Journal of Biogeography (*J. Biogeogr.*) (2004) **31**, 63–77

ORIGINAL ARTICLE

Historical biogeography of olive domestication (*Olea europaea* L.) as revealed by geometrical morphometry applied to biological and archaeological material

Jean-Frédéric Terral[1]*, Natalia Alonso[2], Ramon Buxó i Capdevila[3], Noureddine Chatti[4], Laurent Fabre[1], Girolamo Fiorentino[5], Philippe Marinval[6], Guillem Pérez Jordá[7], Bénédicte Pradat[8], Núria Rovira[3] and Paul Alibert[9]

[1]*Centre de Bio-archéologie et d'Ecologie – CNRS UMR 5059, Institut de Botanique (Université Montpellier 2), Montpellier, France,* [2]*Department de Historia, Universitat de Lleida, Lleida, Spain,* [3]*Museu d'Arqueología de Catalunya-Girona Pedret, Girona, Spain,* [4]*Unité de Recherche UR/09-30, Génétique: Biodiversité et Environnement, Institut Supérieur de Biotechnologie de Monastir, Monastir, Tunisia,* [5]*Laboratorio di Archeobotanica, Dipartimento di Beni Culturali, Università degli Studi di Lecce, Lecce, Italy,* [6]*Centre d'Anthropologie, CNRS – UMR 8555, EHESS – UTM – UPS 39, Toulouse, France,* [7]*Dpt. de Arqueología y Prehistoria, Universitat de Valencia (Facultat de Historia y geografía), Valencia, Spain,* [8]*UFR d'Histoire, Université F. Rabelais, Tours, France and* [9]*Biogéosciences – Dijon, CNRS UMR 5561, équipe 'Différenciation des espèces', Université de Bourgogne, Dijon, France.*

*Correspondence: Jean-Frédéric Terral, Centre de Bio-archéologie et d'Ecologie – CNRS UMR 5059, Institut de Botanique (Université Montpellier 2) – 163, rue Auguste Broussonet, F-34090 Montpellier, France.
E-mail: terral@univ-montp2.fr

ABSTRACT

Aim This study intends to improve our understanding of historical biogeography of olive domestication in the Mediterranean Basin, particularly in the north-western area.

Location Investigations were performed simultaneously on olive stones from extant wild populations, extant cultivated varieties from various Mediterranean countries, and archaeological assemblages of Spanish, French and Italian settlements.

Methods A combination of morphometrics (traditional and geometrical) allowed us to study both the size and shape of endocarp structure. Concerning shape, a size-standardized method coupled with fitted polynomial regression analysis was performed.

Results We found morphological criteria for discriminating between wild and cultivated olive cultivars, and established patterns of morphological variation of olive material according to the geographical origin (for extant material) and to the age of the olive forms (for archaeological material). Levels of morphological convergences and divergences between wild olive populations and cultivated varieties are presented as evidence.

Main conclusions Morphological changes of endocarps of olive under domestication at both geographical and chronological scales provide new criteria for the identification of olive cultivars. They allow to determine the origins of cultivated forms created and/or introduced in the north-western Mediterranean regions and to understand how human migrations affected the rest of the Western Mediterranean regions. A model of diffusion of olive cultivation is proposed. It shows evidence of an indigenous origin of the domestication process, which is currently recognized in the north-western area since the Bronze Age.

Keywords
Olea europaea **L., Mediterranean Basin, morphometrics, domestication, historical biogeography.**

INTRODUCTION

Through the process of domestication, human influence on plant populations undoubtedly constitutes a considerable selective factor in their evolution (Diamond, 2002). Varietal inheritance of numerous cultivated plants results from a long history of peoples and anthropogenic activities, and is nowadays constituted by thousands of cultivated varieties (so-called cultivars) even if their origins (chronological and geographical) are not currently established. The understanding of the history and evolution of plants under domestication, the identification of varietal inheritance and the reconstruction of the beginnings and the exploitation of crop plants must be carried out by conjoint biological, palaeobotanical and archaeological studies. Archaeological discoveries alone are inadequate because the ancient remains of a species is not sufficient to infer that domestication and agriculture had already appeared. The conclusive interpretation must take into account archaeological findings, not only in an ecological and socioeconomical sense, but also in a biological one. In this way, cultural analyses have to be combined with findings from botanical analyses for elucidating geographical areas of crop domestication and to show evidence of diffusion of selected forms in relation to human migrations.

In such context, the olive tree provides a good bio-archaeological model, because, it has occupied since prehistorical times, a major place in the culture of Mediterranean peoples. Indigenous to the Mediterranean Basin, it currently constitutes a complex of wild forms (*Olea oleaster*) and weedy types classified conventionally as *O. europaea* var. *sylvestris*, and cultivars classed as *O. europaea* var. *europaea*. The olive tree model may contribute to exploration of the dynamics of the agricultural and domestic environment by combining biological variations with cultural and archaeological contexts.

Present state of research

Since the first pioneering works based on morphological criteria (de Candolle, 1886; Ruby, 1918; Chevalier, 1948; Turill, 1951; Hauville, 1953), numerous systems of classification and identification of cultivated olive varieties have been established in order to reconstruct their origin, characterize their varietal inheritance and improve their agricultural qualities. The most significant results have been achieved since the 1980s, following the use of biochemical markers and the development of molecular biological techniques. These studies, based on isozyme phenotypes of pollen (Pontikis *et al.*, 1980; Trujillo *et al.*, 1990; Trujillo & Rallo, 1995), foliar enzymatic polymorphism (Ouazzani *et al.*, 1993, 1994, 1995, 1996) and random amplified polymorphism DNA (Bogani *et al.*, 1994; Fabbri *et al.*, 1995) indicated substantial genetic diversity of the olive tree. In spite of an early and intensive domestication, the high overall amount of genetic variability seems to be characteristic of species with a long lifespan and vegetative propagation, such as olive (Hamrick *et al.*, 1979). Nevertheless, no clear relationship was observed between genotypes based on allozyme polymorphism and the geographical locations of the cultivars (Trujillo *et al.*, 1990). This evidences the extreme complexity of the history of olive domestication. Finally, recent genetic studies have shown that selection of cultivars has occurred in different genetic pools, supporting the hypothesis that olive domestication occurred in many locations in the Mediterranean Basin (Besnard & Bervillé, 2000; Besnard *et al.*, 2002a).

Archaeological and palaeobotanical studies can contribute to a better understanding of the origins in time and space of olive domestication and of the diffusion of its cultivation across the Mediterranean. Using biological remains recovered in archaeological contexts, Zohary & Spiegel-Roy (1975) proposed that olive cultivation appeared for the first time since the fourth millennium BC in Palestine. van Zeist (1980) suggested that olive cultivation gradually diffused from East to West carried by the Phoenicians, Etruscans, Greeks and Romans, being brought to Greece around 2500 BC. In north-western Mediterranean areas, introduction of olive cultivation is dated by the discovery of the most ancient oil mill (Brun, 1986; Leveau *et al.*, 1991; Amouretti & Comet, 1992; Pérez Jordà, 2000) dating from the end of the last millennium BC. In Spain, Gilman (1976, 1990) suggests that olive cultivation started during the third millennium BC, but it started there in the second millennium BC (Chapman, 1990; Gil Mascarell, 1992).

Olive stones are recovered in most archaeological sites in the Mediterranean. Because these stones are charred, the fresh matter is missing exploration of the genetic material but morphological approaches are. Despite their hardness, olive stones are often fragmented so that the number of intact samples is limited. Morphological studies of intact olive stones include Kislev (1995) who studied an Israeli Chalcolithic site (3700 BC). He argued that the morphological heterogeneity of these stones was too great to attribute them to domesticated forms and suggested the existence of an olive oil industry prior to the beginning of the domestication process.

The present study applies traditional and geometrical morphometric approaches (Slice *et al.*, 1996 for definitions) to the characterization of modern olive endocarps from 39 cultivars and 11 wild populations. Then, specimens from 21 archaeological sites were analysed and compared with modern samples. This comparative study attempts to identify morphological changes that have occurred during the domestication process. We use these comparisons to suggest a Mediterranean phylogeographical model.

MATERIAL

The olive stone is a fusiform, uni-integumented and sclerified endocarp, composed of two asymmetric valves protecting one seed (Fig. 1a). The surface area shows longitudinally aligned furrows, which are marks of carpellar fascicles. The two valves are separated by a longitudinal suture line and usually have a different size and shape. Owing to the abortion of one ovule, the sterile valve remains flatter than the fertile one.

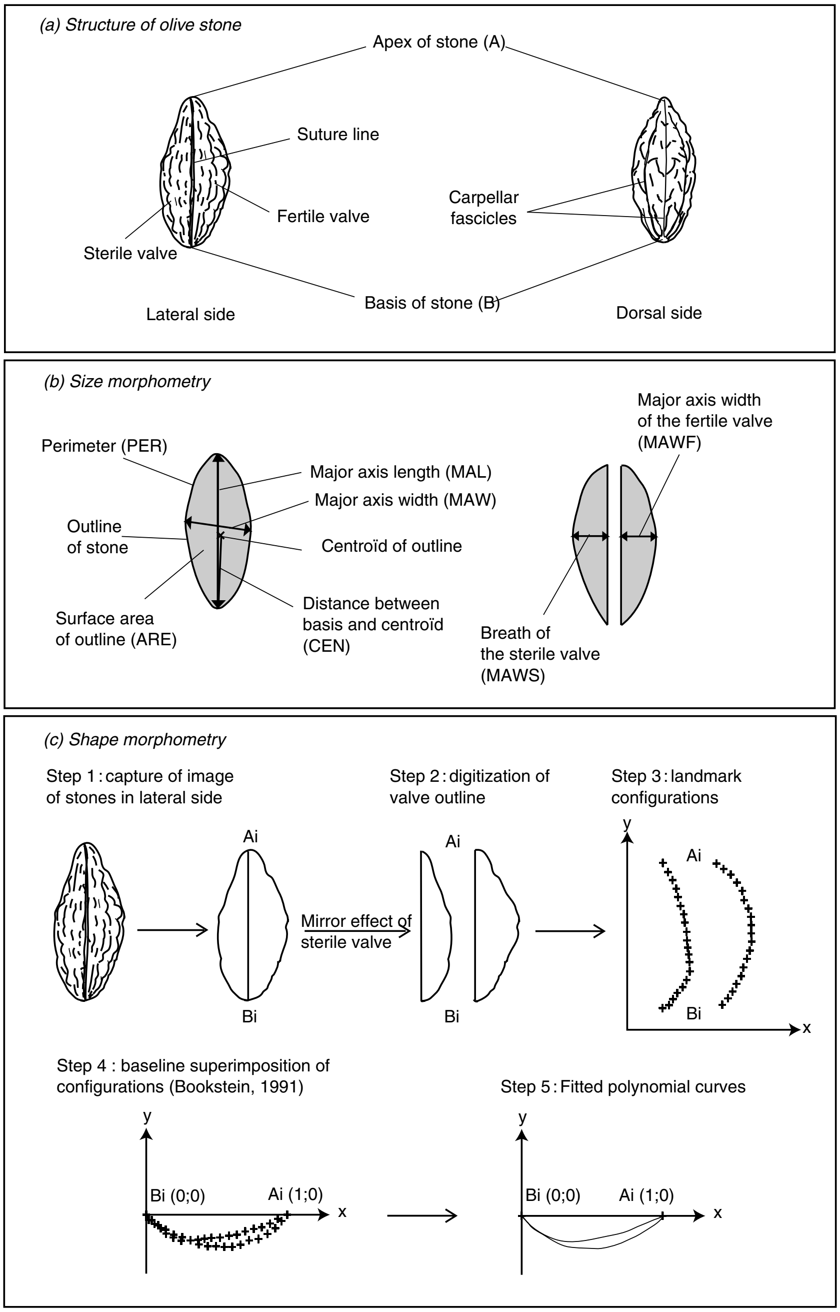

Figure 1 Morphological structure of the olive stone (a) and methodological protocols of traditional (b) and geometrical morphometric analyses (c).

Modern stones

Size measurements have been made using traditional morphometry (size analysis) on 630 olive stones: 180 from wild and 450 from cultivars (Table 1). Then, shape was quantified by a geometrical morphometric approach (shape analysis) on 1500 stones: 330 from wild type and 1170 from cultivars (Table 1). Wild olive stones came from 11 populations situated in different Mediterranean regions (Table 1; Fig. 2a). Olive stones from cultivated varieties were collected from clones growing in the collection of cultivated plants of the Conservatoire Botanique National de Port Cros (Porquerolles Island, Hyères, France – Mesomediterranean bioclimatic stage: mean annual temperature = 15.2 °C; mean annual precipitation = 560 mm) and the collection of the Institut National de la Recherche Agronomique, Domaine Mergueil, Mauguio, France (Mesomediterranean bioclimatic stage: mean annual temperature = 13.9 °C; mean annual precipitation = 750 mm) (Fig. 2a). These two orchards were created in the twentieth century for conservation and study of cultural and genetic diversity in olive (Khadari *et al.*, 2001; Moutier *et al.*, 2001).

Archaeological stones

Two hundred and nine olive stones from nine Spanish, 11 French and one Italian archaeological sites were studied

Table 1 Geographical location, economical use and sample size for studied extant wild olive populations and cultivars.

Olive material	Geographical origin	Production for	*n*
Wild populations			
Moraira* (SP1)	Spain	–	30
Jorox* (SP2)	Spain	–	30
Menzel* (TU1)	Tunisia	–	30
Zaghwan (TU2)	Tunisia	–	30
Meknès (MOR)	Morocco	–	30
Bet Oren* (IS1)	Israel	–	30
Dor* (IS2)	Israel	–	30
Manisa (TUR)	Turkey	–	30
Kambos* (GRE)	Greece	–	30
Ile-Rousse (COR)	Corsica (France)	–	30
Reggio di Calabria (ITA)	Italy	–	30
Cultivars			
Aglandau*	France	Canned fruit and oil	30
Amygdalolia†	Greece	Canned fruit	30
Arbequina*†	Spain	Oil	30
Ascolana Tenera	Italy	Canned fruit	30
Ayvalik	Turkey	Oil	30
Barnea	Israel	Canned fruit and oil	30
Barouni*	Tunisia	Canned fruit	30
Belgentier*	France	Canned fruit	30
Belle d'Espagne	Italy	Canned fruit	30
Bid el Haman*	Tunisia	Canned fruit	30
Cailletier	France	Canned fruit and oil	30
Carolia	Greece	Canned fruit	30
Chemlal of Kabylie	Algeria	Oil	30
Chemlali of Sfax*†	Tunisia	Oil	30
Colombale	France	Canned fruit and oil	30
Corniale	France	Oil	30
Cypressino	Italy	Canned fruit and oil	30
Domat	Turkey	Canned fruit	30
Ecijano	Spain	Canned fruit and oil	30
Gaidouriola*	Greece	Canned fruit	30
Ghjermana	Corsica	Canned fruit and oil	30
Grappola*	Italy	Canned fruit	30
Grossane	France	Canned fruit	30
Kalamata	Greece	Canned fruit	30
Koroneiki*	Greece	Oil	30
Kothreiki*	Greece	Oil	30
Lucques*	France	Canned fruit	30
Manzanilla*†	Spain	Canned fruit and oil	30
Menara	Morocco	Canned fruit and oil	30
Meski*	Tunisia	Canned fruit	30
Olivière*	France	Oil	30
Picholine*†	France	Canned fruit and oil	30
Picholine Marocaine*	Morocco	Canned fruit and oil	30
Picual*	Spain	Oil	30
Razzola	Italy	Oil	30
Sofralik	Turkey	Canned fruit	30
Sourani	Syria	Canned fruit and oil	30
Tanche*	France	Canned fruit and oil	30
Verdale de l'Hérault	France	Canned fruit and oil	30

*Populations and cultivars used for traditional morphometry.
†Cultivars used as test-samples.

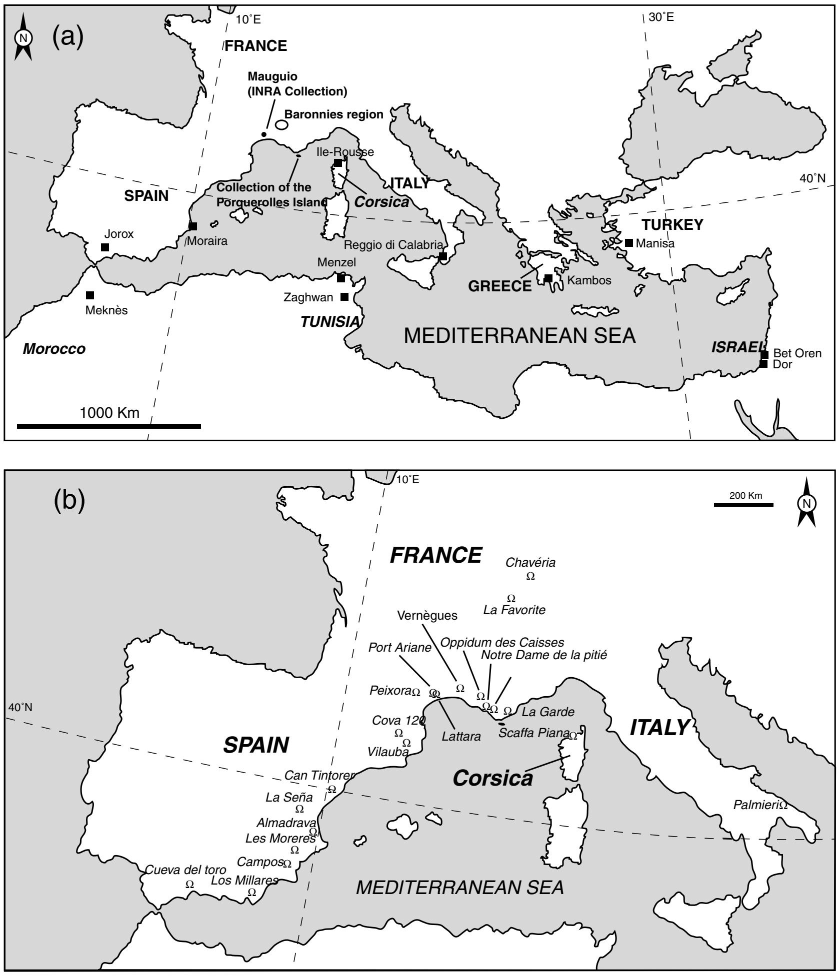

Figure 2 Geographical location of extant reference wild olive populations and cultivars (a) and archaeological sites (b).

Table 2 Archaeological sites and sample size of ancient olive stones analysed.

Archaeological site	*n*	Cultural period	Age
Spain			
Cueva del Toro	1	Early Neolithic	4500–4300 BC
Can Tintorer	1	Middle Neolithic	2900–2700 BC
Campos	2	Chalcolithic	2500 BC
Cova 120	1	Chalcolithic	3190 ± 140 BP
Los Millares	2	Chalcolithic/Bronze age	2500–2000 BC
Les Moreres	40	Chalcolithic	2300–2000 BC
La Seña	14	Iberic period	End of 3rd century BC
Almadrava	40	Roman period	End of 2nd century BC
Vilauba	4	Roman period	500–800 AD
France			
Scaffa Piana	1	Late Neolithic	2825 ± 90 BC
Oppidum de la Cloche	2	Iron age	II–I century BC
Oppidum des Caisses	2	Iron age	End of 2nd century BC
Notre Dame de la Pitié	2	Iron age	220–180 BC
Peixora	1	Roman period	I–II century AD
La Favorite	1	Roman period	I–II century AD
Vernègues	2	Roman period	I–II century AD
La Garde	23	Roman period	II century AD
Chavéria	11	Roman period	End of 2nd century AD
Lattara	11	Iron age/Roman period	400 BC/50 AD
	12	Roman period	50–100 AD
Lattes – Port Ariane	5	Middle age	XIII–XIV century AD
Italy			
Palmieri	30	Bronze age	Undated

(Fig. 2b; Table 2). Their morphology was compared with the modern stones.

Test-samples

In order to test the validity of comparison between modern and archaeological stones, a number of effects had to be previously tested. These preliminary analyses were carried out on subsamples (called hereafter test-samples) from five cultivars (Amygdalolia, Arbequina, Chemlali of Sfax, Manzanilla and Picholine) (Table 1).

First, the effect of carbonization was carried out on stones charred at 400 °C in a electric oven under anaerobic atmosphere, in order to quantify size shrinkage. Shape and geometrical structure of stones, before and after carbonization, were also compared using multivariate analysis of variance (MANOVA) on the shape quantitative parameters (Slice *et al.*, 1996).

A second test concerned changes in shape occurring during the sclerification phase of stone development. Outlines of additional immature stones collected in July/August on the same trees were therefore digitized and their shape was compared with those of the reference collection.

Thirdly, the effects of environmental conditions on shape of stones were appraised at two levels: regional and local. Specimens from five trees of the Porquerolles plantation were compared with specimens of those used to create the orchard. On a local scale, stones from two distinct trees of the same cultivar of the Porquerolles orchard were compared with the Picholine and Arbequine cultivars (the only two cultivars for which several trees were available for sampling).

Finally, errors of measurement were estimated by an additional session of digitization and morphometric analyses performed on subsamples of 60 specimens.

METHODS

Size analysis

The outline of the olive stone was digitized in lateral view using a stereo-microscope coupled to a computerized image analysis system. For each stone, the following seven measurements were taken (Fig. 1b): major axis length (MAL, mm); major axis width or maximum diameter (MAW, mm); width of the fertile valve (MAWF, mm); width of the sterile valve (MAWS, mm); surface area of outline (ARE, mm^2); perimeter of outline (PER, mm); distance between base of stone and centroid (CEN, mm).

Measurements were treated by canonical variate analysis (CVA) carried out on the 630 specimens (modern stones) and eight variables (seven quantitative and one qualitative, expressing 21 classes corresponding to the 21 wild populations and cultivars). The analysis intended to show evidence of discriminant criteria between populations and to compare, if possible, archaeological stones with the reference samples.

Shape analysis

On digitized views of external outlines (i.e. an open outline) (step 1 – Fig. 1c), 20 landmarks (x; y) per valve were captured (step 2). The landmarks comprise two homologous ones; B (basis of stone) and A (apex of stone) and 18 pseudohomologous ones equally spaced between B and A (step 3).

Each valve was translated and rotated into a standard orientation on the x-axis, by assigning to the two homologous landmarks B and A, the coordinates (0; 0) and (1; 0), respectively (step 4). Thus, each valve was superimposed onto the baseline (B; A), and the 18 pseudohomologous landmarks took coordinates scaled to the length of the valve (Bookstein, 1991). A least-squared third-degree polynomial curve was then fitted to the outline of each valve (step 5). The choice of the third-degree of polynomial adjustment constitutes a suitable compromise between quadratic polynomial curves which are not very precise and fourth-degree polynomial curves which exaggerate some of the local irregularities (as demonstrated by Rohlf, 1990).

Finally, each stone was defined by two equations:

$$\text{fertile valve: } y = b_0 + b_1x^1 + b_2x^2 + b_3x^3$$
$$\text{sterile valve: } y = b'_0 + b'_1x^1 + b'_2x^2 + b'_3x^3$$

The eight regression parameters 'b_i' were used as quantitative variables (Table 3). A CVA was then carried out on 1500 stones and nine variables (the eight quantitative and one qualitative expressing 50 classes corresponding to the 50 wild populations and cultivars).

Discriminant power of CVA is evaluated by the dispersion of individuals around the centroid of their populations in the canonical space. The Mahalanobis distance matrix between each sample centroids (called hereafter consensus population individual) expresses their convergences and divergences in shape. This method was used as the basis for an UPGMA cluster analysis performed to establish a taxonomy based on morphological relationships among samples and distinct morphological groups. In such a classification method, one considers a horizontal hierarchical tree plot constructed from a given group, in our case the occidental wild populations. As a result, more and more olive populations and cultivars were linked together and aggregated in larger clusters of increasingly dissimilar elements.

Archaeological olive stones were compared with extant samples studied by CVA as additional individuals. Then, the classification of archaeological stones may help us to identify the earliest cultivated forms, hereby enabling us to replace this information in a phylogeographical framework. In some cases, it was impossible to classify archaeological stones, either because they were naturally or accidentally morphologically remote to modern forms. The probability that an archaeological stone belongs to a specified olive morphological group identified by clustering was calculated using the Mahalanobis distance between stones and each group centroid in the canonical space. If $P \geq 0.75$, we have considered the allocation as reliable. If P is between 0.65 and 0.75, classification can be

Table 3 Mean of geometrical parameters (b_i) for each population and cultivar from morphometric analysis of modern olive stones.

	Mean shape descriptors of olive endocarps							
Populations/cultivars	b_0	b_1	b_2	b_3	b'_0	b'_1	b'_2	b'_3
Wild populations								
Moraira (Spain)	−0.043	−1.253	1.250	0.135	−0.041	−0.755	0.672	0.162
Jorox (Spain)	−0.042	−1.061	1.057	0.213	−0.047	−0.957	0.799	0.169
Menzel (Tunisia)	−0.031	−1.034	0.807	0.235	−0.026	−0.915	0.654	0.203
Zaghwan (Tunisia)	−0.036	−1.064	1.030	0.147	−0.034	−0.704	0.645	0.203
Meknès (Morocco)	−0.042	−1.072	1.245	0.139	−0.050	−0.096	0.652	0.182
Bet Oren (Israel)	−0.021	−1.038	1.072	−0.020	−0.021	−0.846	1.001	−0.136
Dor (Israel)	−0.022	−0.992	0.707	0.281	0.000	−0.889	1.072	−0.196
Manisa (Turkey)	−0.023	−0.905	0.512	0.376	−0.016	−0.658	0.386	0.264
Kambos (Greece)	−0.021	−0.740	0.250	0.566	−0.011	−0.725	0.221	0.512
Ile-Rousse (Corsica, France)	−0.018	−0.575	0.401	0.365	−0.011	−0.599	0.459	0.135
Reggio di Calabria (Italy)	−0.032	−1.101	0.852	0.274	−0.021	−0.894	0.867	−0.103
Cultivars								
Aglandau	−0.040	0.044	0.738	0.201	−0.017	−0.535	0.983	−0.326
Amygdalolia	−0.036	0.343	0.780	0.291	−0.016	−0.394	0.770	0.071
Arbequina	−0.055	−1.272	1.151	0.125	−0.035	−1.162	1.153	0.013
Ascolana Tenera	−0.039	0.625	1.034	0.064	−0.016	−0.508	0.942	−0.173
Ayvalik	−0.024	−0.991	0.458	0.309	−0.027	−0.812	0.321	0.213
Barnea	−0.010	−1.139	1.522	−0.392	−0.006	−0.594	0.810	−0.214
Barouni	−0.054	−0.518	0.802	0.243	−0.036	−0.457	0.671	−0.061
Belgentier	−0.035	0.800	1.816	−0.459	−0.025	−0.436	1.780	−0.528
Belle d'Espagne	−0.060	−0.924	0.911	0.003	−0.081	−0.817	0.859	−0.029
Bidelhaman	−0.013	0.137	0.903	0.098	−0.007	−0.559	0.538	0.173
Cailletier	−0.029	0.115	0.715	0.360	−0.017	−0.654	0.439	0.220
Carolia	−0.011	−0.706	0.237	0.470	−0.010	−0.275	0.007	0.277
Chemlal of Kabylie	−0.041	−1.206	1.358	−0.126	−0.008	−1.042	1.486	−0.451
Chemlali of Sfax	−0.020	−0.681	0.290	0.442	−0.012	−0.613	0.373	0.239
Colombale	−0.016	−0.916	0.868	0.064	−0.004	−0.690	0.857	−0.160
Corniale	−0.025	−0.877	1.049	−0.162	−0.018	−0.520	0.814	−0.290
Cypressino	−0.047	−1.102	1.183	−0.058	−0.032	−0.903	1.112	−0.191
Domat	−0.021	−1.033	0.481	0.317	−0.022	−0.647	0.309	0.038
Ecijano	−0.012	−0.528	0.368	0.168	−0.014	−1.099	1.045	0.280
Gaidouriola	−0.012	−0.613	0.400	0.316	−0.009	−0.262	−0.031	0.295
Gjhermana	−0.030	0.454	0.548	0.495	−0.012	−0.530	0.283	0.332
Grappola	−0.042	−0.645	0.451	0.360	−0.033	−0.657	0.583	0.102
Grossane	−0.054	−1.289	1.234	0.062	−0.027	−1.013	1.205	−0.181
Kalamata	−0.025	−0.860	0.214	0.635	−0.009	−0.476	0.200	0.300
Koroneiki	−0.020	0.275	0.902	0.110	−0.009	−0.560	0.813	−0.016
Kothreiki	−0.023	0.393	0.957	0.098	−0.010	−0.693	0.865	−0.097
Lucques	−0.023	−0.333	0.857	0.079	−0.022	−0.525	0.724	−0.117
Manzanilla	−0.036	0.131	0.612	0.453	−0.028	−0.565	0.619	0.193
Menara	−0.046	−1.233	1.193	0.056	−0.021	−0.749	0.789	−0.032
Meski	−0.018	−0.015	0.720	0.227	−0.009	−0.630	0.513	0.124
Olivière	−0.029	1.021	1.842	−0.588	−0.016	−0.295	1.666	−0.631
Picholine	−0.002	−0.252	1.091	−0.172	−0.004	−0.545	0.760	−0.228
Picholine Marocaine	−0.028	0.710	0.890	0.191	−0.020	−0.092	0.861	0.112
Picual	−0.045	−0.002	1.008	−0.007	−0.031	−0.258	1.072	−0.264
Razzola	−0.025	−0.124	0.836	0.108	−0.020	−0.581	0.703	0.015
Sofralik	−0.012	−0.612	0.402	0.325	−0.011	−0.263	−0.029	0.148
Sourani	−0.017	−0.923	0.650	0.278	−0.008	−0.630	0.513	0.119
Tanche	−0.057	0.780	1.223	−0.041	−0.039	0.045	1.237	−0.129
Verdale de l'Hérault	−0.029	−0.249	0.324	0.608	−0.023	−0.509	0.097	0.588

subject prone to guarantee. If $P \leq 0.65$, a specimen was affiliated at an upper level (node) of clustering (i.e. a 'group' of morphological group). Finally, if in spite of this procedure, probability does not reach an acceptable value, the stone was classifiable with no actual morphological group ('unclassified' in Table 5).

RESULTS

Size analysis

Canonical score 1 (CS1) of the CVA (expressing 56.7% of the total variance of individuals explained by the multivariate analysis) discriminates between stones with high MAL (CS1 > 0) and stones with low MAL (CS1 < 0) (Fig. 3). Canonical score 2 (CS2) (20.1% of variance explained) separates stones with high width (CS2 > 0) from stones with low width (CS2 < 0). The discrimination power of the analysis is equal to 60%. A Guttman effect was however noticed, indicating that the two canonical scores are at least partly correlated. Nevertheless, wild olive stones appear to have a low MAL but appear intermediate in term of width, when compared with cultivars (Fig. 3).

Measurements of charred stones from Amygdalolia, Arbequina, Chemlali of Sfax, Manzanilla and Picholine cultivars revealed that size shrinkage after carbonization is equal to 9–10% for variables of distance (e.g. 'MAL') and 17–19% for 'surface area of stone outline'. These coefficients are comparable with those reported by Kislev (1995). As the developmental state of olive stones collected by ancient human populations is not known, it is not possible to determine whether they reached their definitive size after fruit maturation.

Finally, the existence of correlations among size variables emphasizes limits of traditional morphometry to characterize olive stones and discriminate different populations. This shows that stone 'MAL', previously considered as a discriminant criterion between wild olive (MAL < 10 mm) and cultivated olive (MAL > 10 mm) as reported by Renfrew (1973), Marinval (1988), Leveau *et al.* (1991) and Buxó i Capdevila (1993), is insufficient to distinguish individuals from both botanical varieties. This constitutes a serious restriction for a comparative approach (modern/archaeological stones) and thus, for the assignment of archaeological specimens to extant wild populations or cultivated forms.

Shape analysis

Table 4 presents the results of analysis performed on test-samples. The effect of carbonization on stone shape was not significant. Similarly, no shape differences were observed between mature and immature stones and effects of environmental conditions were not significant at a regional and local scale. Finally, morphometric data from the two measurement sessions showed that measurement error is not responsible for a significant heterogeneity. Altogether, these results indicate the absence of significant confounding factors. This means that ancient specimens can be analysed together with wild modern specimens and cultivars.

On the two first dimensions of the CVA conducted on the regression parameters (67.7% of the variance), two groups of wild olive populations are clearly discriminated in relation to their geographical location in the Mediterranean Basin, except the Corsican population (Fig. 4). Western wild olive populations are distinguished from eastern wild olive populations on the basis of geometrical morphometric criteria. Moreover, 76% of wild olive stones are well classified in the CVA, whereas 99% of stones from cultivated varieties are distinguished from the wild.

UPGMA achieved according to the minimum Mahalanobis distance between clustered populations and cultivars is presented in Fig. 5. At a distance linkage equal to 5.12, cluster analysis distinguishes seven groups. Compared with olive

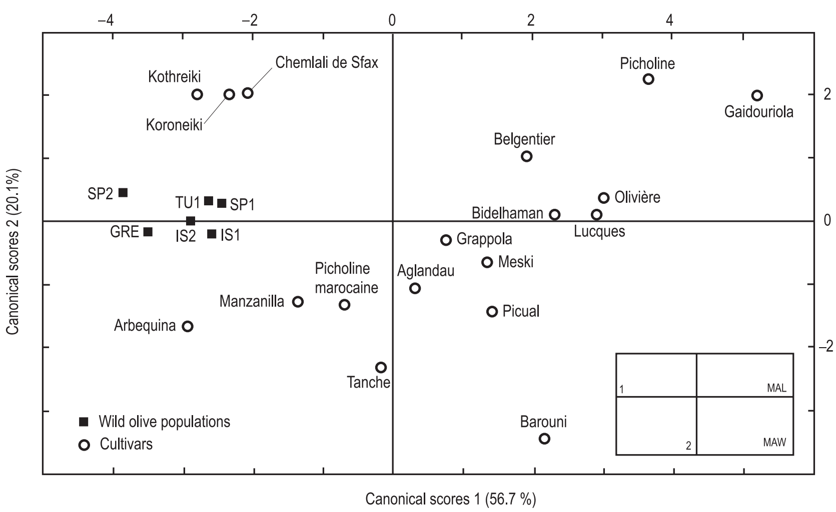

Figure 3 Canonical variate analysis biplot 1–2 showing extant wild olive populations and cultivars discriminated according to size. For more clarity, only consensus are represented.

Table 4 Effects of carbonization, maturation, environment and measurements errors on stone shape descriptors (bi parameters) tested by MANOVA.

		MANOVA		
Effect	Cultivars	Wilks test	*F*(8.51)	*P*-value
Maturation	Amygdalolia	0.92	0.57	0.80
	Arbequina	0.92	0.58	0.79
	Chemlali of Sfax	0.96	0.27	0.97
	Manzanilla	0.75	1.86	0.17
	Picholine	0.78	1.75	0.11
Carbonization	Amygdalolia	0.58	4.68	0.05
	Arbequina	0.99	0.45	0.94
	Chemlali of Sfax	0.94	0.41	0.92
	Manzanilla	0.98	0.15	0.99
	Picholine	0.99	1.84	0.99
Environment				
Regional conditions	Amygdalolia	0.78	1.85	0.11
	Arbequina	0.86	1.07	0.40
	Chemlali of Sfax	0.80	1.59	0.15
	Manzanilla	0.77	1.66	0.27
	Picholine	0.76	2.01	0.06
Local conditions	Arbequina	0.84	1.19	0.32
	Picholine	0.95	0.32	0.95
Measurement errors	Arbequina	0.99	0.05	0.99
	Picholine	0.98	0.15	0.98

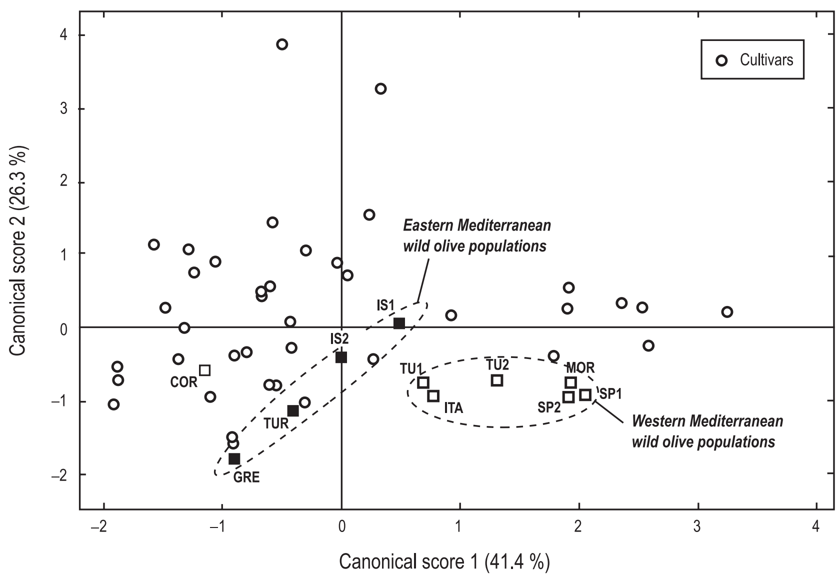

Figure 4 Canonical variate analysis biplot 1–2 showing extant western Mediterranean wild olive populations and eastern Mediterranean wild olive populations discriminated according to geometrical morphometric criteria.

groups defined *a priori* for the CVA (wild populations and cultivars), the overall posterior discriminant ratio (DR) corresponding to percentage of well-classified stones is, at this level of aggregation, higher than 75%. This threshold may be considered as reliable. These groups consist of:

- group I [subgroup Ia: Western Mediterranean wild olive populations except the Corsica one (DR = 75%); subgroup Ib: Arbequina, Tanche, Grossane, Chemlal of Kabylie, Cypressino and Menara (DR = 77.8%)],
- group II [Belle d'Espagne (DR = 50%)],
- group III [Israeli wild olive populations, Colombale, Barnea, Corniale and Picholine (DR = 75.3%)],
- group IV [subgroup IVa: Turkish and Corsican wild olive populations, Sourani, Chemlali of Sfax, Ayvalik, Domat and Kalamata (DR = 74.8%); subgroup IVb: Greek wild olive population and Verdale de l'Hérault (DR = 76.1%)],
- group V [subgroup Va: Aglandeau, Picual, Ascolana Tenera, Barouni and Grappola (DR = 75%); subgroup Vb: Amygdalolia, Manzanilla, Cailletier, Gjhermana, Bidelhaman, Meski, Koroneiki, Kothreiki, Lucques, Razzola and Picholine Marocaine (DR = 80%)],
- group VI [Ecijano (DR = 80%)],
- group VII [Belgentier and Olivière (DR = 75%)].

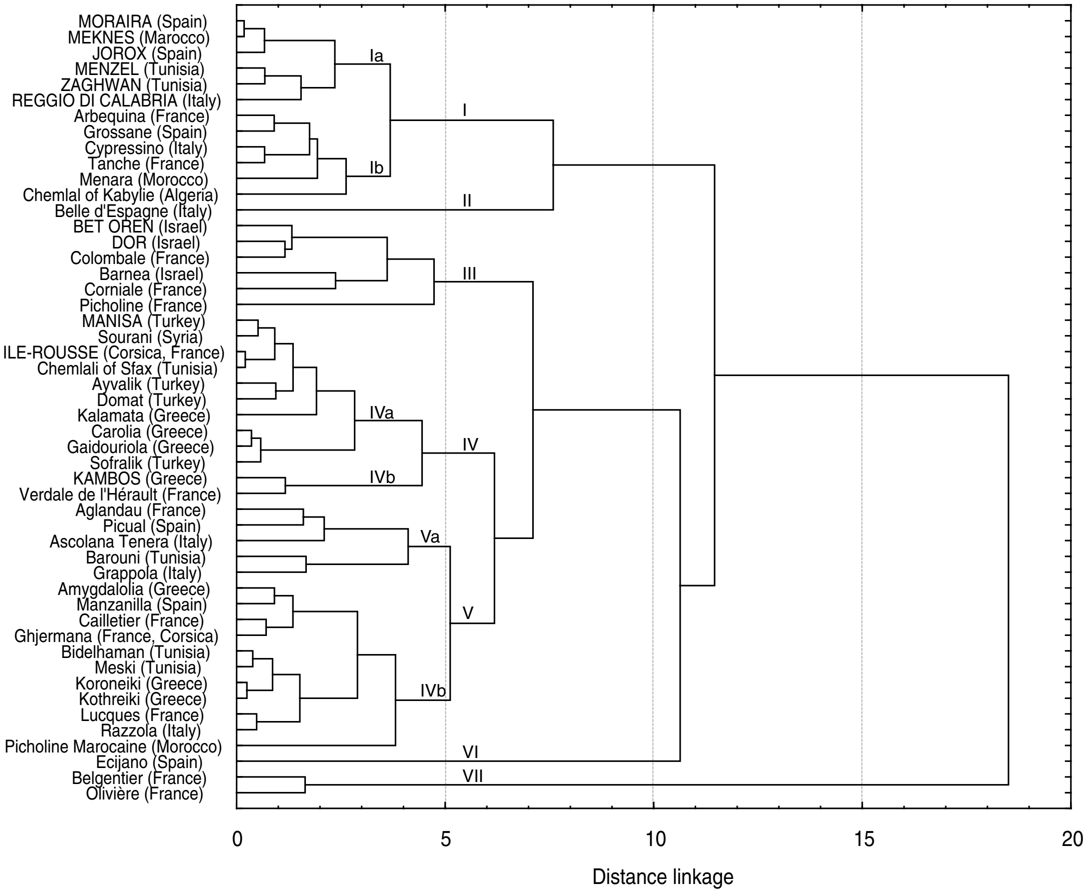

Figure 5 Cluster analysis (UPGMA) based on the minimum Mahalanobis distances among each wild olive populations and cultivars.

Allocation of archaeological stones at a chrono-geographical scale

Table 5 presents the allocation of archaeological stones to morphological types defined on the basis of results from CVA carried out on shape quantitative b_i parameters and cluster analysis. All the archaeological specimens dated before the Chalcolithic are allocated to the wild samples constituting the morphotype Ia. The first occurrence of a 'cultivated shape' appears during the Chalcolithic in Spain (Les Moreres) and the Bronze Age at Palmieri (Italy). This means that cultivated morphotypes appeared in Spain and Italy long before the introduction of oleiculture. In France, except the single Neolithic sample of Scaffa Piana (Corsica) identified as a stone from wild type, stones are contemporary or posterior than the introduction of the classical oleiculture.

Most of the sample specimens from the Iberic Period (around 200 BC at La Seña) in Spain and the Iron Age in France are allocated the IV morphotype. The fifth type appears in Spain during the Iberic Period and later in France, during the Roman Period. In these countries, it is only since the Roman Period that stones of the morphological type III seem to emerge. Finally, at Lattes-Port Ariane (Middle Age), one specimen was classified in the VII morphotype. The classification of one specimen to this group could constitute, in the present state of research, the first attestation of this morphotype. Types II and VI are never represented.

DISCUSSION

'East–west' distribution of wild olive populations and cultivars

Two morphological groups of wild populations can be distinguished (Fig. 4). Interestingly, they reflect the biogeographical division of the Mediterranean Basin proposed by Blondel & Aronson (1995). Based on climatic, ecological, historical and sociocultural factors, the Mediterranean Basin may be divided into four zones, among which the western and eastern Mediterranean areas are separated by a line running Adriatic Sea–Libyan Desert.

This relationship between morphological differentiation in olive trees and biogeographical divisions concord with results from studies based on chloroplast and mitochondrial DNA polymorphisms (Besnard & Bervillé, 2000; Besnard *et al.*, 2002a,b). The analysis of the cytoplasmic genetic

Table 5 Allocation of ancient stones to extant morphological types defined by UPGMA.

Archaeological site	Cultural period	n	Morphotype	Probability of allocation
Spain				
Cueva del Toro	Early Neolithic	1	Ia	0.89
Can Tintorer	Middle Neolithic	1	Unclassified	0.82
Campos	Chalcolithic	2	Ia	0.86
			Ia–Ib	0.76
Cova 120	Chalcolithic	1	Ia	0.92
Los Millares	Chalcolithic/Bronze Age	2	Ia	0.83
			Ib	0.79
Les Moreres	Chalcolithic	40	Unclassified ($n = 7$)	
			Ia ($n = 8$)	$0.76 \le P \le 0.91$
			Ib ($n = 10$)	$0.79 \le P \le 0.89$
			Ia–Ib ($n = 5$)	$0.69 \le P \le 0.93$
Seña	Iberic Period	14	Unclassified ($n = 2$)	
			IV ($n = 9$)	$0.76 \le P \le 0.89$
			III–IV ($n = 2$)	$0.63 \le P \le 0.73$
			V ($n = 1$)	0.65
Almadrava	Roman Period	40	Unclassified ($n = 4$)	
			Ia ($n = 3$)	$0.71 \le P \le 0.76$
			Ib ($n = 5$)	$0.80 \le P \le 0.90$
			Ia–Ib ($n = 3$)	$0.74 \le P \le 0.77$
			III ($n = 1$)	0.76
			IV ($n = 10$)	$0.74 \le P \le 0.78$
			III–IV ($n = 10$)	$0.72 \le P \le 0.81$
			V ($n = 4$)	$0.79 \le P \le 0.83$
Vilauba	Roman Period	4	Unclassified ($n = 1$)	
			Ib ($n = 1$)	0.87
			Ia–Ib ($n = 2$)	$0.74 \le P \le 0.78$
France				
Scaffa Piana	Late Neolithic	1	Ia	0.86
Oppidum de la Cloche	Iron Age	2	Ia–Ib	0.92
			IVa	0.70
Oppidum des Caisses	Iron Age	2	Ia	$0.74 \le P \le 0.90$
Notre Dame de la Pitié	Iron Age	2	Unclassified	
			Ib	0.86
Peixora	Roman Period	1	Ib	0.91
La Favorite	Roman Period	1	Ib	0.83
Vernègues	Roman Period	2	Vb ($n = 2$)	$0.76 \le P \le 0.79$
La Garde	Roman Period	23	Unclassified ($n = 3$)	
			Ib ($n = 6$)	$0.76 \le P \le 0.79$
			III ($n = 3$)	$0.76 \le P \le 0.86$
			IV ($n = 11$)	$0.75 \le P \le 0.89$
Chavéria	Roman Period	11	Ib ($n = 4$)	$0.77 \le P \le 0.94$
			Ia–Ib ($n = 4$)	$0.75 \le P \le 0.79$
			III ($n = 3$)	$0.70 \le P \le 0.77$
Lattara	Iron Age/Roman Period	11	unclassified ($n = 4$)	
			IV ($n = 2$)	$0.75 \le P \le 0.77$
			IV–V ($n = 5$)	$0.75 \le P \le 0.95$
	Roman Period	12	Unclassified ($n = 3$)	
			IV ($n = 5$)	$0.80 \le P \le 0.92$
			V ($n = 4$)	$0.77 \le P \le 0.89$
Lattes – Port Ariane	Middle Age	5	Unclassified ($n = 1$)	
			III ($n = 1$)	0.76
			IV ($n = 1$)	0.80
			V ($n = 1$)	0.86
			VII ($n = 1$)	0.87

Table 5 *continued.*

Archaeological site	Cultural period	n	Morphotype	Probability of allocation
Italy				
Palmieri	Bronze Age	30	Unclassified ($n = 7$)	
			Ia ($n = 9$)	$0.74 \leq P \leq 0.97$
			Ib ($n = 2$)	$0.79 \leq P \leq 0.82$
			Ia–Ib ($n = 9$)	$0.72 \leq P \leq 0.79$
			V ($n = 3$)	$0.71 \leq P \leq 0.79$

diversity has demonstrated a east–west segregation of wild olive populations characterized by two distinct groups of mitotypes. These morphological and genetic differentiations related to this biogeographical distribution can be explained by geographical isolation processes which have occurred over the last millennia. During the Quaternary period, climatic oscillations (Allen *et al.*, 1999) and anthropogenic pressures on vegetation (Blondel & Aronson, 1995) could have led to the scission of the former distribution area of *O. europaea* into two distinctive entities: one including Maghreb and south-eastern Europe and the other concerning Greece and near east. The probable rupture of the gene flow between these two geographical zones, as suggested by Besnard *et al.* (2002a,b) resulting from this geographical segregation, may explain the preservation of the integrity of the two olive morphotypes on both sides of the Mediterranean Basin.

As no relationship was shown between shape and developmental as well as environmental factors (in reference to Table 3), we may consider that clustering could represent the historical biogeography of wild populations and cultivars. Morphological proximity between the cultivars and the two wild morphotypes (east–west morphotypes) could attest from their geographical origin and shape comparison with archaeological stones may provide a temporal scale of these events.

Geography and history of olive domestication

The group constituted by the cultivars Arbequina, Tanche, Grossane, Chemlal of Kabylie, Cypressino and Menara (group Ib) is morphologically the nearest group to occidental Mediterranean wild populations. It is noteworthy that the first archaeological specimens closely resembling in shape to these cultivar stones are assigned to group Ib. This means that (1) olive domestication could have occurred at the Chalcolithic/Bronze Age in Spain, long before the introduction of oleiculture by classical people and (2) from ancestral wild forms, certainly by empirical selection.

From an agricultural point of view, two varieties of group Ib are remarkable. Nowadays, Arbequina cultivation is located in north-eastern Spain whereas the Tanche variety is confined to a small geographical area in the Baronnies region (see Fig. 2a). However, Cluster analysis indicates that these two cultivars are morphologically similar.

At an upper level of clustering, group II constituted by a single cultivar (Belle d'Espagne) indicates a morphology close to an ancestral one. However, as no archaeological specimens are similar to this group, it is not possible to date its probable appearance. The next level of clustering includes wild eastern Mediterranean samples and cultivars originated from the Mediterranean Basin. Interestingly, group IV expresses a clear geographical unity. Actually, except Verdale, Chemlali of Sfax and the wild olive form from Ile-Rousse (Corsica, France) which is probably a feral form (A. Bervillé, pers. comm.), the fourth group is constituted by cultivars from the eastern Mediterranean Basin. The fifth group covers a large geographical area and includes cultivars from the eastern and western Mediterranean. We note the strong morphological convergence between Greek (Kothreiki and Koroneiki) and Tunisian cultivars (Bidelhaman and Meski). Moreover, in the case of Palmieri, the allocation of three archaeological stones to this group gives rise to the problem of an early introduction in Italy of cultivars from eastern Mediterranean areas and/or from North Africa.

Similarly, group III expresses a morphological heterogeneity. It pools Israeli samples (wild and cultivated) together with three French cultivars. This heterogeneity may reflect the scale of human migrations, which spread olive cultivation through the Mediterranean Basin.

An interesting result concerns the extreme differentiation of the Belgentier and Olivière cultivars (group VII). The shape divergence that characterizes these two samples with regard to all others appears quite higher than those observed between wild and cultivated varieties. Until the beginning of the twentieth century, culture of Olivière was very widespread in Languedoc (Southern France) (Degrully, 1907). Nowadays it is confined to the Occidental Pyrenees, whereas cultivation area of Belgentier is restricted to south-eastern France. From a genetic point of view, Olivière is a male sterile variety characterized by a specific mitochondrial DNA marker (MCK mitotype) common in some Languedocian and Kabylian cultivars (Besnard & Bervillé, 2000). This genetic specificity has been considered as evidence of an indigenous origin of Olivière domestication in the western Mediterranean.

Although our morphometric results correlated with molecular data, we were not able to date the origin of their domestication. Concerning Belgentier, we have no data other than its geographical proximity to Olivière. The hypothesis that the Belgentier cultivar would derive from the Olivière should be tested.

The classical history of the Mediterranean region and particularly of human populations provides additional elements to argue the chronological appearance of cultivated forms. The geographical distribution of cultivars of groups IV and V may be related to our knowledge about trading contacts between Greeks and Phoenicians, which occurred *c.* 1000 years BC in the Aegean Sea. Later, Phoenicians conquered the southern Mediterranean coast and founded several countries and cities in Northern Africa, particularly Carthage in 814 years BC. Carthage became the hub of Phoenician trade from where merchant ships sailed to Spain (Gras, 1995). The existence of the Andalousian Manzanilla in the fifth group may support the classification of this group V to a Phoenician route. The distribution of cultivars, morphological differentiation and chronological appearance of forms of these groups may be affiliated to the expansion of Roman Empire which, after the fall of Carthage around 150 years BC, spread around the Mediterranean Basin.

In archaeological stones, the chronological differentiation of cultivated forms identified is remarkable; this phenomenon may be consistent with importation of cultivated varieties. Stones from the Can Tintorer and Cueva de Toro Neolithic sites and from the Chalcolithic/Bronze Age site are attributed to the wild type. Among the Bronze Age sites, the earliest stones from cultivated olive (one sample from Los Millares and 10 from Les Moreres) are identified under a form close to stones of group Ib. As mentioned above, this is the earliest evidence of selective practices applied to olive in Spain. It confirms previous hypotheses consistent with the emergence from the Neolithic of a selective exploitation of olive and, from the Bronze Age, with a management of populations for fruit production (Terral & Arnold-Simard, 1996; Terral, 2000). Later, at La Seña and L'Almadrava, this cultivated form seems to have been supplanted by allochthonous cultivated forms (group IV). This observation seems to confirm the preponderant influence of classical cultures on autochthonous human populations that inherited progressively foreign ways, customs and traditions.

Finally, during the Roman Period and in the Middle Age, we see further diversification of olive varieties. Stones from Greek and north African types become the most frequent. At the end of the last millennium BC, the diversification of cultivars during the Roman Period may be related to the development of olive cultivation and demands for derived products: fruits, oil for domestic use (lighting and cooking) and unguents. But it appears that Romans have only restructured and developed cultivation practices and olive oil economy, already well implanted since the Iron Age (Pérez Jordà, 2000).

CONCLUSION

Morphometric analyses applied to wild and cultivated olive stones from various Mediterranean origins give a basis for comparing archaeological specimens in order to infer the historical biogeography of olive domestication.

Wild olive stones may be distinguished from cultivated forms by shape analysis but not by size. At the Mediterranean scale, patterns of morphological changes testify the complexity of exchanges among classical populations which spread olive cultivation from east to west through the Mediterranean Basin (Besnard & Bervillé, 2000).

When archaeological olive stones are compared with stones of modern cultivars, an early and autochthonous olive domestication in north-western Mediterranean areas is suggested. The appearance of cultivated forms at the Chalcolithic/Bronze Age seems to corroborate that farming and selective practices have been operated at least since that time.

These results support hypotheses from previous bioarchaeological and palaeoenvironmental studies that evidence the emergence of cultivation practices from the Neolithic and the Bronze in Spain (Terral & Arnold-Simard, 1996; Terral, 2000). In this case, new, more successful operations of selection and cultivation practices would have begun during the Bronze Age.

ACKNOWLEDGMENTS

We thank Stéphanie Thiébault (CNRS, Nanterre) and Jean-Paul Roger (Parc National de Port Cros), Nathalie Moutier (INRA, Mauguio) and Cristóbal Rubio (Paleontología, Zaragoza) for their help and assistance during sampling sessions. We are also grateful to J.-C. Auffray (ISEM, Montpellier) for his technical support, suggestions and criticisms during the preparation of this present work, G. Besnard (Univ. Nancy) and A. Bervillé (INRA, Montpellier) for discussions, as well as Isabel Figueiral (CEB, Montpellier) and Nick Rowe (AMAP, Montpellier) for English improvement. This work is supported by the CNRS APN project 'Fruticulture et patrimoines variétaux' and the GDR CNRS 2474 'Morphométrie et Evolution des Formes'. We thank the two anonymous referees for their interesting and constructive comments.

REFERENCES

Allen, J.R.M., Brandt, U., Brauer, A., Hubberten, H.-W., Huntley, B., Keller, J., Kraml, M., Mackensen, A., Mingram, J., Negendank, J.F.W., Nowaczyk, N.R., Oberhänsli, H., Watts, W.A., Wulf, S. & Zolitschka, B. (1999) Rapid environmental changes in southern Europe during the last glacial period. *Nature*, **400,** 740–743.

Amouretti, M.-C. & Comet, G. (1992) *Le livre de l'olivier*. Edisud, Aix-en-Provence.

Besnard, G. & Bervillé, A. (2000) Multiple origins for Mediterranean olive (*Olea europaea* L. ssp. *europaea*) based upon mitochondrial DNA polymorphisms. *Comptes Rendus de l'Académie des Sciences, Paris (Sciences de la Vie)*, **323,** 173–181.

Besnard, G., Khadari B., Baradat, P. & Bervillé, A. (2002a) *Olea europaea* (Oleaceae) phylogeography based on chloroplast DNA polymorphism. *Theoretical and Applied Genetics*, **104,** 1353–1361.

Besnard, G., Khadari B., Baradat, P. & Bervillé, A. (2002b) Combination of chloroplast and mitochondrial DNA polymorphisms to study cytoplasm genetic differentiation in the olive complex (*Olea europaea* L.). *Theoretical and Applied Genetics*, **105,** 139–144.

Blondel, J. & Aronson, J. (1995) Biodiversity and ecosystem function in the Mediterranean Basin: human and non-human determinants. *Mediterranean-type Ecosystems. The function of biodiversity* (ed. by G.W. Davis and D.M. Richardson), pp. 43–119. Springer-Verlag, Berlin.

Bogani, P., Cavalieri, D., Petruccelli, R., Polsinelli, R. & Roselli, G. (1994) Identification of olive tree cultivars by using random amplified polymorphism DNA. *Acta Horticulturae*, **356,** 98–101.

Bookstein, F.L. (1991) *Morphometric tools for landmark data. Geometry and biology*. Cambridge University Press, Cambridge.

Brun, J.-P. (1986) *L'oléiculture antique en Provence, les huileries du département du Var. Sup. Revue Arch*. Narbonnaise, Paris.

Buxó i Capdevila, R. (1993) Des semences et des fruits. Cueillette et agriculture en France et en Espagne méditerranéenne du Néolithique à l'Age du Fer. Unpublished PhD Dissertation, University Montpellier II, Montpellier.

de Candolle, A. (1886) *Origine des plantes cultivées*, 379 p. Deuxième édition. Librairie Germer Baillière et Cie, Paris.

Chapman, R. (1990) *Emerging Complexity. The later prehistory of south-east Spain, Iberia and the west Mediterranean*, 304 p. Cambridge University Press, Cambridge.

Chevalier, A. (1948) L'origine de l'olivier et de ses variations. *Revue internationale de Botanique appliquée et d'agriculture tropicale*, **303/304,** 1–24.

Degrully, L. (1907) *L'olivier*, 223 p. Coulet et fils éditeurs, Montpellier.

Diamond, J. (2002) Evolution, consequences and future of plant and animal domestication. *Nature*, **418,** 700–707.

Fabbri, A., Hormaza, J.I. & Polito V.S. (1995) Random amplified polymorphic DNA analysis of olive (*Olea europaea* L.) cultivars. *Journal of the American Society for Horticultural Science*, **120,** 538–542.

Gil Mascarell, M. (1992) La agricultura y la ganadería como vectores económicos del desarrollo del Bronce valenciano. *Saguntum*, **25,** 49–68.

Gilman, A. (1976) Bronze age dynamics in southeast Spain. *Dialectical Anthropology* **1,** 307–319.

Gilman, A. (1990) The mafia hypothesis. *When worlds collide: the Indo-European and the Pre-Indo-Europeans* (ed. by T. L. Markey and J. A. C. Greppin), pp. 151–169. Ann Arbor, Karoma Publishing.

Gras, M. (1995) *La Méditerranée archaïque*. Armand Colin eds, Paris.

Hamrick, J.L., Linhart, Y.B. & Mitton, J.B. (1979) Relationships between life history characteristics and electrophoretically detectable genetic variation in plants. *Annual Review of Ecology and Systematics*, **10,** 173–200.

Hauville, A. (1953) La répartition des variétés d'oliviers en Algérie et ses conséquences pratiques. *Bulletin de la Société Agricole d'Algérie*, **580,** 1–8.

Khadari, B., Breton, C., Besnard, G., Roger, J.-P. & Bervillé, A. (2001) Molecular characterization and genetic structure of olive germplasm collection in Conservatoire Botanique National Méditerranéen de Porquerolles using Nuclear RAPD markers and RFLP of Mitochondrial DNA. *Acta Horticulturae*, **546,** 433–437.

Kislev, M.E. (1995) Wild olive endocarp at submerged Chalcolithic Kfar Samir, Haifa, Israel. *Journal of the Israel Prehistoric Society*, **26,** 134–145.

Leveau, P., Heinz, C., Laval, H., Marinval, P. & Medus, J. (1991) Les origines de l'Oléiculture en Gaule du sud. Données historiques, archéologiques et botaniques. *Revue d'Archéométrie*, **15,** 83–94.

Marinval, P. (1988) Cueillette, agriculture et alimentation de l'Epipaléolithique jusqu'au deuxième Age du Fer. Unpublished PhD Dissertation, EHESS, Paris.

Moutier, N., Lauri, P.E., Khadari, B., Besnard, G., Bervillé, A. & Dosba, F. (2001) Olive research programmes at the INRA, Montpellier. *Olivae*, **86,** 30–33.

Ouazzani, N., Lumaret, R., Villemur, P. & Di Guisto, F. (1993) Leaf alloenzyme variation in cultivated and wild olive trees (*Olea europaea* L.). *Journal of Heredity*, **84,** 34–42.

Ouazzani, N., Lumaret, R. & Villemur, P. (1994) An evaluation of approach the genetic variability of olive tree using enzymatic markers. *Acta Horticulturae*, **356,** 91–94.

Ouazzani, N., Lumaret, R. & Villemur, P. (1995) Apport du polymorphisme alloenzymatique à l'identification variétale de l'olivier (*Olea europaea* L.). *Agronomie*, **15,** 31–37.

Ouazzani, N., Lumaret, R. & Villemur, P. (1996) Genetic variation in the olive tree (*Olea europaea* L.) cultivated in Morocco. *Euphytica*, **91,** 9–20.

Pérez Jordà, G. (2000) La conservación y la transformación de los productos agricolas en el mundo ibérico. *Saguntum Extra*, **3** (III reunion sobre economia en el Món ibèric), 47–68.

Pontikis, C.A., Loukas, M. & Kousounis, G. (1980) The use of biochemical markers to distinguish olive cultivars. *Journal of Horticultural Science*, **55,** 333–343.

Renfrew, J.M. (1973) *Palaeoethnobotany. The food plants of the Near East and Europe*, 248 p. Columbia University Press, New York.

Rohlf, F.J. (1990) Fitting curves to outlines. *Proceedings of the Michigan Morphometric Workshop* (ed. by F.J. Rohlf and F.L. Bookstein), pp. 167–177. The University of Michigan Museum of Zoology, Ann Arbor, MI.

Ruby, J. (1918) *Recherches morphologiques et biologiques sur l'olivier et sur ses variétés cultivées en France*. Première thèse de Doctorat es Sciences Naturelles, Paris.

Slice, D.E., Bookstein, F.L., Marus, L.F. & Rohlf, F.J. (1996) A glossary for morphometrics. *Advances in morphometrics* (ed. by L.F. Marcus, M. Corti, A. Loy, G.J.P. Naylor and D.E. Slice), pp. 531–551. Plenum Press, New York.

Terral, J.-F., (2000) Exploitation and management of the olive tree during Prehistoric times in Mediterranean France and Spain. *Journal of Archaeological Science*, **27,** 127–133.

Terral, J.-F. & Arnold-Simard, G. (1996) Beginnings of olive cultivation in relation to Holocene bioclimatic changes. *Quaternary Research*, **46,** 176–185.

Trujillo, I. & Rallo, L. (1995) Identifying olive cultivars by isozyme analysis. *Journal of the American Society for Horticultural Science*, **120,** 318–324.

Trujillo, I., Rallo, L., Carbonell, E.A. & Asins, M.J. (1990) Isoenzymatic variability of olive cultivars according to their origin. *Acta Horticulturae*, **296,** 137–140.

Turill, W.B. (1951) Wild and cultivated olives. *Kew Bulletin*, **3,** 339–342.

van Zeist, W. (1980) Aperçu de la diffusion des végétaux cultivés dans la région méditerranéenne. *La mise en place, l'évaluation et la caractérisation de la flore et des végétations circum méditerranéennes*, pp. 129–145. Coll. Fondation L. Emberger, Naturalia Monspeliensa.

Zohary, D. & Spiegel-Roy, P. (1975) Beginning of fruit growing in the Old World. *Science*, **187,** 319–327.

BIOSKETCHES

Jean-Frédéric Terral is a University Lecturer in Biology and Botany at the University of Montpellier 2 (Sciences et Techniques du Languedoc). His main research interests include palaeoenvironmental and palaeoclimatic changes, history of cultivation and evolution of woody plants under domestication through quantitative ecoanatomical and morphometric approaches.

Natalia Alonso, Ramon Buxó i Capdevila, Girolamo Fiorentino, Philippe Marinval, Guillem Perez Jorda, Bénédicte Pradat and **Núria Rovira** are archaeobotanists focusing their studies on the history of cultivated plants and human vegetal feeding.

Noureddine Chatti is a University Lecturer in evolutionary genetics at the Institut de Biotechnologie de Monastir (Tunisia). His main research interest concerns chromosomal and genetic differentiation in local populations and reproductive isolating mechanisms.

Laurent Fabre is an archaeobotanist and biologist. His researches are centred on reconstruction of palaeoenvironments under anthropogenic impact (INRAP – Montpellier and UMR 5059 CNRS).

Paul Alibert is a University Lecturer in Evolutionary Biology at the University of Bourgogne (Dijon, France). His main research interest concerns morphometric appraisal of population differentiation and speciation.