery of obsidian from Sardinia in some Catalan sites (Gibaja et al., 2013; Terradas et al., 2014). If we assume a more intense coastal trading, the populations from these regions would be exposed to

a more diverse biological background than those from inner land. In contrast, the sample from Los Cascajos, although it is inland, shows affinities similar to those from the Catalonian coastal samples, separating from the Pyrenean samples. In this case, aDNA analyses have shown that Los Cascajos is a sample with high genetic variability and would not be an isolated group (Hervella et al., 2016). Los Cascajos is situated in the Ebro basin, where there was an intense exchange network that intensely ran Northwest to Southeast and *vice versa* following the river, from inland to the Mediterranean coast (Cava et al., 2008; Baldellou et al., 2011; Montes and Alday, 2011; Tarriño and Terradas, 2013). This network was more intense than the trades documented between coastal valley and mountainous areas in the Catalan region (Villalba et al., 1986; Bosch and Borrel, 2009).

Although the following interpretations should be taken cautiously due to the lack of interobserver error test between our samples and the Italian data (Coppa et al., 2007), all French and Iberian samples significantly diverge from the Italian groups. However, these differences are smaller with the Neolithic than with the Hunter-Gatherer sample. Concretely, the Languedoc-Midi Pyrenees and Solsonian samples (inland) are the most divergent from the Italian Neolithic one, while Bòbila Madurell (Vallès area) and Los Cascajos present slighter differences with it. Hence, it is plausible that some of the migration from the East that arrived into French and Iberian territory with the spread of the agriculture had the same substrate as the Italian. Nevertheless, this seems to have been less intense than that observed in the Italian Peninsula (Coppa et al., 2007). Furthermore, the Italian Palaeolithic-Mesolithic sample diverges significantly from the Iberian one when dental morphology is analysed (López-Onaindia et al., 2019), which would result in different previous biologic backgrounds in each area.

Finally, it must also be mentioned that in those two Middle-Neolithic groups that diverge most from the rest, Solsonian area and Languedoc-Midi Pyrenees, there are representations of burials done in stone slab cists, while in the other studied areas these are not present. In the case of the Late-

Neolithic, these samples are also diverse, but show similar affinities with most Middle-Neolithic samples. This trend has previously been observed in our works, as groups get uniform between them towards the Bronze Age (López-Onaindia & Subirà, 2017; López-Onaindia et al., 2018). This trend towards the uniformity of the biological make-up of the population by the end of the Neolithic is also observed in the genetic studies (Szécsény-Nagy et al., 2017; Olalde et al., 2019; Villalba-Mouco et al., 2019). These studies also show that the Hunter-Gatherer component becomes more important at this period.

In summary, our results are compatible with a dual pattern model for the dispersion of the Neolithic in the Northwest of the Mediterranean, although the impact of incoming eastern farmers would not be as important as in other areas of the Mediterranean. In addition, we observe that this effect is similar in the Iberian Peninsula and South of France, and that the affinities that are observed in material culture between the Chasséen and Sepulcres de Fossa cultures have a parallel in biological means. Lastly, the similarities between inhabitants from coastal areas are greater, as probably these were more open to external influences related to exchange networks; moreover, the inner groups also present some variation in funerary culture with the presence of burials in cists.

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