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The Demeter project: eight millennia of agrobiodiversity changes in the northwest Mediterranean basin

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Abstract

The development of agricultural societies is closely entangled with that of domestic animals and plants. Local and traditional domestic breeds and varieties are the result of millennia of selection by farmers. DEMETER (2020-2025) is an international project which is aiming to characterize the changes in animal and plant agrobiodiversity (pigs, sheep, goats, and barley) in relation with environmental and socioeconomic factors in the northwestern Mediterranean basin since the beginnings of agriculture. The project is based on a combination of approaches including phenomics (through geometric morphometrics), databasing, zooarchaeology, archaeobotany, climate modeling, paleoproteins (ZooMs) and statistical analyses. Several hundreds of archaeological sites from the South of France and Catalonia will be studied, covering the maximum environmental, societal and cultural diversity of context over the course of the last eight millennia.

Keywords

Archaeozoology, Archaeobotany, Diachrony, Domestication, Agriculture

INTRODUCTION

The onset of plant and animal domestication marks a major transition in human history and a key element in the development of modern societies (Dodson, Dong 2016; Vigne et al. 2011; Zeder 2015). Domestication led to important changes in ecology, demography, and the social organization of human populations (Bocquet-Appel, Bar-Yosef 2008). Domesticated plants and animals play a pivotal role in our modern Western societies, being the primary sources of food. However, we are now experiencing a major worldwide crisis, with losses in the diversity of food production systems and the progressive disappearance of traditional due to the imposition of industrial intensive farming models. Local knowledge and the farming culture are under threat, as well as the diversity and sustainability of cultivated species, varieties and breeds. Our current breeds and varieties are the result of never-ending artificial selection of morphological, physiological and behavioral traits resulting from thousands of years of human-plant-animal interactions. To date, bioarchaeological research has focused more on the earliest stages of the domestication process, in order to trace the origins of domestic populations, rather than on their subsequent evolution within and alongside human societies involved in intensive and continuous relationships with them outside the “domestication centers”. In this context, the DEMETER project (2020-2025), funded by the European Research Council, pursues three main questions: How have domestic plants and animals changed through time, far from their centers of origin? Which socioeconomic, cultural and environmental transformations interacted with this agrobiodiversity? In what way was this process achieved?

Among the many possible factors affecting the past diversity of domestic plants and animals, it is necessary to consider the chronocultural and socioeconomic context (e.g., household production, long/short distance trade networks), the geography (e.g., topology, distance to the coast) (Alonso, BoubY 2017), the type of site (e.g., open- air, urban, rural, etc.), its function (i.e., main activities, specialization) (Bréhard et al. 2010) and the prevailing environmental parameters, such as climate (Arbogast et al. 2006). However, a holistic approach to disentangle the respective roles of these factors in shaping ancient agrobiodiversity has not yet been undertaken. Here we will present our overall objective and the three main methodological approaches, i.e., geometric morphometrics, paleoclimatic modeling and databasing that have been implemented during the first year of the project, in addition to progress on current research.

THE NORTHWESTERN OCCIDENTAL MEDITERRANEAN BASIN

DEMETER is focused on the Northwestern Occidental Mediterranean basin (southern France and Catalonia), i.e., outside the core domestication area of the selected species. Several reasons make this an excellent area for investigating the different parameters that may have contributed towards the development of new breeds and varieties : various socioeconomic dynamics (e.g., agricultural strategies, exchanges between populations, selection), long chronology, large number of archaeological settlements with various functions and status (e.g., rural, urban sites) and rich environmental contexts, since the region hosts varied geography including littoral plains, mountains, valleys, lagoons and deltaic areas. Moreover, the climatic evolution of the Mediterranean basin during the Holocene has been well described (Azuara et al. 2015; Frigola et al. 2007; Jalali et al. 2016; Sabatier et al. 2012). This region has a rich and complex history that cannot be easily synthesized. Six major chronocultural periods nevertheless emerge (fig. 1). The first being the Neolithic (5,850-2,300 BC). The Northwestern Occidental Mediterranean basin witnessed the arrival of the

Mediterranean stream of Neolithic expansion through the impressed ware cultural complex, which influenced inland Europe ; received continental influences during the Bronze Age (2,300-750 BC) ; developed considerably in the Iron Age (750-50 BC), entering into contact with Phoenicians, Greek and Etruscan populations before Roman colonization and the foundation of large cities ; it underwent the deconstruction of the Roman Empire (ca 480 AD), the arrival of the Visigoths and the subsequent Islamic conquest, both of whom contributed to its prosperity during the Middle Ages (480-1,492 AD), while important trade routes across the Mediterranean and northern Europe became increasingly integrated (Wickham 2005) with such developments continuing during the Modern period (1,492- 1,800 AD). Thus far, no regional synthesis of the evolution of the targeted species and diachronic changes in cultivation and husbandry practices has yet covered the large time span selected by DEMETER. However, a relatively large amount of grey literature (i.e., site reports, monographs) has been produced and provides essential information about the changes that occurred during specific time periods or a specific focus on a single species (e.g., cattle during historic periods; Forest, Rodet-Belarbi 2002). By the end of the project, DEMETER should include the study of at least 100 archaeological sites spread across the last eight millennia (fig. 1).

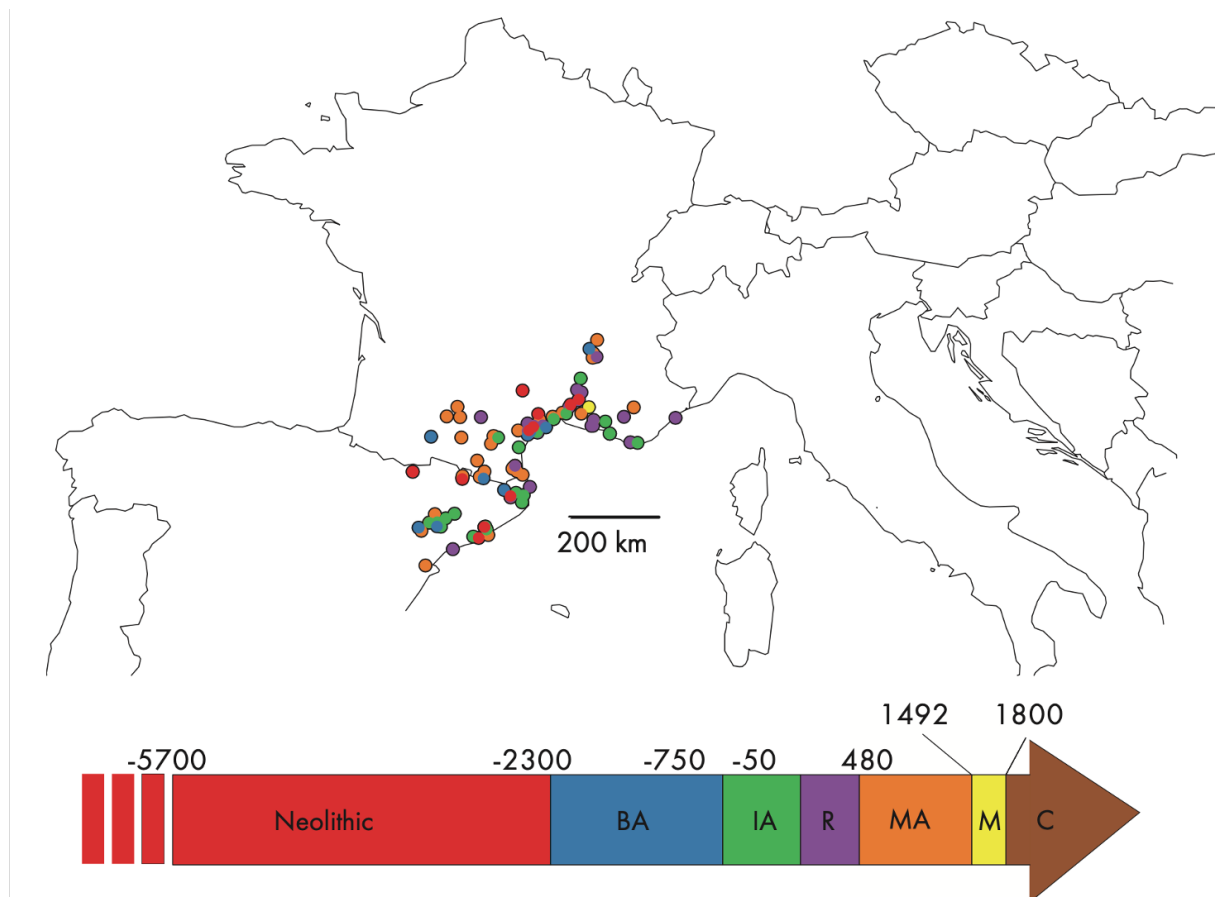


Fig. 1. Preliminary list and locations of 140 archaeological sites identified for the DEMETER project. Dots on the map and the timeline are colored according to the following timeframe: Neolithic (5700-2300 BC), Bronze Age-BA (2300-750 BC), Iron Age-IA (750-50 BC), Roman-R (50 BC-480 AD), Middle Ages-MA (480-1492 AD), Modern-M (1492-1800 AD) and Contemporaneous-C periods (since 1800).

SHEEP, GOATS, PIGS AND BARLEY

We focus on a series of species domesticated during the Neolithic that spread into Western Europe along with the first farming communities as part of the Neolithic package, together with agricultural practices, ceramic production, increases in storage activities and sedentariness, and marked demographic expansion (Bocquet-Appel, Bar-Yosef 2008). The selected model species are of major economic importance today and have been continuously valued in the region: sheep (*Ovis aries*), goats (*Capra hircus*), pigs (*Sus scrofa*), and barley (*Hordeum vulgare*).

In general, sheep have been the dominant mammalian species found among archaeological remains from the final Neolithic until today (e.g., Antolín et al. 2018; Nieto-Espinet et al. 2021; Saña et al. 2020), with some exceptions, such as those sites showing a particularly large predominance of goats (e.g., medieval sites in a borough of Montpellier; Fabre et al. 2002). Sheep and goats have been among the main domestic mammals (with pigs and cattle) of the Mediterranean since the Neolithic and are the two inseparable emblematic species of the Mediterranean basin landscapes. They have the advantage that their wild ancestors (i.e., the Asian mouflon [*Ovis orientalis*] and the bezoar ibex [*Capra aegagrus*], respectively) are absent from Europe, making taxonomic identifications easier. The earliest known evidence of morphological modifications linked with domestication were identified ~10,500 years ago in the Upper Euphrates basin (Peters et al. 2005). The two species are morphologically close, but several studies have confirmed a clear differentiation based on metrical (Salvagno, Albarella 2017) and macroscopic (e.g., Gillis et al. 2011) analyses of bones and teeth.

Pigs were consumed at all times, but their remains are rare in the Neolithic and become abundant during the Roman Empire (50 BC-480 AD; Forest 2000; Nieto-Espinet et al. 2021), likely linked with the social differentiation of consumers (Forest 2009). Pig is certainly the species whose history of domestication is best known from archaeological remains and has been the subject of many studies. Pigs were domesticated from the wild boar, which naturally occurs in Europe, and makes the identification of wild and domestic archaeological specimens particularly challenging (Albarella et al. 2006). Nonetheless, recent geometric morphometric studies have allowed traditional identifications to be refined (Evin et al. 2013). Additionally, pigs have been the subject of numerous bioarchaeological studies over the last decade (e.g., Duval et al. 2015 ; Evin et al. 2015b ; Krause-Kyora et al. 2013 ; Larson et al. 2007 ; Ottoni 2012).

Domestic barley is divided into two morphological types: two-rowed (subsp. *distichum*) and six-rowed (subsp. *vulgare*) barley, which both include naked and hulled forms (Zohary et al. 2012). Barley has been one of the main cereals in Mediterranean agriculture since the Neolithic, and a major element of both human and animal diets. Carbonized grains are commonly found in archaeological sites (Zohary et al. 2012) from all periods. Barley is found from the Neolithic to Modern times in the study region. Two-row and six-row varieties have been identified, as well as lax-eared and dense-eared forms, and naked and hulled types. Naked 6-row barley was important in the Neolithic, being replaced by hulled 6-row barley from the 3rd/2nd millennium cal. BC onwards. This species becomes of major importance in regional agriculture from the end of the Bronze Age (ca 1,400-750 BC). Two-row barley is present in the early Neolithic but it remains undetected in later periods until Roman times (Alonso, Bouby 2017; Antolín et al. 2015; Antolín, Buxó 2012; Bouby 2001; 2014; Ros 2020). Barley is used for many purposes, and adapts to more environmental conditions than most wheat species.

A MULTI-METHODOLOGICAL APPROACH

The project is based on a combination of approaches, including phenomics (through geometric morphometrics), databasing, zooarchaeology, archaeobotany, climate modeling, paleoproteins (ZooMs) and statistical analyses.

Geometric morphometrics

Recent methodological advances in geometric morphometrics (i.e., the study of forms in multi-dimensional spaces allowing in-depth investigation of morphological change) (Rohlf, Marcus 1993), allow us to address questions regarding the micro-evolutionary processes that accompanied the long history of domestic species in an unprecedented way. Geometric morphometrics (GMM) is increasingly used for bioarchaeological studies in order to track differences between diachronic populations (Bouby et al. 2020; Cucchi et al. 2014; Ottoni et al. 2013; Pagnoux et al. 2021; Price, Evin 2017; Terral et al. 2004), domestication signatures (Bonhomme et al. 2020; Cucchi et al. 2011; Evin et al. 2013; Evin et al. 2015b), or husbandry practices (Bopp-Ito et al. 2018; Duval et al. 2015; Duval et al. 2018; Price, Evin 2017). Geometric morphometrics provide highly resolute tools to quantify and analyze morphometric variation, which pick up from the previous traditional biometric analyses and are applied to archaeological plant and animal remains to investigate domestication and the morphometric variation of domestic populations (Bouby et al. 2013; Evin et al. 2013; Evin et al. 2015b; Ottoni et al. 2013; Ros et al. 2014; Terral et al. 2010; Terral et al. 2004). Moreover, morphometric analyses are often the only available approach with sufficient fine-scale resolution, suffer less from preservation limitations than other approaches (e.g., aDNA, isotopes) and can be carried out on a large scale in a non-destructive manner. We have a relatively good understanding of the morphological changes that took place at the early stages of the domestication process in the near-eastern center (e.g., Colledge, Conolly 2007; Conolly et al. 2011; Vigne et al. 2005; Zeder 2006; Zeder et al. 2006), but how domesticated populations evolved and diversified after the initial steps and outside the “domestication centers” remains largely unknown, due to the lack of large-scale diachronic studies. During the evolution of domesticates, local environmental and anthropic contexts will have led to subtle differences in the morphology of the populations (Balasse et al. 2016). Thus, DEMETER seeks to precisely quantify this morphological variation using cutting-edge geometric morphometric approaches.

The teeth of mammals and charred cereal grains have the advantage of being well preserved in archaeological assemblages, in comparison to other types of remains. In addition, they are frequently found in large numbers and are known to be taxonomically informative, and protocols and modern specimens of known taxonomy (species, breed/variety, wild/domestic status) are already available (Burger et al. 2011; Cucchi et al. 2011; Larson et al. 2007; Terral et al. 2010). Therefore, pig, sheep and goat teeth and barley grains will be primarily used as phenotypic markers. The link between human selection and mammal tooth morphology is not yet well understood, but previous work on wild and domestic pigs revealed strong tooth shape differences between wild and domestic populations, as well as strong differences between wild populations as well as marked differences between domestic breeds (Evin et al. 2015a). Thus, this work demonstrated the power of geometric morphometrics when applied to tooth morphology to quantify fine-scale differences. This link between human selection and morphology is more straightforward for cereal grains, since they were directly targeted for food production, even if their shape was not likely the target of selection itself. For cereals, an additional constraint comes from the taphonomic preservation of the remains, which are

usually found carbonized. Charring can significantly modify the size and shape of the grain (Boardman, Jones 1990; Bonhomme et al. 2017; Braadbaart 2008; Ros et al. 2014). Nevertheless, it has already been demonstrated that carbonization is not detrimental to the discrimination of two-rowed and six-rowed hulled barley grain shapes (Ros et al. 2014). The size and shape of the cereal grains are quantified using outline analyses (Bonhomme et al. 2014; Kuhl, Giardina 1982; Mayer et al. 1998, fig. 2A), while the teeth and mandibles of mammals are quantified using outline, landmark and sliding semi-landmark based approaches (fig. 2B). Because the use of geometric morphometrics requires specific computational and analytical training, we will ultimately develop an expert system (a computer knowledge-based system), based on geometric morphometric techniques, aiming at fostering morphometric analysis of archaeological remains to study domesticated species. Tooth measurements are based on a landmark and sliding semi-landmark geometric morphometric approach (fig. 2B). Pig teeth are measured following Evin et al. (2013), while new geometric morphometric protocols have been established for measuring sheep and goat teeth and mandibles (fig. 2B), and repeatability tests performed (following Evin et al. 2020). Initial work has focused morphometric differences between modern sheep and goats (Jeanjean et al. in prep.), which can now be used to identify archaeological specimens before exploring the spatiotemporal variation of the two species. In parallel, linear measurements from a maximum number of sites are also analyzed.

The evolution of barley is studied using both archaeological seeds and a reference collection of seeds from 58 modern varieties from France. Because archaeological seeds are mainly preserved charred, fresh barley seeds are being charred to allow a more realistic comparison. Based on the literature (Bonhomme et al. 2017; Charles et al. 2015; Ros et al. 2014; Styring et al. 2013) and numerous preliminary experiments, modern samples are charred for 3 h 30 in an anoxic environment and a temperature of 240 °C. Morphometric analyses are based on automatic extraction of outline point coordinates from a black and white mask of the original photograph of the grain (fig. 2A). The next line of research will involve the study of grains from archaeological sites of different chrono-cultural phases.

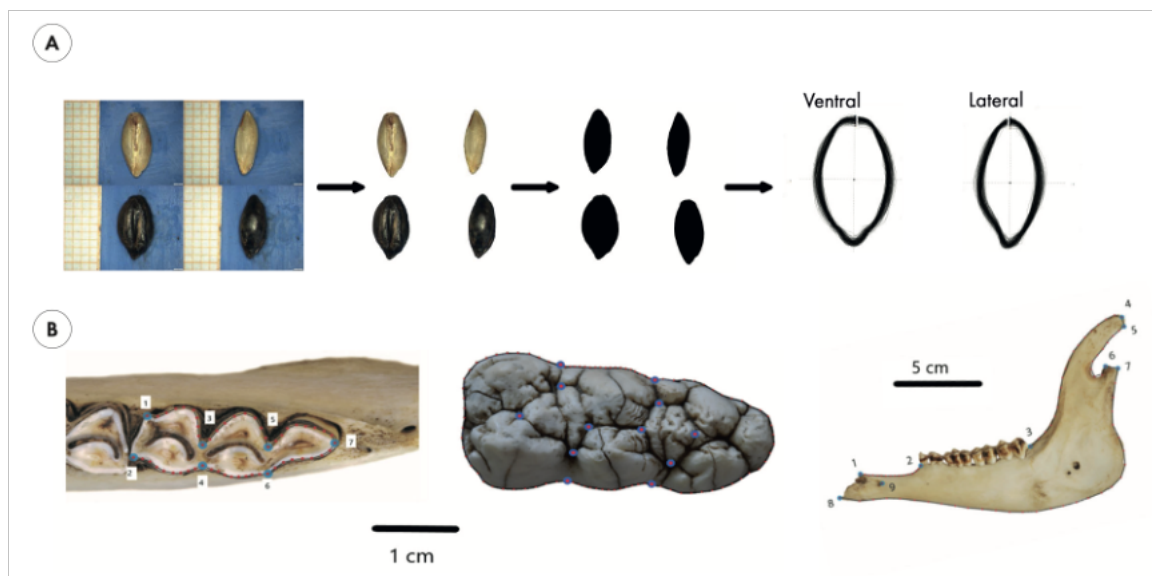


Fig. 2. Geometric morphometric protocols used for capturing the size and shape of barley grain (A), the lower third molar of sheep (left), pig (middle), and the mandible of sheep (right). A: Acquisition steps of the grain outline coordinates. B: Landmarks and sliding-semi landmark positions on teeth and mandibles.

Climate reconstruction and modeling

Climate is certainly a determining factor, through natural selection, in the evolution of breeds and landraces, as exemplified by the presence of traditionally small, stocky and heavy-headed horses in the colder north compared to Arabian horses living in hot and arid regions, which possess fine heads, long and slender legs, each being thus adapted to their local environments (Clutton-Brock 2012). Climate changes can be reconstructed quantitatively from fossil pollen data obtained from sediment cores using several methods (review in Chevalier et al. 2020). Here, quantitative climate reconstruction of seasonal and annual temperatures are obtained using three independent mathematical methods: (i) the Modern Analogue Technique (Guiot 1990), (ii) the Weighted Average Partial Least Square regression (Ter Braak, Juggins 1993) and, for the first time for the Mediterranean area, (iii) Boosted Regression Trees (Salonen et al. 2014). This multi-method approach is applied to approximately 20 pollen records from the studied area with satisfactory age controls and aggregated to reconstruct past climate changes over the last 10,000 yrs. This classical approach (Davis et al. 2003) optimizes the signal-to-noise ratio to provide reliable climate values at the regional scale, and is potentially less sensitive to biases such as the impact of human activities on the vegetation and thus the pollen assemblages. Future research will include a new paleoclimatology proxy: the Branched Glycerol Dialkyl Glyceryl Tetraethers (brGDGTs), which offers new perspectives on continental temperature reconstructions (Martin et al. 2020).

Databasing

Archaeology has a long tradition in databasing, as a way for gathering, updating and managing (Corboud 2002) all the artifacts and information recorded during an excavation in a lasting fashion. The analysis of a large number of sites and specimens requires the establishment of carefully designed and rigorously maintained databases. For each archaeological site and occupation level, the following information is specifically recorded: geography (latitude, longitude, and altitude) and environment (e.g., mountain, low land, etc.); archaeology: chrono-cultural information, relative dating, absolute dating, type (e.g., open-air) and function of the site (e.g., sheepfold-caves, funerary sites, etc.). For each site and occupation level, we review the published and grey literature, including archaeobotanical and archaeozoological data to register the human food spectrum and the relative importance of the species in the local economy. In addition, available osteometric measurements and mortality profiles are recorded. During the first year of the project, carpological, zooarchaeological and archaeological files have been collected and rigorously formatted, and are now ready to be analyzed. In future, all databases will be integrated into an open-source relational database (PostgreSQL) including a geographic information system (GIS).

CONCLUSION

DEMETER aims to test the following hypotheses : 1) the diversity of ancient domesticates has varied non-linearly through time and space, with periods of homogenization and periods of diversification, 2) human selection for desired traits is associated with other forces acting on domesticated species and contributing to shape many aspects of their morphology, 3) the influence of human and environmental factors in the domesticated species has varied in time and space, according to cultural and biological conditions, 4) domestication is a complex biological and cultural process during which each species follows its own path. This paves the way for the exploration of fundamental changes in farmed animals and crops, in connection

to different, past rural communities and their evolution under new farming practices in a given geographic area.

This multi-disciplinary project will provide a better understanding of the resilience of agrobiodiversity in an ever-changing socioeconomic and environmental world. Furthermore, we will be able to increase awareness of the risks associated with current policies, which lead towards highly specialized, homogeneous and centralized production, and a greater disconnection between human populations and domestic plants and animals.

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