RETRIEVING FAMILY DYNAMICS THROUGH PALAEOGENETIC AND ISOTOPIC ANALYSIS

A JOINT PROPOSAL FOR THE STUDY OF THE LAST HUNTER-GATHERERS AND EARLY FARMERS' DAILY LIVES

HUGO H. HERNÁNDEZ Universidad del País Vasco, Facultad de Letras, Departamento de Geografía, Prehistoria y Arqueología, hugo.hernandez@ehu.eus
IZASKUN SARASKETA-GARTZIA Universidad del País Vasco, Facultad de Letras, Departamento de Geografía, Prehistoria y Arqueología, izaskun.sarasketa@ehu.eus

RESUMEN La Prehistoria reciente viene marcada desde sus inicios por cambios medioambientales, pero también en el modo de vida de los seres humanos, lo que se refleja en las nuevas formas económicas y culturales. Por ello, el estudio bioarqueológico de los restos humanos resulta de gran importancia, jugando un importante papel la paleogenética de poblaciones y autosómica, así como la bioquímica isotópica, que pueden resolver, en gran medida, incógnitas en el seno del discurso prehistórico. El presente artículo tratará de reflejar esta realidad metodológica a través de casos neolíticos europeos, donde las analíticas mencionadas han dado resultados satisfactorios, y proponer su aplicación en yacimientos del noroeste de la Península Ibérica. Un enfoque integrado de estos métodos revelará aspectos de gran interés, como puedan ser patrones diferenciales entre poblaciones mesolíticas y neolíticas. Realzamos la importancia del estudio de los yacimientos mesolíticos para poder llevar a cabo una comparativa estadísticamente válida respecto a los datos obtenidos de entornos neolíticos y aportar nueva información sobre el tránsito a la economía de producción, enunciando las limitaciones propias del registro arqueológico para poblaciones cazadoras-recolectoras finales.

PALABRAS CLAVE Transición Mesolítico-Neolítico, ADN antiguo, análisis isotópicos, paleodietas, patrones de movilidad

ABSTRACT Recent Prehistory is characterized not only by a combination of changes in palaeoenvironmental terms, but also in the daily life of humans, reflected in new economic and cultural habits. Therefore, bioarchaeological studies of human remains play an important role in archaeology. Within this field, population palaeogenetics, autosomal DNA and isotopic biochemistry analyses can answer several questions in the prehistoric speech. Our present article attempts to reflect this reality through methodological cases from Neolithic European sites, where these analytics have been performed with satisfactory results. We also propose their application in various sites in the Iberian Peninsula. An integrated approach of these methods reveals some issues of interest (demographics and daily life), as differential patterns among Mesolithic and Neolithic populations in a diachronic reconstruction. We claim the study of the Mesolithic sites in order to conduct a statistically valid comparative regarding the larger number of Neolithic evidences, with the aim to provide new data about the transition economies to food production, despite the limitations of the archaeological record of the last hunter-gatherer communities.

KEYWORDS Mesolithic-Neolithic transition, ancient DNA, isotopes analysis, paleodietary, mobility patters

INTRODUCTION: FUNERARY CONTEXTS IN TRANSITION (13,000-5,000 CAL BP)

During the Mesolithic-Neolithic transition in the north of the Iberian Peninsula, we face climatic and human cultural changes, within the end of Pleistocene and the rising of the Holocene (Aura *et al.*, 1998). The climatology became warmer, and new plant and animal species supplanted the previously ones, adapted to cold weather (Scott *et al.*, 2007). Hunter-gatherer human populations probably became more sedentary and technical improvements related to food production, new social practices and demographic events expanded across Iberia (Alday *et al.*, 2012; Fernández-Eraso *et al.*, 2015).
Funerary contexts allow us to retrieve ancient family dynamics. However, not all are clear enough to draw good conclusions. Focusing on northern Iberia, burial variability grows in Neolithic contexts, mainly due to the

beginning of the megalithic phenomenon (Arias, 2007). In contrast, Mesolithic human remains are generally scarce and isolated (Iriarte-Chiapusso *et al.*, 2005). Certain funerary contexts are massive, with chaotic disposals of the buried corps, which do not allow conclusions in our regard; a good example may be the Late Neolithic collective burial of San Juan Ante Portam Latinam (Laguardia, Basque Country) (Vegas and Armendariz, 1999). However, such sites enable other detailed bioarchaeological research, including studies on physical anthropology, related to violence in Prehistory, or population genetic studies (Izagirre and De-la-Rúa, 1999).

MATERIALS AND METHODOLOGY

INTRODUCING THE METHODOLOGY OF PALAEOGENETICS

The current methodologies of ancient DNA (aDNA) have been applied to prehistoric contexts with an increasing rate of success (Hofreiter *et al.*, 2001; Deguilloux *et al.*, 2012), with two main research lines; on one hand, the archaeological remains of domesticated species could retrieve the genealogy of plants and animals lineages (Glémin and Bataillon, 2009; Larson *et al.*, 2014). On the other hand, the study of human aDNA can let us know about aspects like human lactase persistence, skin/hair pigmentation, incidence of diseases, etc., in the case of the autosomal or non-sexual DNA (Olalde *et al.*, 2014). By contrast, uniparental or sexual aDNA, from the mitochondria within human cells for female lineages and Y-chromosome aDNA for male lineages, can inform us about several issues related to population movements throughout the biological history of women and men (Soares *et al.*, 2010).

Among conventional methodologies of aDNA replication, Polymerase Chain Reaction (PCR) and Restriction Fragment Polymorphism (RFPLS) discriminates Single-Nucleotid Polymorphism or SNPs in both male and female aDNA (De-la-Rúa and Hervella, 2013). These cumulative polymorphisms define several DNA haplotypes, who grouped are called mitochondrial and Y-chromosome human haplogroups. They show affinities or differences among demographic groups from a human DNA reference sequence (CRS) and several developed human molecular clocks (Soares *et al.*, 2010). Recent methodological improvements known as New Generation Sequencing (NGS) are performed to sequence the whole genome from the sample and discriminate aDNA and potential contaminations (Pinhasi *et al.*, 2012).

From mitochondrial data, easier to obtain through this methodology, we can concrete several human cladistic groups (Haak *et al.*, 2010; Soares *et al.*, 2010; Brandt *et al.*, 2013; Hernández, 2015). In the case of neolithisation process, we can simplify into four relevant groups of population:

- Cladistic Group 1 (CG1): haplogroups of hunter-gatherer populations. The most important haplogroup of European hunter-gatherers are the variations of haplogroup U*.
- Cladistic Group 2 (CG2): haplogroups of early farmer populations. They changed the european genetic pool, with the introduction of various haplogroups mostly derived from Near East (N*, T*, K*, J*, HV*, W*, X*).
- Other cladistic groups. We can include there the postneolithic populations (CG3, probably from other migration events, like I*) or several unaffiliated haplogroups (CG4), like the halogroup H, the most numerous today, or V*.

INTRODUCING THE METHODOLOGY OF ISOTOPIC ANALYSES

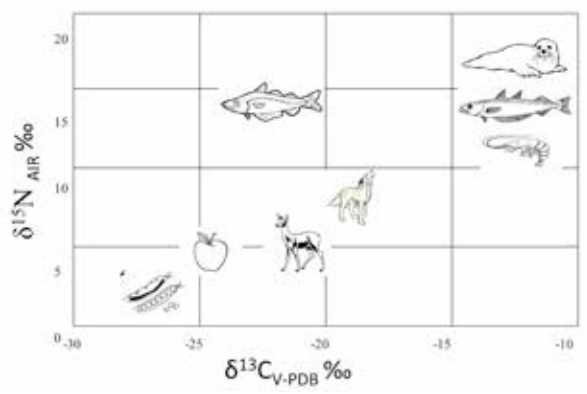
Since the decade of 1980, we have new lines of investigation to obtain information about the paleodietary and mobility patterns. In this text, we will focus on isotopes of carbon and nitrogen for the study of paleodietary patterns and on sulphur and strontium isotopes for the mobility patterns. Thanks to these studies, we have the chance to know details about the analysed groups: if they were local or not, the access to the food and, linked with it, the presence of hierarchies, the possible *women market*, etc.

CARBON AND NITROGEN

The study of carbon isotopes ($\delta^{13}C$, which shows the difference between C12 and C13) allows us to know the relative weight of the protein dependent on their origin: terrestrial, fluvial or marine, and of plants C3 and C4 (Salazar-García, 2009).

In the case of nitrogen ($\delta^{15}N$), values are related to the complexity of the trophic chain of the organism consumed by the studied individual. For example, organisms of marine ecosystems are much complex than the terrestrial ones, and that is the reason why they have higher values (Sarasketa-Gartzia, 2015).

We can obtain a lot of information about the dietary habits relating both nitrogen and carbon values (figure 1). However, the vegetal proteins are usually masked by the higher animal protein values (Richards *et al.*, 2003). If the analysed individual is a child, the nitrogen values could be higher, owing to the intake of the mother's

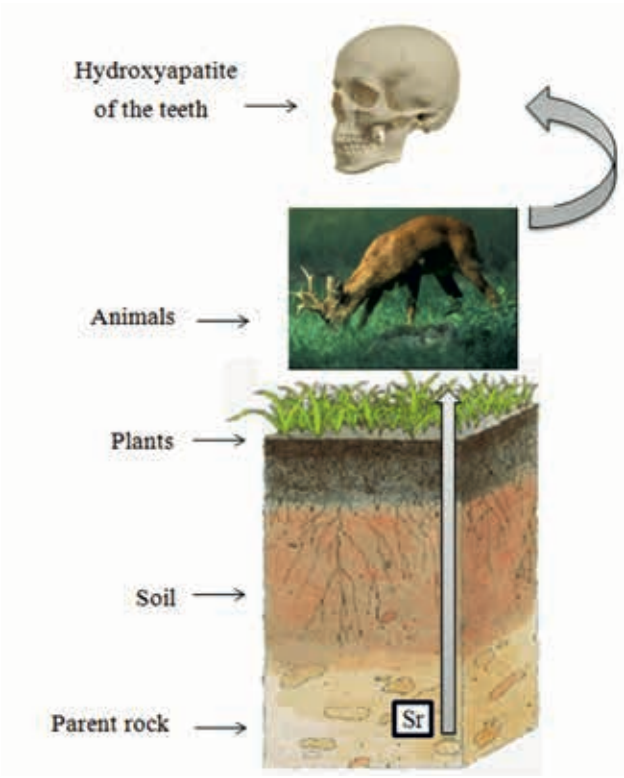


1. Graphic with the different food patterns dependent on the nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) values. The right side of the graphic would corresponds to C4 sources and the left side to C3, with variable data of nitrogen.

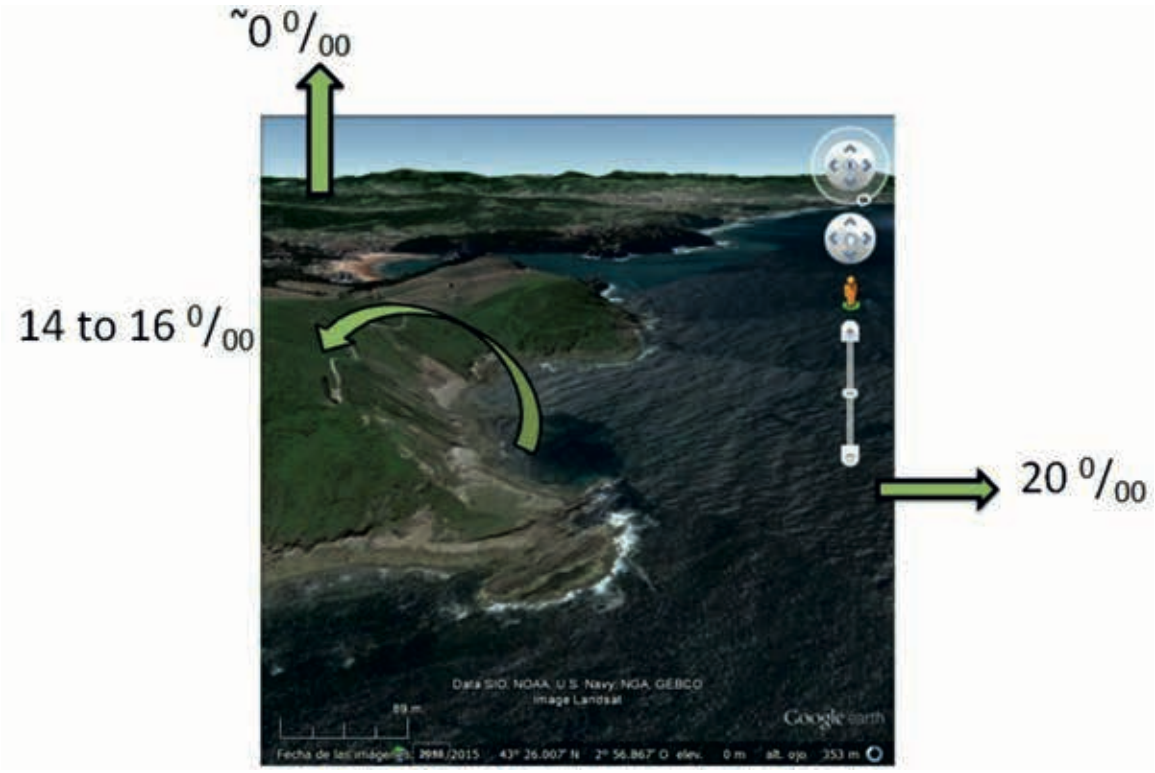
nitrogen values during the lactation. Additionally, it is important to remark, that the results of stable isotopes refer only to consumption of the last 10-15 years of the individual (Meiklejohn, 2009).
The study of carbon, nitrogen and sulphur isotopes requires the same process (Salazar-García *et al.*, 2014). The bone samples of 300-500 mg have to be cleaned, before obtaining the collagen following Richards and Hedges (1999) with an additional ultrafiltration step (Brown *et al.*, 1988). After that, the solution is frozen and lyophilized before being weighed into tin capsules and finally loaded into the mass spectrometer (Salazar-García *et al.*, 2014).

SULPHUR AND STRONTIUM

The values of sulphur increase according to the distance between the organism analysed and the marine coast, because of the sea-spray effect (figure 2) (Nehlich *et al.*, 2010). Moreover, it is very important to analyse archaeological fauna remains too, especially if we have to interpret results in complex ecosystems as estuaries (Richards *et al.*, 2001).
The strontium ($^{87}Sr/^{86}Sr$) analyses are based on the isotopic proportions of different geological zones: each geological zone has a concrete value, because radioactive strontium isotope (Sr^{87}) derives from the decomposition of the rubidium (Rb^{87}) and, because of that, it depends on the antiquity of rocks. The most ancient rocks have the highest values, between 0.700 and 0.750 (Bentley, 2006). The strontium values present on the rocks pass through the trophic change by the lithosphere, and then to the plants, the animals and, finally, to the human body tissues (figure 3). In the archaeological study, we use the values of the teeth enamel, in order to relate it with the period of its formation.



3. Graphic with the movement of $\delta^{87}Sr$ through the parent rock to the humans enamel.



2. $\delta^{34}S$ values in different geographical zones.

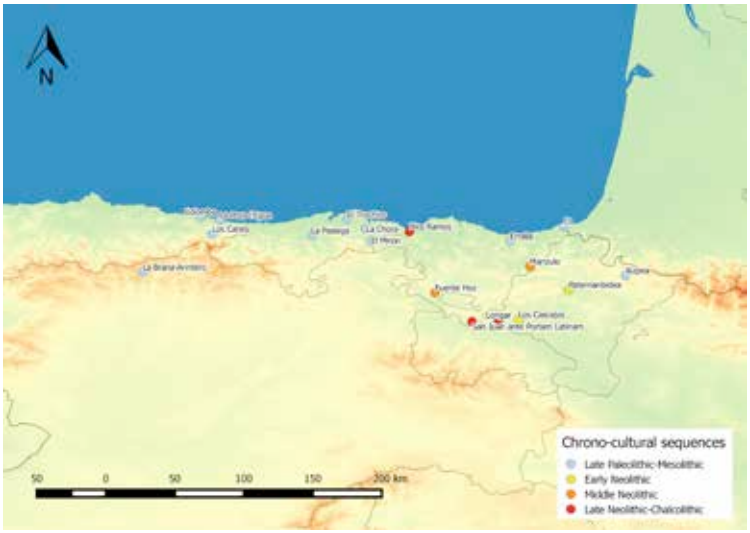
SAMPLE: ARCHAEOLOGICAL SITES IN WESTERN PYRENEES AND CANTABRIAN COAST

Stable isotopes and palaeogenetics research in the selected area and chronology are performed in the following archaeological sites, shown in the map (figure 4). Research actions in both methodological areas are not correlated:

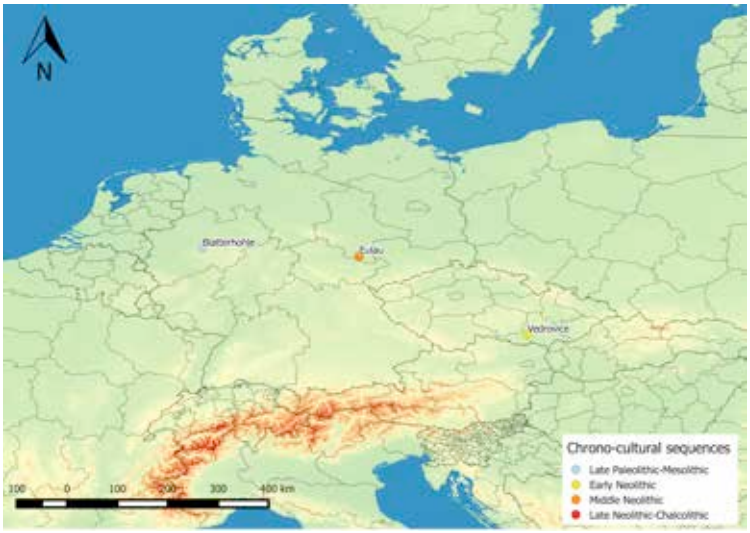
- Stable isotopes studies are more frequent in Mesolithic (n=10) and Neolithic individuals (n=4) (Arias, 2005). Its dispersal is more centralized in the Cantabrian Coast.
- Palaeogenetic studies (Izagirre and De-la-Rúa, 1999; Hervella *et al*., 2012; De-la-Rúa *et al*., 2015) are more frequent in Neolithic sites, with numerous individuals analysed (n=153). Its dispersal is more centralized in Western Pyrenees and the Upper Ebro Valley. There are several analysed individuals from Late Palaeolithic and Mesolithic chronologies (n=7), across the Cantabrian fringe.
- Only two archaeological sites (La Braña-Arintero and Marizulo) have researches in both methodologies (Arias, 2005; Arias and Schulting, 2010; Hervella *et al*., 2012; Sánchez-Quinto *et al*., 2012; Olalde *et al*., 2014). However, the low number of analysed individuals (n=3), unable us to draw relevant conclusions.

In order to emphasize the contribution of a joint palaeogenetic-isotopic methodology, several examples from other European areas have been selected (figure 5). They share Mesolithic-Neolithic chronologies, and they have large samples that enable researchers to identify several social and familiar patterns:

- Blatterhöle (Hagen, Nordrhein-Westfalen, Germany) is a cave and archaeological site with Mesolithic (11,200-10,500 cal BP) and Late Neolithic (5,950-4,850 cal BP) occupations (Bollongino *et al*., 2013). Burials of both populations are in the same location. This site brings a prolonged occupation, emphasizing the transition and interactions between hunter-gatherers and Neolithic groups.
- Vedrovice (Hungary) is a LBK burial context (Bramanti, 2008; Zvelebil and Pettitt, 2008). Its human occupation is dated in Early Neolithic (7,300-6,900 cal BP). This site provides very valuable information about the early spread of agriculture in Central Europe. Isotopes and



4. Map of Western Pyrenees and Cantabrian coast of Iberia, showing archaeological sites with stable isotopes and palaeogenetic researchs performed.



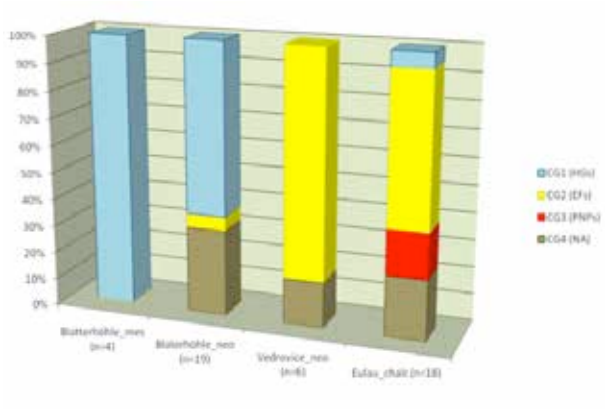
5. Location of selected methodological cases (Blatterhöhle, Vedrovice, Eulau).

palaeogenetic data from Vedrovice can test hypothesis about the neolithisation process through the study of Neolithic migratory events from Near East and the first contacts between this intrusive populations and the Late Mesolithic regional societies (Divišová, 2012).
- Eulau (Saxony-Anhalt, Germany) is an archaeological site dated in Late Neolithic and Chalcolithic times (4,850--3950 cal BP), concerning Corded Ware and Bell Beaker cultures. Despite its late chronology, its importance lies in direct child-parent patterns detected among individuals buried together, with the oldest molecular evidence of a nuclear family ever. Different isotopes and palaeogenetic results show an exogamous and patrilocal society (Haak *et al.*, 2008; Brandt *et al.*, 2013).

RESULTS AND DISCUSSION

METHODOLOGICAL CASES

In the case of Blatterhöhle (Nordrhein-Westfalen, Germany), the results concerning the ancient DNA are based in matrilineal lineages. Twenty-three individuals provided valid results (Bollongino *et al.*, 2013). Mesolithic results (n=4) offers homogeneity in the gene pool of hunter-gatherer populations (Haak *et al.*, 2015). However, Late Neolithic individuals analysed (n=19) revealed genetic continuity with Mesolithic lineages up to 60% (figure 6). These evidences have suggested a model of "parallel societies" during all Neolithic period, but the lack of information for Early Neolithic populations in the cave would be related to different economic or social practices, perhaps associated to population origins (Haak *et al.*, 2010).
By contrast, Vedrovice (Hungary) results are scarce, with only six individuals showing valid mitochondrial results (Bramanti, 2008) (figure 6). They draw a genetic discontinuity between them and the potential western hunter-gatherer genetic pool, with high values for haplogroups associated to early European farmers (Soares *et al.*, 2010). However, due to the reduced sample, it would be explained by different burial practices among human groups (Deguilloux *et al.*, 2012).
In the case of Eulau (Saxony-Anhalt, Germany), palaeogenetic valid results are performed for nineteen individuals (Corded Ware, n=16; Bell-Beaker, n=3) for maternal lineages and three individuals for paternal lineages (Corded Ware) (Haak *et al.*, 2008; Brandt *et al.*, 2013). Results show a high incidence of populations not associated with first Neolithic events (figure 6). However, both hunter-gatherer and early farmer genetic pools are present in Eulau samples. Also, Y-chromosome results (n=3) draw the possibility of a patrilocal society, as shown in other simultaneous archaeological sites as well as Les Treilles (southern France) or Cova de l'Avellaner (Catalogne, Spain) (Lacan *et al.*, 2011a, 2011b). The particularity of Eulau lies in the demonstrated relationship between individuals from the same grave. This is the case of Eulau grave 99, where female and children shared the same mitochondrial haplogroup (K*). Among males, they shared the same Y-chromosome haplogroup too (R1a).
If we focus on isotopic analysis, there are also differences

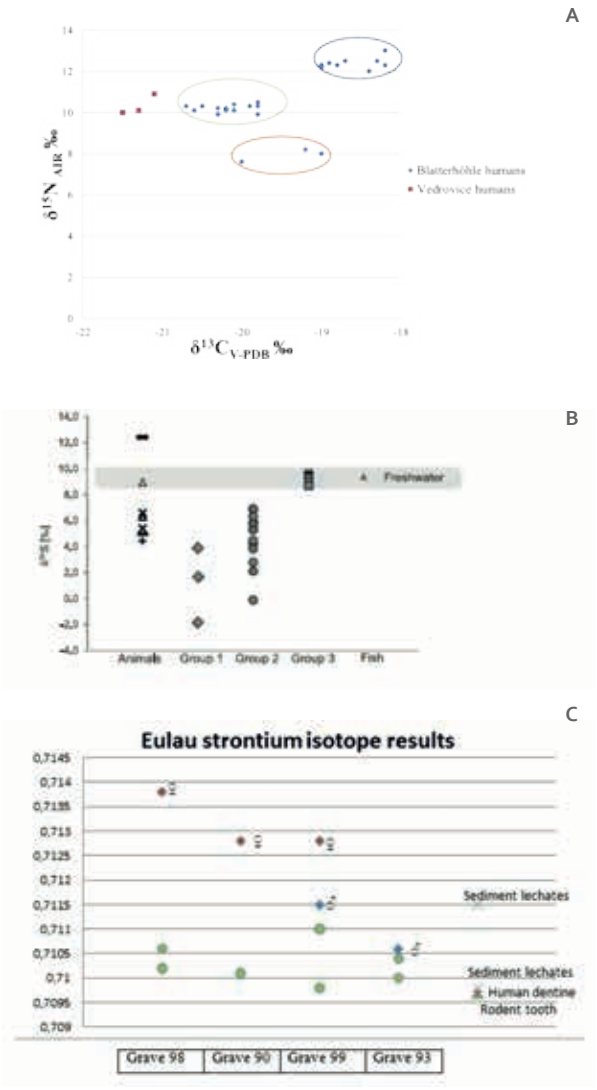


6. aDNA results for Blatterhöhle, Vedrovice and Eulau individuals.

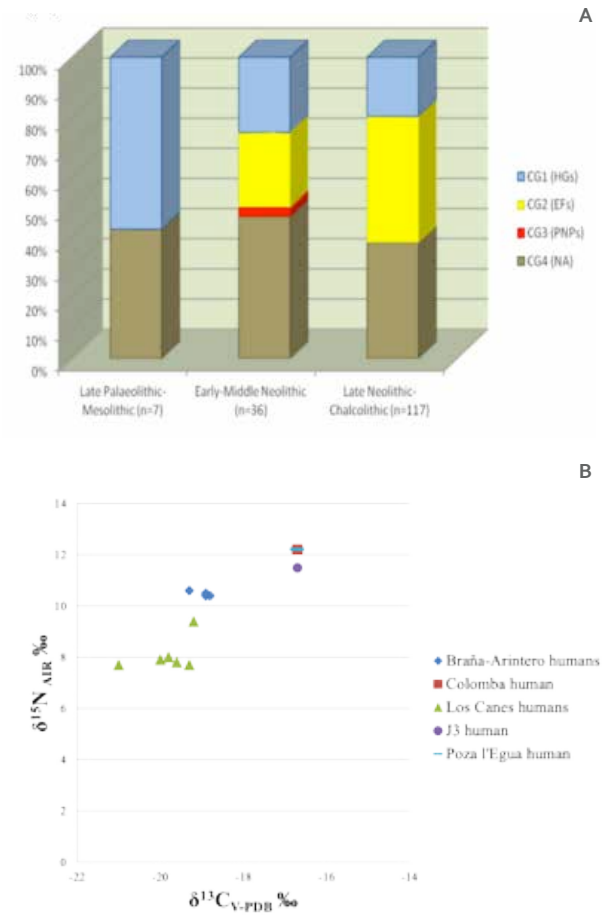
between the three cases. First of all, in Blatterhöhle (n=24) we can differentiate three groups. The first one (n=9), with high values of $\delta^{15}N$, clearly shows a main consumption of marine resources. Secondly, an important amount of analysed individuals (n=12) have a high consumption of herbivorous. The last group (n=3) has lower nitrogen values, emphasizing the consumption of wild fauna (Bollongino *et al.*, 2013). Sulphur isotopes data shows that the Neolithic hunter-gatherers, with higher values of sulphur, are well distinguished comparing with the other two groups.
Secondly, in Vedrovice site, sulphur results (n=50) show that most of humans spent their childhood and adulthood near or at Vedrovice, with the exception of eight individuals with different strontium and sulphur values. Consumption of vegetables is almost restricted to adult females, while both old males and females had access to meat, which could be some kind of *dietary status* (Divišová, 2012; Zvelebil and Pettitt, 2013). On the other hand, nitrogen results show a relative homogeneous diet, what means that the dietary protein was derived mainly form animal sources, with the exception of one infant (related to breastfeeding) (Zvelebil and Pettitt, 2013).
Finally, in the case of Eulau, we only have strontium isotopes results; values of children (green circles) form a homogeneous group around 0.7103 (figure 7), consequent with the local ratio. In contrast, the females (in red) have higher values of strontium, indicating that they spent their first years of their lives in other region and, afterwards, they moved to the location of males (in blue), which were more local.

WHAT WE HAVE IN WESTERN PYRENEES AND THE CANTABRIAN COAST, IBERIA?

In the selected area, palaeogenetic results are numerous (n=160), spread over thirteen archaeological sites from Upper Palaeolithic to Early Eneolithic (15,000-4,850 cal BP). Unified results show consistent patterns for hunter-gatherer and early farmers maternal lineages (figure 8a). It would reproduce the central European situation (Haak *et al.*, 2005; Haak *et al.*, 2010; Bramanti *et al.*, 2009; Brandt *et al.*, 2013), but the high value for unaffiliated mitochondrial haplogroups is an important regional difference (Hervella *et al.*, 2012).



7. Isotopes results for (A) Blatterhöhle (adapted from Bollongino *et al.*, 2013) and Vedrovice (adapted from Divisovà, 2012) stable isotopes results; (B) Blatterhöle sulphur results (from Bollongino *et al.*, 2013) and (C) Eulau strontium results (adapted from Haak et al. 2008).



8. aDNA and stable isotopes analyses performed in Western Pyrenees and Cantabrian coast archaeological sites.

Isotope analyses for the Mesolithic and Neolithic periods are, unfortunately, limited (n=14), principally because of the reduced number of human remains in the analysed zone (especially during the Mesolithic), and the scarce researches in this line. However, we can observe an increment in the consumption of marine resources during Mesolithic times, while in the Neolithic this trend changes, becoming terrestrial sources the main feed (figure 8b).

Archaeological sites in Western Pyrenees with combined isotopes and palaeogenetics results are scarce (La Braña-Arintero and Marizulo, figure 4) (Arias, 2005; Arias and Schulting, 2010; Hervella *et al.*, 2012; Sánchez-Quinto *et al.*, 2012; Olalde *et al.*, 2014). La Braña-Arintero (León, Spain), is a Mesolithic burial context with two individuals analysed. Both samples show correlative mitochondrial aDNA results with other Mesolithic remains across Europe (Haak *et al.*, 2015). They belong to the cladistic group of western hunter-gatherers (U5b). The isotope analysis, on the other hand, show a diet based mainly in terrestrial resources, probably with an important ingest of herbivorous animals, and probably with a punctual consumption of aquatic foods, as the nitrogen value is slightly higher than 10°/$_{oo}$ (figure 8b) (Arias and Schulting, 2010).

By contrast, Marizulo (Gipuzkoa, Basque Country), an archaeological Late Neolithic site, displays an individual who, despite his clear Neolithic affiliation, shows genetically patterns close to hunter-gatherers (U5) Thus, this individual shows a gene flow between hunter-gatherer and early farmers in Western Pyrenees. We have a carbon value near -20%$_{o}$ which corresponds to a typical terrestrial dietary pattern (Arias, 2005). However, this carbon value is provided from the fractionation control of the radiocarbon analysis, and because of that we can only use this data as guidance.

CONCLUSIONS AND PERSPECTIVES

Through all these examples, we would like to reflect that the joint methodology of stable isotopes and palaeogenetic studies are capable to shed light to several prehistoric research fields, as well as:

(1) Familiar and social relationships: bioarchaeological research can be able of provide explanation about the origin of family members, or define a prehistoric society as exogamous, patrilocal, etc.

(2) Neolithisation process: these methodologies can assess migratory events and human admixtures in the past, and the different history of men and women.

(3) Daily life of prehistoric individuals, across palaeodiets, degree of genetic lactase persistence, etc.
We want to emphasize the need of continuity of human bioarchaeological research, in order to extend the isotope and ancient DNA databases with the study of new burial contexts and a proper collaboration among different areas of study concerning the prehistoric settlement. In this line, there are now some researches, as few doctoral theses in project (I. Sarasketa-Gartzia, A. Higuero, A. Villalba-Mouco, etc.) with the aim to analyse prehistoric human remains with isotopes; and, even more, some recent papers which content both aDNA and isotopes analysis (Alt *et al*., 2016; Esparza *et al*., in press).

ACKNOWLEDGEMENTS

H. H. Hernández benefits from a postgraduate grant from the University of the Basque Country (UPV/EHU). I. Sarasketa-Gartzia benefits from a postgraduate grant from the Basque Government. They have partially funded by the research projects of Spanish Science Ministry HAR2014-53536-P (*La ruta occidental del poblamiento de la Península Ibérica durante el Paleolítico medio y superior),* as well as the Research Team in Prehistory of UPV/EHU (IT-622-13). We would like to thank the organizers of VIIIth JIA (Lisbon-2015), specially the coordinators of *Traditional Session 6 Microarchaeology: tracking the hidden archaeological record through multidisciplinary analysis*.

BIBLIOGRAPHY

ALDAY, A.; CARRETERO, J.; ANDERUNG, C.; GÖTHERSTRÖM, A. (2012) – Uros, Genética, Indígenas y Colonos. A propósito de la neolitización de Europa. *Veleia,* 29, p. 335-358.

ALT, K.; ZESCH, S.; GARRIDO-PENA, R.; KNIPPER, C.; SZÉCSÉNYI-NAGY, A.; ROTH, C.; TEJEDOR-RODRÍGUEZ, C.; HELD. P.; GARCÍA-MARTÍNEZ-DE-LAGRÁN, Í.; NAVITAINUCK, D.; ARCUSA, H.; ROJO-GUERRA, M. (2016) – A Community in Life and Death: The Late Neolithic Megalith Tomb at Alto de Reinoso (Burgos, Spain). *PLoS ONE,* 11: 1, e0146176.

ARIAS, P. (2005) – Determinaciones de isótopos estables en restos humanos de la región Cantábrica. Aportación al estudio de la dieta de las poblaciones del Mesolítico y Neolítico. *Munibe,* 57, p. 359-374.

ARIAS, P. (2007) – La muerte en la Prehistoria. Introducción al comportamiento funerario en el territorio de Navarra desde el Mesolítico a la Edad del Bronce (VII-II milenio a.C.). In HURTADO, M., coord., *La tierra te sea leve: arqueología de la muerte en Navarra.* Pamplona: Gobierno de Navarra, Departamento de Cultura y Turismo, Institución Príncipe de Viana, p. 29-41.

ARIAS, P.; SCHULTING, R. (2010) – Análisis de isótopos estables sobre los restos humanos de la Braña-Arintero. Aproximación a la dieta de los grupos mesolíticos de la cordillera cantábrica. In VIDAL, J.; PRADA, M., coords., *Los Hombres Mesolíticos de la cueva La Braña-Arintero (Valdelugueros, León).* León: Diputación de León, p. 130-137.

AURA, J.; VILLAVERDE, V.; GONZÁLEZ, M.; GONZÁLEZ, C.; ZILHÃO, J.; STRAUS, L. (1998) – The Pleistocene-Holocene transition in the Iberian Peninsula: continuity and change in human adaptations. *Quaternary International,* 49/50, p. 87-103.

BENTLEY, R. (2006) – Strontium isotopes from the Earth to the Archaeological Skeleton: A Review. *Journal of Archaeological Method and Theory*, 13, p. 135-187.

BOLLONGINO, R.; NEHLICH, O.; RICHARDS, M.; ORSCHIEDT, J.; THOMAS, M.; SELL, C.; FAJKOŠOVÁ, Z.; POWELL, A.; BURGER, J. (2013) – 2000 Years of Parallel Societies in Stone Age Central Europe. *Science,* 342, p. 479-481.

BRAMANTI, B. (2008) – Ancient DNA: genetic analysis of aDNA from sixteen skeletons of the Vedrovice collection. *Anthropologie,* XLVI: 2-3, p. 153-160.

BRAMANTI, B.; THOMAS, M.; HAAK, W.; UNTERLAENDER, M.; JORES, P.; TAMBETS, K.; ANTANAITIS-JACOBS, I.; HAIDLE, M.; JANKAUSKAS, R.; KIND, C.J.; LUETH, F.; TERBERGER, T.; HILLER, J.; MATSUMURA, S.; FORSTER, P.; BURGER, J. (2009) – Genetic discontinuity between local hunter-gatherers and Central Europe's first farmers. *Science,* 326, p. 137-140.

BRANDT, G.; HAAK, W.; ADLER, C.; ROTH, C.; SZÉCSÉNYI-NAGY, A.; KARIMNIA, S.; MÖLLER-RIEKER, S.; MELLER, H.; GANSLMEIER, R.; FRIEDERICH, S.; DRESELY, V.; NICKLISCH, N.; PICKRELL, J.; SIROCKO, F.; REICH, D.; COOPER, A.; ALT, K.; THE GENOGRAPHIC CONSORTIUM (2013) – Ancient DNA Reveals Key Stages in the Formation of Central European Mitochondrial Genetic Diversity. *Science,* 342, p. 257-261.

BROWN, T.; NELSON, D.; VOGEL, J.; SOUTHON, J. (1988) – Improved collagen extraction by modified Longin method. *Radiocarbon,* 30, p. 171-177.

DE-LA-RÚA, C.; HERVELLA, M. (2013) – Paleogenética humana. In GARCÍA-DÍEZ, M.; ZAPATA, L., eds, *Métodos y Técnicas de Análisis y Estudio en Arqueología Prehistórica.* Leioa: Universidad del País Vasco, p. 427-439.

DE-LA-RÚA, C.; IZAGIRRE, N.; ALONSO, S.; HERVELLA, M. (2015) – Ancient DNA in the Cantabrian fringe populations: a mtDNA study from Prehistory to Late Antiquity. *Quaternary International,* 364, p. 306-311.

DEGUILLOUX, M.-F.; LEAHY, R.; PEMONGE, M.-H.; ROTTIER, S. (2012) – European Neolithization and Ancient DNA: An Assessment. *Evolutionary Anthropology,* 21, p. 24-37.

DIVIŠOVÁ, M. (2012) – Current Knowledge of the Neolithisation Process: a Central European Perspective. *Interdisciplinaria Archaeologica,* III: 1, p. 141-153.

ESPARZA, A.; PALOMO, S.; VELASCO, J.; DELIBES, G.; ARROYO, E.; SALAZAR-GARCÍA, D. (in press) – Familiar Kinship? Palaeogenetic and isotopic evidence from a triple burial of the Cogotas I archaeological culture (Bronze Age, Iberian Peninsula). *Oxford Journal of Archaeology*.

FERNÁNDEZ-ERASO, J.; MUJIKA-ALUSTIZA, J.; ZAPATA-PEÑA, L.; IRIARTE-CHIAPUSSO, M.; POLO-DÍAZ, A.; CASTAÑOS, P.; TARRIÑO-VINAGRE, A.; CARDOSO, S.; SESMA-SESMA, J.; CARCÍA-GAZOLAZ, J. (2015) – Beginnings, settlement and consolidation of the production economy in the Basque region. *Quaternary International,* 364, p. 162-171.

GLÉMIN, S.; BATAILLON, T. (2009) – A comparative view of the evolution of grasses under domestication. *New Phytologist,* 183, p. 273-290.

HAAK, W.; BALANOVSKY, O.; SÁNCHEZ, J.; KOSHEL, S.; ZAPOROZHCHENKO, V.; ADLER, C.; DER SARKISSIAN, C.; BRANDT, G.; SCHWARZ, C.; NICKLISCH, N.; DRESELY, V.; FRITSCH, B.; BALANOVSKA, E. (2010) – Ancient DNA from European Early Neolithic Farmers Reveals Their Near Eastern Affinities. *PLoS Biology,* 8: 11, e1000536.

HAAK, W.; BRANDT, G.; DE JONG, H.; MEYER, C.; GANSLMEI-

ER, R.; HEYD, V.; HAWKESWORTH, C.; PIKE, A.; MELLER, H.; ALT, K. (2008) – Ancient DNA, Strontium isotopes, and osteological analyses shed light on social and kinship organization of the Later Stone Age. *PNAS,* 105: 47, p. 18226-18231.

HAAK, W.; FORSTER, M.; BRAMANTI, B.; MATSUMURA, S.; BRANDT, G.; TÄNZER, M; VILLEMS, R.; RENFREW, C.; GRONENBORN, D.; ALT, K.; BURGER, J. (2005) – Ancient DNA from the first European farmers in 7500-year-old Neolithic sites. *Science,* 310, p. 1016-1018.

HAAK, W.; LAZARIDIS, I.; PATTERSON, N.; ROHLAND, N.; MALLICK, S.; LLAMAS, B.; BRANDT, G.; NORDENFELT, S.; HARNEY, E.; STEWARDSON, K.; FU, Q.; MITTNIK, A.; BÁNFFY, E.; ECONOMOU, C.; FRANCKEN, M.; DIEDERICH, S.; GARRRIDO PENA, R.; HALLGREN, F.; KHARTANOVICH, V.; KHOKHLOV, A.; KUNST, M.; KUZNETSOV, P.; MELLER, H.; MOCHALOV, O.; MOISEYEV, V. (2015) – Massive migration from the steppe was a source for Indo-European languages in Europe. *Nature,* 522, p. 207-211.

HERNÁNDEZ, H. (2015) – ¿Reemplazo demográfico en el Neolítico europeo? El punto de vista de la Genética. *CKQ,* 5, p. 111-140.

HERVELLA, M.; IZAGIRRE, N.; ALONSO, S.; FREGEL, R.; ALONSO, A.; CABRERA, V.; DE-LA-RÚA, C. (2012) – Ancient DNA from Hunter-Gatherer and Farmer Groups from Northern Spain Supports a Random Dispersion Model for the Neolithic Expansion into Europe. *PLoS ONE,* 7: 4, e34417.

HOFREITER, M.; SERRE, D.; POINAR, H.; KUCH, M.; PÄÄBO, S. (2001) – Ancient DNA. *Nature Reviews. Genetics,* 2, p. 353-359.

IRIARTE-CHIAPUSSO, M.; ARRIZABALAGA, A.; ETXEBARRÍA, F.; HERRASTI, L. (2005) – La inhumación humana en conchero de J3 (Hondarribia, Gipuzkoa). In ARIAS, P.; ONTAÑÓN, R.; GARCÍA-MONCÓ, C., eds, *Actas del III Congreso del Neolítico en la Península Ibérica.* Santander: Universidad de Cantabria, p. 607-614.

IZAGIRRE, N.; DE-LA-RÚA, C. (1999) – An mtDNA Analysis in Ancient Basque Populations: Implications for Haplogroup V as a Marker for Major Paleolithic Expansion from Southwestern Europe. *The American Journal of Human Genetics*, 65: 1, p. 199-207.

LACAN, M.; KEYSER, C.; RICAUT, F.-X.; BRUCATO, N.; DURANTHON, F.; GUILAINE, J.; CRUBÉZY, E.; LUDES, B. (2011a) – Ancient DNA reveals male diffusion through the Neolithic Mediterranean route. *PNAS,* 108: 24, p. 9788-9791.

LACAN, M.; KEYSER, C.; RICAUT, F.-X.; BRUCATO, N.; TARRÚS, J.; BOSCH, A.; GUILAINE, J.; CRUBÉZY, E.; LUDES, B. (2011b) – Ancient DNA suggest the leading role played by men in the Neolithic dissemination. *PNAS,* 108: 45, p. 18255-18259.

LARSON, G.; PIPERNO, D.; ALLABY, R.; PURUGGANAN, M.; ANDERSSON, L.; ARROYO-KALIN, M.; BARTON, L.; CLIMER VIGUEIRA, C.; DENHAM, T.; DOBNEY, K.; DOUST, A.; GEPTS, P.; GILBERT, M.; GREMILLION, K.; LUCAS, L.; LUKENS, L.; MARSHALL, F.; OLSEN, K.; PIRES, J.; RICHERSON, P.; RUBIO DE CASAS, R.; SANJUR, O.; HOMAS, M.; FULLER, D. (2014) – Current perspectives and the future of domestication studies. *PNAS,* 111: 17, p. 6139-6146.

MEIKLEJOHN, C. (2009) – Radiocarbon dating of Mesolithic human remains in Spain. *Mesolithic Miscellany,* 2: 2, p. 2-20.

NEHLICH, O.; BORIC, D.; STEFANOVIC, S.; RICHARDS, M. (2010) – Sulphur isotope evidence for freshwater fish consumption: a case study from the Danube Gorges, SE Europe. *Journal of Archaeological Science,* 37, p. 1131-1139.

OLALDE, I.; ALLENTOFT, M.; SÁNCHEZ-QUINTO, F.; SANTPERE, G.; CHIANG, C.; DEGIORGIO, M.; PRADO-MARTÍNEZ, J.; RODRÍGUEZ, J.; RASMUSSEN, S.; QUILEZ, J.; RAMÍREZ, O.; MARIGORTA, U.; FERNÁNDEZ-CALLEJO, M.; PRADA, M.; VIDAL, J.; NIELSEN, R.; NETEA, M.; NOVEMBRE, J.; STURM, R.; SABETI, P.; MARQUÈS-BONET, T.; NAVARRO, A.; WILLERSLEV, E.; LALUEZA-FOX, C. (2014) – Derived immune and ancestral pigmentation alleles in a 7,000-year-old Mesolithic European. *Nature,* 507, p. 225-228.

PINHASI, R.; THOMAS, M.; HOFREITER, M.; CURRAT, M.; BURGER, J. (2012) – The genetic history of Europeans. *Trends in Genetics,* 10, p. 496-505.

RICHARDS, M., DOUGLAS PRICE, T.; KOCH, E. (2003) – Mesolithic and Neolithic subsistence in Denmark: New isotope data. *Current Anthropology*, 44: 2, p. 288-295.

RICHARDS, M.; FULLER, B.; HEDGES, R. (2001) – Sulphur isotopic variation in ancient bone collagen from Europe: implications for human palaeodiet, residence mobility, and modern pollutant studies. *Earth and Planetary Science Letters*, 191, p. 185-190.

RICHARDS, M.; HEDGES, R. (1999) – Stable isotope evidence for similarities in the types of marine foods used by Late Mesolithic humans at sites along the Atlantic coast of Europe. *Journal of Archaeological Science*, 26, p. 717-722.

SÁNCHEZ-QUINTO, F.; SCHROEDER, H.; RAMÍREZ, O.; ÁVILA-ARCOS, M.; PYBUS, M.; OLALDE, I.; VELAZQUEZ, A.; PRADA, M.; VIDAL, J.; BERTRANPETIT, J.; ORLANDO, L.; GILBERT, M.; LALUEZA-FOX, C. (2012) – Genomic Affinities of Two 7,000-Year-Old Iberian Hunter-Gatherers. *Current Biology,* 22, p. 1494-1499.

SALAZAR-GARCÍA, D. (2009) – Estudio de la dieta en la población neolítica de Costamar. Resultados preliminares de análisis de isótopos estables de carbono y nitrógeno. In FLORS, E., coord, *Monografíes de Prehistòria i Arqueologia Castellonenque, 8: Torre la Sal (Ribera de Cabanes, Castellón), evolución del paisaje antrópico desde la prehistoria hasta el Medievo.* Castelló: Servei d'investigacions arquèologiques i prehistòriques, p. 411-418.

SALAZAR-GARCÍA, D.; EMILI, J.; OLÀRIA, C.; TALAMO, S.; MORALES, J.; RICHARDS, M. (2014) – Isotope evidence for the use of marine resources in the Eastern Iberian Mesolithic. *Journal of Archaeological Science*, 42, p. 231-240.

SARASKETA-GARTZIA, I. (2015) – La aplicación de los isótopos estables en la reconstrucción de paleodietas. In SÁEZ DE LA FUENTE, I.; TEJERIZO, C.; GONZÁLEZ, L.; HERNÁNDEZ, B.; HERNANDO, C., coords, *Arqueologías sociales. Arqueología en Sociedad. Actas de las VII Jornadas de Jóvenes en Investigación Arqueológica*. Vitoria-Gasteiz: Arkeogazte, p. 310-317.

SOARES, P.; ACHILLI, A.; SEMINO, O.; DAVIES, W.; MACAULAY, V.; BANDELT, H.-J.; TORRONI, A.; RICHARDS, M. (2010) – The Archaeogenetics of Europe. *Current Biology,* 20: 4, p. R174-R183.

VEGAS, J.; ARMENDARIZ, Á.; ETXEBERRIA, F.; FERNÁNDEZ, M.; HERRASTI, L.; ZUMALABE, F. (1999) – La sepultura colectiva de San Juan ante Portam Latinam (Laguardia, Álava). In BERNABEU, J.; OROZCO, T., eds, *SAGVNTUM-PLAV*, 2: N.º Extra, p. 439-445.

ZVELEBIL, M.; PETTITT, P. (2008) – Human condition, life, and death at an early Neolithic settlement: Bioarchaeological analyses of the Vedrovice cemetery and their biosocial implications for the spread of agriculture in Central Europe. *Anthropologie,* XLVI: 2-3, p. 195-218.

ZVELEBIL, M.; PETTIT, P. (2013) – Biosocial archaeology of the Early Neolithic: Synthetic analyses of human skeletal population from the LBK cemetery of Vedrovice, Czech Republic. *Journal of Anthropological Archaeology*, 32, p. 313-329.