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Article

Shape Diversity of Olive Stone, Resulting from Domestication and Diversification, Unveils Traits of the Oldest Known, 6500-Years-Old Table Olives from Hishuley Carmel Site (Israel)

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Abstract: The first exploited and domesticated olive forms are still unknown. The exceptionally well-preserved stones from the submerged Hishuley Carmel site (Israel), dating from the middle of the 7th millennium BP, offer us the opportunity to study the oldest table olives discovered so far. We apply a geometrical morphometric analysis in reference to a collection of modern stones from supposed wild populations and traditional varieties of various origins, genetic lineages and uses. Analyses carried out on modern material allow to characterize the extent of stone morphological variation in the olive tree and differentiate distinct morphotypes. They also allow to discuss the status of supposed wild populations and interpret the divergence between groups of varieties and their wild progenitors in an evolutionary and biogeographical perspective. Shape of archaeological stones compared to the differentiation model, unveils morphological traits of olives most likely belonging to both wild olive trees and domesticated forms, some of them showing a notable domestication syndrome. This forms at the early stages of domestications, some of which surprisingly morphologically close to modern varieties, were probably used for dual use (production of olive oil and table olives), and possibly contributed to the dispersion of the olive tree throughout the Mediterranean Basin and to its subsequent diversification.

Keywords: archaeobiology; domestication and diversification; morphometrics; *Olea europaea* L. subsp. *europaea* (olive tree); perennial crop history; shape diversity; table olives

1. Introduction

The olive tree (*Olea europaea* L. subsp. *europaea*.) is undoubtedly the iconic fruit tree of the Mediterranean Basin. Its origins are enrooted in a palaeogeographical and palaeoecological history of several million years and linked with the Mediterranean climate [1–3]. The wild olive tree or oleaster (*O. e.* subsp. *e.* var. *sylvestris*), the ancestor of all the cultivated varieties (*O. e.* subsp. *e.* var. *europaea*) [4], is a characteristic element of the Mediterranean vegetation, in particular of the meso-thermomediterranean bioclimatic stages of which it is one of its main markers [5]. It can be found, often mixed with numerous feral individuals escaped from cultivation [6], in the matorrals and woodlands of xerophytic Mediterranean areas. It is currently present in the Levant, Turkey, the Peloponnese and coasts of mainland Greece, the Maghreb, the Southern Iberian Peninsula, Southern Italy, Cyrenaica (Lybia), the Mediterranean islands and, much more sporadically on the Northern Mediterranean coast [7]. Its distribution area is less extensive than that of the cultivated olive tree. Nowadays, more than 1200 olive varieties are cultivated all around the Mediterranean which accounts for 90% of the cultivated area globally [8], to produce oil and table olives (<https://www.internationaloliveoil.org/> (accessed on 25 October 2021)).

Palaeobotanical and archaeobotanical findings show that the oleaster persisted in the Mediterranean, even at the height of the pleniglacial cooling [9,10]. Very scarce carpological data are related to Palaeolithic and Mesolithic hunter-gatherer populations that lived on the shores of the Mediterranean during the last glacial period and the early Holocene. The occasional recordings of olive stones, however, show that wild olives were sometimes consumed. As such, the example of the underwater site of Ohalo II, in the Sea of Galilee, is quite exceptional because of the discovery of thousands of charred fruits and seeds, including olive stones, which are evidence of the diet of the Epipaleolithic hunter-gatherers who lived in this habitat around 21,000–18,000 BP [11,12]. The existence of refuges during the Last Glacial Maximum, in the Near East, in the south of the Iberian Peninsula, as well as probably in North Africa and Sicily, would have favored a rapid expansion of the oleaster on the shores of the Mediterranean with the Holocene warming. The rapid Holocene expansion of olive populations was driven first by climatic factors and then by human activity, as shown by *Olea* palynological records, increasing over time in both the Eastern and Western Mediterranean Basin [10,13–15]. Olive macro-remains become more common between 11,000 and 5000 BP and penetrated new regions, particular in Western Mediterranean areas [16,17].

Recent genetic studies based on nuclear microsatellite and plastid markers revealed an East-West differentiation of oleaster populations [18–22]. A coalescent-based Bayesian approach has further specified the geographic structure of the oleaster genetic diversity in the Mediterranean, consisting of 3 distinct lineages [21–23]: E1, from the Peloponnese (Greece) to the Levant; E2 and E3 in the western part of the Mediterranean Basin.

Olive domestication is considered to have begun in the Levantine region during the Chalcolithic period (6000–5500 BP) [7,13,24–27]. The beginnings of oleiculture in the Near East are already well documented, both by archaeology and archaeobotany, but also by written sources [7,28,29]. Rock-hewn structures observed at several sites in Jordanian highlands were interpreted as olive mills dating back to the Chalcolithic period [30]. Around the same period, archaeobotanical remnants (stones, charcoal) of olive trees are more frequent. Stones found in archaeological excavations are often fragmented what is generally regarded as a marker of oil extraction. In reference to the Oleaster distribution range assessed by a genetic model [21], some of these sites located outside of the bioclimatic zone where the oleaster can grow today, were interpreted as a reliable sign of cultivation and agronomical developments (crop irrigation, seedling transplantation and probably grafting) [7,27,31,32]. Olive remains from Kfar Samir, a submerged site off the Carmel Coast located some 1800 m north of Hishuley Carmel site, provide an early evidence (around 7000 BP) for oil extraction [25,33]. Their morphometric patterns were studied using traditional morphometry [34]. Results show new evidence of olive exploitation, probably oleaster, supporting the hypothesis that olive exploitation and management

emerged centuries before domestication. A similar pattern of pre-domestication phase was recorded in Spain in the 3rd and 2nd millennium BP [35,36]. At Ebla (Syria), during the Bronze Age (5th millennium BP), administrative records engraved on clay tablets show vast olive plantations under royal control, with tax royalties paid by peasants in the form of oil [28].

According to archaeological and archaeobotanical data, from the Levantine primary domestication centre, selected olive forms, slowly and gradually diffused, probably by vegetative propagation through cuttings or grafting, and so is the associated agronomic knowledge and techniques. They first reached the Aegean around 4500 BP, then the central and western Mediterranean where domesticated olives have been found in Italy and Spain in the Late Bronze Age, around 3200–3000 BP [26,37,38]. Finally, they reached Southern France around 2800–2600 BP.

In many occidental areas, domesticated olive forms introduced from the Eastern Mediterranean have crossed with local wild or domesticated ones [39]. These secondary domestication centres have played a fundamental role in the adaptation of non-native varieties and the diversification of the olive tree. Hence, selection events took place independently of the primary centre, as in Southwestern Spain, 1500–1000 years before the introduction of new varieties probably through the Phoenicians [40]. Subsequently massive and repeated arrival of new domesticated forms totally blurred the original local genetic diversity. Later, the Roman oleiculture has left in all Mediterranean countries numerous and varied archaeological remains which provide valuable documentation for apprehending the development of this production in space and time [28,41]. Olive oil production sites can be identified by the presence of mills or grinders, presses, vats, and cellars with storage jars, as well as crushed stones representing waists of extraction. Amphora manufacturing workshops are generally located in the production areas. These containers, often characteristic of a particular content (e.g., oil, wine, fish sauces) and intended for exchanges and trades transport for exchange, also make it possible to follow commercial interactions in the ancient world [42].

In spite of this abundance of archaeological, bio-archaeological, historical and genetic data acquired over the last 20 years, the characteristics and identity of the first domesticated varieties, especially those that were used for the production of table olives, are still unknown. Moreover, the ancient texts and treatises mentioning different types of olive trees do not seem to be usable for identifying ancient varieties [43]. In these texts, there is mainly mention of methods, recipes and preparation processes that may vary according to the degree of fruit maturity (green and black olives) such as debittering, use of condiments to improve the taste (seasoning) and preservation processes for commercial purposes and transport.

The discovery of numerous waterlogged stones in Hishuley Carmel (Figure 1), a submerged site off the Carmel Coast (Israel) in the heart of the olive domestication cradle, offers an unprecedented opportunity to provide new insights into the possible first olive varieties. Some of these stones have been analysed in a preliminary way using a comparative approach of traditional morphometry [33]. Sizes of these archaeological stones were compared to those of stones of two current local varieties (Souri, a traditional local variety and Barnea, a modern variety developed in the 1970s in Israel). This previous analysis study, based on a narrow modern reference collection and morphological characters greatly influenced by environmental conditions [40,44,45], suggested that the stones from the Hishuley Carmel site could belong to wild forms ('undomesticated'), without excluding the hypothesis that they could be derived from domesticated olive trees [33].

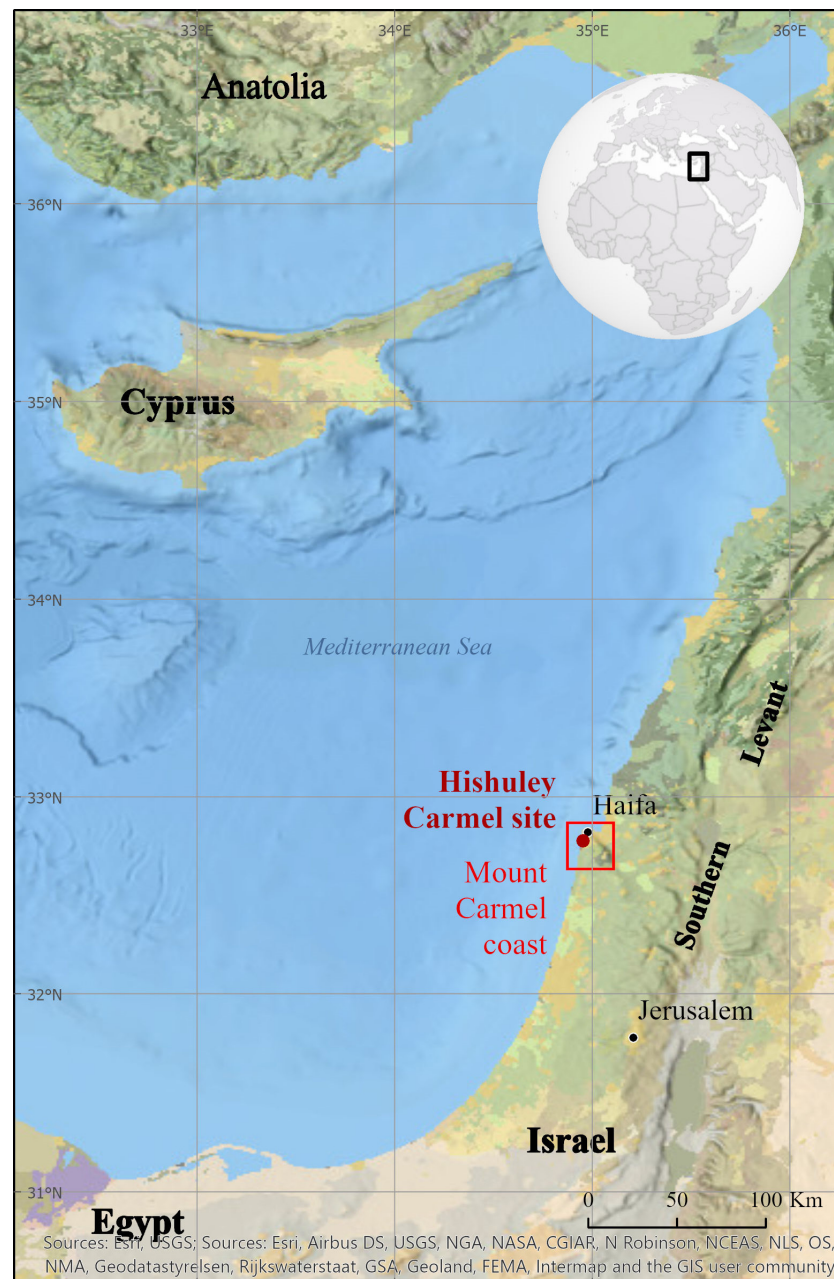


Figure 1. Location of Hishuley Carmel site (Israel).

The present study focuses on the morphological changes of olive stones associated with their domestication and on identification of shape changes that accompanied, the selection pressures occurring during the domestication process (domestication syndrome). It uses geometric morphometry applied to archaeological stones, further compared to a reference collection of wild olives, feral forms and modern varieties. Firstly, it aims at deciphering the morphological diversity of olive stones and identify the relationships between stone shape, use of varieties and biogeographical, biological and genetic traits of the modern olives. Then, comparison of such morphological signatures of waterlogged olive stones recovered from two distinct structures in Hishuley Carmel site, with this reference discriminant model is performed for the first time. It is expected to reveal the features of some of the oldest domesticated forms in the Levantine cradle of olive domestication, whose fruits were used to produce table olives, as shown by archaeology. Results are placed in a more general context, relating to the evolutionary and biogeographical history of the olive tree in the Mediterranean.

2. Materials and Methods

2.1. Plant Material

Archeological stones were recovered in 2011 in the submerged prehistoric site of Hishuley Carmel, on the Mount Carmel coast (Israel) (Lat. 32.77714—Long. 34.95371), in the course of underwater surveys (Figure 2). Stones were located in 2 distinct constructed structures (A and B), 3 m apart, and interpreted as installations used for table olives production [33]. Archaeological data and experiments demonstrated that stones are issued from fruits prepared (debitting, pickling or dry salting) to be consumed as a whole (table olive).



Figure 2. Olive stones from Hishuley Carmel site during cleaning, sorting and recovery (photo taken by Sarah Ivorra).

Numerous stones were collected from these two structures and have been carefully examined. Ninety-nine from A and 148 from B, apparently undeformed, unbroken, and thus well-preserved olive stones were sampled to be analyzed using the geometric morphometric method presented below. A subsample of few olive stones from each structure were dated by ^{14}C .

The modern material consists of 319 stones from supposed 17 wild olive populations (Table S1) and 1641 stones from 55 varieties (Table S2) from various geographical origins in the Mediterranean Basin. Some of them are synonymic varieties such as Koroneiki and Psilolia (Crete) and, Athalassa and Lefkara (Cyprus). They correspond to the same cultivar, thus to the same genotype, but are named differently according to geographical and/or cultural factors. Three varieties from different countries [Souri (Israel), Sourani (Syria) and Istambuli (Turkey)] are suspected to be the same cultivar. Thus, the shape of these varieties is supposed to be identical or very similar.

Stones were collected between 1994 and 2019 in the course of field surveys, either by our team or through collaborations. All the stones from varieties were collected in the 'Conservatoire Botanique National Méditerranéen de Porquerolles' (Porquerolles Island, France), the Melgueil INRAE collection (Maugio, France), the experimental station of Tassaout (WOGB-Marrakech, INRA-Morocco), olive groves of the Peloponnese, Phocis and Crete (Greece), and orchards of Galilee (Israel), in order to have a representative sample of the current diversity of olive cultivated around the Mediterranean Basin.

2.2. Stone Shape Analysis

All analyses were performed in the R 4.0.0 [46] with the *Momocs* 1.3.1 package for morphometrics [47,48], *MASS* 7.3.51.6 [49] for discriminant analyses and their cross-validation, hierarchical clustering analysis and *ape* for unrooted tree representation [50].

The olive stone is a sclerified endocarp whose shape varies from subspherical to fusiform, according to its genetic origin (Figure 3). It is composed of two merged asymmetric valves (fertile and sterile) protecting one seed and merged at the level of a suture line. Each valve is a carpellar leaf, itself asymmetrical when observed in dorsal view. In order to remove the potential effect of asymmetry, the outlines are positioned so that Size (Right side) > Size (Left side) (Figure 3).

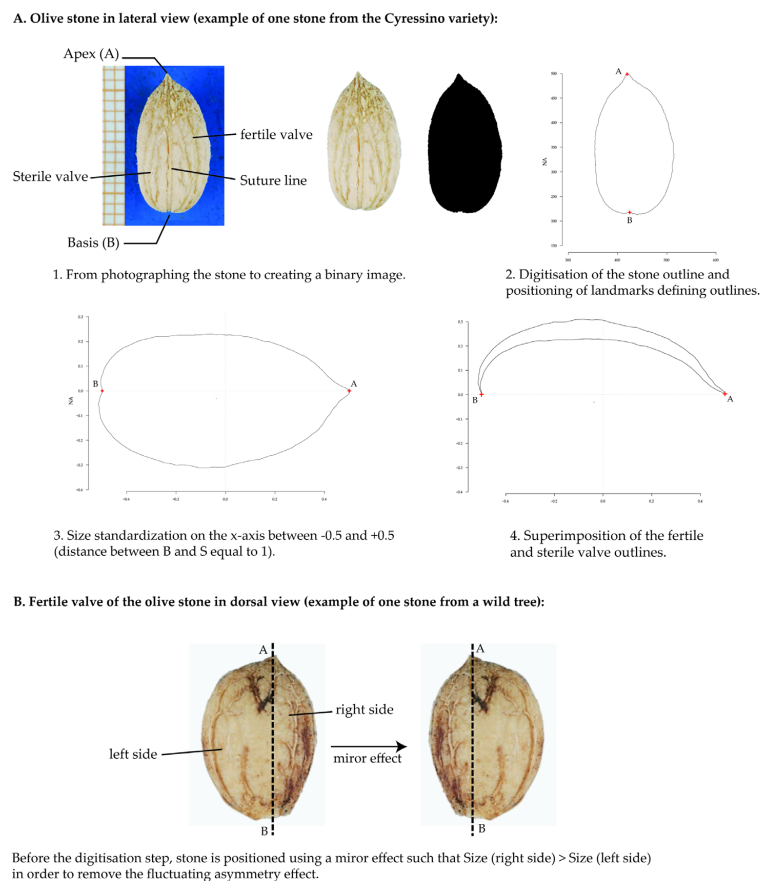


Figure 3. The morphometric protocol applied to olive stones described step by step (Sarah Ivorra and Jean-Frédéric Terral, CNRS/UM—ISEM).

The 4 open outlines (fertile and sterile valves in lateral view; right and left sides of sclerified carpellar leaf in dorsal view) were defined in a first session by 20 and in a second by 120 landmarks ($x; y$) including the 2 homologous points [Basis (B) and apex (A) of stone]. Our objective was to test the descriptive power of open outlines in relation to the number of landmarks used, in other words, to test if the use of a large number of landmarks allowed to better capture the morphology of open outlines (Figure 3).

In previous works, such open outlines were fitted using a polynomial regression [40,51], a third-polynomial curve was used to characterize olive valve open outlines. This fitting appears to be a suitable compromise between quadratic polynomial curve (x^2 —parabolic) which is too imprecise and a fourth-degree polynomial curve which tend to exaggerate local irregularities of outline. Unfortunately, the use of the third-polynomial curve does not make it possible to record the acuminate or pointed apex, characteristic of stones of certain varieties such as ‘Olivière’.

Finally, each stone was defined by 2 equations: (1) Fertile valve: $y_F = b_0 + b_1x + b_2x^2 + b_3x^3$; (2) Sterile valve: $y_S = b'_0 + b'_1x + b'_2x^2 + b'_3x^3$

The b_i coefficients, including the intercept b_0 , were used as quantitative variables in further statistical analyses. But, in such natural polynomial equations b_i coefficients are correlated and change along increasing fitting degrees. This is why we use finally the orthogonal polynomials, also called Legendre's polynomials, as a method of fitting a least-squares curve along each valve outline and providing uncorrelated coefficients.

Legendre polynomials are the simplest of the orthogonal polynomials because their weight function is equal to 1. For n -Legendre polynomials, $P(x)$, that are recursive [52], and n -Legendre coefficients, c , that are used as shape descriptors, expansion of the width function, $W(x)$, is:

$$W(x) = \sum_1^N C_n P_n(x)$$

The width function $W(x)$ is a linear combination of Legendre polynomials of degree n in x , and each Legendre coefficient, C_n , is an independent shape descriptor because of orthogonality. Legendre polynomials form a complete orthogonal system based on the interval $[-1, 1]$ and a weight function (ρ) of 1. Expansion of the width function represents the expression of Legendre polynomials as a series. From (x, y) coordinates of olive stone valve outline, uncorrelated coefficients from orthogonal polynomial regression are used as numerical shape descriptors. Practically, they were obtained using the *opoly* function in the *Momocs* package [47].

Each stone (modern and archaeological) generated 16 quantitative parameters (8 for the lateral side—4 for the fertile valve and 4 for the sterile valve; 8 for the dorsal side—4 for the right side and 4 for the left). These 16 quantitative parameters of shape are used for multivariate statistical analyses.

2.3. Statistical Analyses

The descriptive power of the two digitalization approaches (open outlines defined by 20 and 120 landmarks) was tested using RV test by comparing the 2 morphological distance matrices expressing morphological disparity between both wild populations and varieties. Potential differences in shape among the 2 archaeological stone sets were tested using a multivariate analysis of variance (MANOVA) on the polynomial coefficients. Linear discriminant analysis (LDA) was performed on the modern reference collection of 1940 olive stones in order to test the morphological discrimination between 71 accessions of olive trees defined as 15 supposed wild populations with 20 stones per population except for Dor (19 stones) and 55 varieties with 30 stones per variety, except 'Djlot Shami' (27), 'Gaidouriola' (29), 'Kortbi' (29), 'Souri' (27) and 'Tanche' (29). Indeed, some stones with slight malformations caused by parasite attacks, have been excluded. A hierarchical ascendant clustering using the Ward method on the distance between each supposed wild population and variety allowed us to highlight the underlying grouping structure among accessions. Each cluster corresponds to a morphotype including wild population, varieties or a mixture whose mean shape may be calculated. The discrimination of each morphotype was recalculated at different levels of aggregations of the clustering hierarchical tree using the confusion matrix established by the LDA. Different levels of aggregations are possible and we chose a 75% of discrimination accuracy threshold as robust enough to be further used for archaeobotanical inference, and to stop refining aggregation.

The archaeological olive stones were then compared to the retained morphotypes. They were included in the LDA as predicted individuals and then assigned to a morphotype with a probability of identification which corresponded to the sum of assigned probabilities of inferred wild and feral populations and/or varieties that made up the morphotype. Stones with a posterior probability of assignation < 0.75 were filtered out.

3. Results

3.1. Number of Landmarks to Be Used to Define the Stone Outline

On the whole available material, the open outlines of all olive stones (4 curves: fertile and sterile valves in lateral view; large and small sides of the fertile valve in dorsal view) were defined by 20 and 120 landmarks in two measurement sessions, aimed at testing the descriptive power of open outlines in relation to the number of landmarks used. The polynomial coefficients are synthetic shape variables, and were treated as quantitative variables in a Linear Discriminant Analysis (LDA) whose explanatory variable takes 72 modalities corresponding to supposed wild populations and cultivars. The morphological disparity between wild populations and cultivars is summarized within two Mahalanobis distance matrices between each population or cultivar centroid (for 20 and 120 points per outline, respectively). The two distance matrices were compared using a RV test. The results of the test ($RV = 0.97, p < 0.0001$) indicate high similarity between distance matrices. Therefore, defining the contours using 120 points does not provide a more precise description of the morphology of the olive stones, than that of 20 points. The following analyses are thus performed on the basis of 20 landmarks per outline for both modern material and archaeological stones. Shape descriptors of modern and archaeological stones are presented in Tables S3 and S4, respectively.

3.2. Morphological Differentiation between Current Wild Populations and Varieties

A hierarchical clustering was calculated using Ward approach on the Mahalanobis distance matrix calculated on accession (supposed wild populations and varieties) centroid. A typology based on morphological relationships among accessions and distinct morphological groups was established (Figure 4). In such a classification method, more and more olive populations and cultivars were linked together and aggregated in larger clusters of increasingly dissimilar elements. The robustness of the clusters was assessed through their accuracy, that is the correct proportion of accession correctly classified in this cluster, versus all others.

Cluster analysis and Linear Discriminant Analysis (LDA) carried out from the morphometric data emphasize 4 main sets or morphological clusters of modern reference olive stones within which several morphotypes can be distinguished. A total of 12 main morphotypes are evidenced with a discrimination rate greater than or equal to 75% (Figure 4; Table S5).

The first set includes two morphotypes (MT1 and MT2). MT1, mainly composed of stones from supposed wild populations, characterizes rounded and rather symmetrical stones. MT2 is characterized by slightly asymmetrical stones in lateral view (the sterile valve less voluminous than the fertile valve) with a rounded base and a slightly narrowed apex. The second set (MT3 and MT4) comprises more tapered, elliptical, non-acuminate and slightly asymmetric stone morphologies in lateral view for MT3, and slightly acuminate stone with relatively pronounced asymmetry in lateral view for MT4. The third set consists of 5 morphotypes that are distinguished by a very tapered stone (reduces in thickness toward one end). The stones of MT5 are weakly acuminate and asymmetrical, essentially in lateral view. Those of MT6 resemble the morphology of the MT5 stones but the apical tip is slightly more pronounced and the centre of gravity of the stone is shifted towards the apex. MT7 has very tapered and asymmetrical stones, especially in lateral view, with a centre of gravity located in the middle part of the stone or even slightly below. MT8 has stone features with the same characteristics as MT7, but with the centre of gravity located at the upper part of the stone. MT8 associates elliptical, slightly tapered, relatively symmetrical stones in dorsal view which are asymmetrical in lateral view. MT9 is similar to MT8 but its stones are much more tapered. The fourth and last set is defined by 3 distinct morphotypes: MT10 is characterized by elliptical stones that are slightly asymmetrical in lateral view. MT11 is distinguished from MT10 by its slightly acuminate apex. For MT12, the stone apex becomes more pronounced, so the centre of gravity shifts slightly towards the base of the stone.



The varieties constituting these morphotypes were compared to: (1) the origins of populations and varieties according to the biogeographical context in the Mediterranean basin [53] (Tables S1 and S2; Figure S1A), (2) the main use for varieties (Table S2; Figure S1B), (3) their geographical origin inferred by DNA nuclear markers (gene pool) [21,54,55] (Table S2; Figure S1C), (4) their affiliation of a specific maternal lineage (cpDNA) [20,21,55] (Table S2; Figure S1D).

3.3. Morphological Variability of the Two Sets of Archaeological Stones (A and B) from Two Distinct Structures in the Hishuley Carmel Site

In order to compare shape of stones from the two archaeological sets sampled in the two distinct structures of olive processing, the MANOVA carried out on the 16 orthogonal polynomial coefficients to compare morphology of the two stone sets shows that there are no significant differences between them (Wilks' Lambda = 0.922, $p = 0.262$). For further analyses such as the comparison of archaeological stone shape to current morphotypes, the two sets are treated together as a single entity. Results of morphometric analysis performed on the archaeological stones are presented in Table S4.

3.4. Dating of Archaeological Olive Stones

Olive stones from the two sets corresponding to two distinct archaeological structures were dated by radiocarbon (Figure 5). They were both dated in the mid-7th millennium BP (A: cal. 6638–6449 BP and B: cal. 6679–6498 BP) and from a cultural point of view in the Chalcolithic period [33].

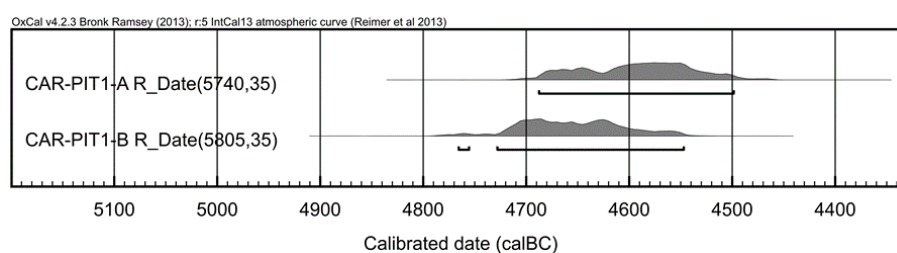


Figure 5. Report on C-14 dating of olive from structures A and B in Hishuley Carmel site, in the Poznań Radiocarbon Laboratory, Poland [33].

3.5. Identification of Morphotypes in the Archaeological Material

The LDA trained on the modern material was used to predict the domestication status of the 247 archaeological stones. The LDA were then assigned to a morphotype with a probability of identification which corresponded to the sum of posterior probabilities of assignment of wild populations and/or varieties that made up the 12 morphotypes. Identifications associated with a posterior probability greater than or equal to 0.75 were retained; those below were filtered out.

Ninety stones (36.8%) could not be classified, probably due to deformations not detected during their initial examination or because these archaeological stones do not have any current analog in our reference collection. Among the morphotypes distinguished in the current reference material, 8 morphotypes were highlighted in the archaeological material but with a different relative frequency. While some morphotypes are represented by only a few stones (MTs 3, 4), 5 main morphotypes dominate (Figure 6):

- MT1 (40 stones—25.5% of the classified archaeological material) consisting of stones from supposed wild populations and one variety with a ‘primitive’ morphology (Arbequina) differing from wild forms by a larger size, although this trait was not considered in this study. Arbequina may be distinguished from wild populations with a rate of 86.7%,
- MT2 (12 stones—7.6%) defined by stones of varieties (all for table or mixed use) from the Eastern Mediterranean and one French variety. All varieties are allocated to the Eastern gene pool,

- MT10 (15 stones—9.6%), composed of varieties of the Eastern maternal lineage, relatively different in terms of geographical origin (cultivation area and nuclear genetic data) and use of the fruit,
- MT11 (25 stones—15.9%) constituted of supposed wild populations and varieties from diverse origins, uses and maternal lineages,
- MT12 (15 stones—9.6%) including mainly oriental varieties used primarily for oil or mixed use.

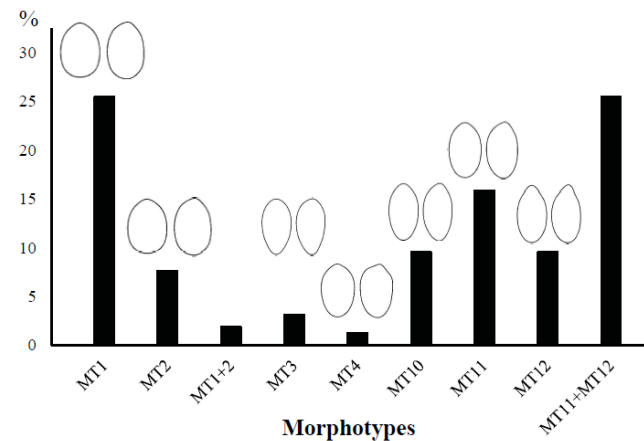


Figure 6. Percentages of archaeological stones affiliated with defined morphotypes Percentage of archaeological stones affiliated with LDA-defined morphotypes.

Finally, 3 stones (1.9%) and 40 stones (25.5%) have been classified in MT1 + 2 and MT11 + 12 at a higher level of aggregation, respectively.

4. Discussion

It is clearly admitted that the Levant region is the cradle of olive domestication [13,28,39]. Although this issue has long been debated, all the studies from various domains (archaeology, archaeobotany and genetics) agree that the Eastern genetic resources provided the bulk of the cultivated pool, today very diversified and widespread around the Mediterranean Basin, and beyond. However, this primary domestication model does not challenge the existence during glacial periods of refuges located south of Iberian and Italian peninsulas, which enabled the oleaster, the ancestor of the cultivated olive, to progressively recolonize north European areas. Prehistoric and protohistoric cultures exploited the local oleasters and probably, unconsciously or not, selected interesting variants that further resulted in morphological types [36,56,57]. However, these likely punctual and minor events of human selection are nowadays almost totally masked by the diversity of oriental forms introduced and spread all over the Mediterranean throughout ancient and medieval times. The main areas where eastern varieties were introduced, probably vegetatively propagated and then crossed with local clones, constituted secondary domestication and diversification centres favoring olive adaptation. The Picholine Marocaine variety is a very demonstrative example. In fact, it belongs to the Near-Eastern maternal lineage (E1) but is characterized by Western nuclear markers [21,54,55]. Its genetical duality shows that its ancestors are of eastern origin, but since they were introduced further west, they have been progressively admixed by Western forms involving the substitution of the former nuclear genetic material by a ‘Western genome’.

While palaeogenomics opens promising perspectives in the evolutionary history and genealogy of ancient cultivated forms, morphometric tools remain essential, accurate and complementary to decipher in a non-destructive way, the morphology of the bioarchaeological material, and contribute to characterize its status and relationships to modern populations. Even if morphometrics, like palaeogenomics, face post-depositional constraints that may partially or totally degrade the material, its acuity and resolution power

are not dismantled. The quantification of shapes by means of mathematical and statistical approaches is both descriptive and decisional by providing very efficient biosystematic criteria. As concerns grapevine, the validation of geometric morphometric results in the history and identity of Roman French grape varieties [44] by palaeogenomics [58] illustrates the level of resolution achieved by shape analysis, often at the infraspecific level [59]. Measuring the phenotype also means integrating genotype expression through the filter of development. This is modulated by the environment and thus by abiotic (climatic or cultivation practices in the case of cultivated plants) and biotic (extrinsic and intrinsic, such as inter-individual or intra-individual competition) factors. Competition between seeds developing within a closed structure, such as the pips in a grape berry, illustrates the role played by developmental and endogenous factors within the same individual [45]. The use of the geometric component of morphology (shape), independently of size (by size standardization), allows us to work on conservative criteria as demonstrated by previous studies showing that environmental factors do not significantly influence stone geometry [26,40]. Moreover, geometric morphometrics allow to overcome a number of interpretative barriers related to changing environmental pressures. This technique also enables to limit or annihilate phenotypic plasticity (i.e., size change across an environmental gradient) and finally, to reveal variations of genetic origin such as those related to artificial selection pressures, thus to domestication (see for example [60,61]). Using traditional measurements provide size variations that has been developed over long chronological periods and that the reproducibility of trait measurements has been beforehand tested.

In this study, the quantified morphological variations, ranging from rounded stones to more elliptical, tapering and asymmetrical shapes, describe the diversity of spontaneous forms growing today in Mediterranean plant communities. The supposedly wild forms are distributed in several distinct morphotypes (MTs: 1, 3, 6, 10, 11 and 12) (Figure 4). To interpret such morphological diversity, Terral et al. [40] invoked different geographical origins, arguing that the morphology of the oleaster stones have differentiated as a result of the Quaternary fragmentation of its former distribution area. This fragmentation resulted in the rupture of gene flows between regions during ice ages, especially between the Eastern and Western Mediterranean. This hypothesis was supported by genetic data [18]. However, more recent studies have shown that this geographical differentiation actually is indirect, through the feral status of these populations [26,62,63]. Indeed, these populations were morphologically differentiated because they derived from varieties of different morphological features and distinct geographical origins. Thus, in order to infer the status of these populations, it is necessary to refer directly to the morphology. The morphotype 1 (MT1) corresponds to round-shaped stones, a simple and minimalist morphology that is also found in other wild relatives or ancestors of cultivated perennial species such as grapevine (*Vitis vinifera* subsp. *sylvestris*) [44,45,59,64] or the palm genus (*Phoenix* spp.) [60,61,65]. The single variety enclosed in MT1 would be one variety with a 'primitive' (*sensu* plesiomorphic) morphology that human breeding pressures have barely impacted. In contrast, other morphological types of supposed wild populations would most likely represent feral forms, as noticed for Israeli populations [6]. Feral olive trees are omnipresent in the Mediterranean region, and exploited in some areas for different purposes (rootstock, food, cosmetics, medicinal uses) [66,67]. The issue of feral olives in Mediterranean plant communities raises the question of the future of genuine wild populations subject to increasing human disturbances and genetic pollution (gene flows between cultivated orchards and local wild populations), especially since olive is wind-pollinated. Finally, it is important to stress that MT1 is not geographically structured. Stones of this morphotype may be considered as the ancestral morphotype showing a robust phenotype (canalization process according to the theoretical model of Waddington [68] revisited more recently by Siegal and Bergman [69], i.e., an inexistent or very low phenotypic plasticity, despite genetic variations and heterogeneous environmental constraints. The same trend has been demonstrated in other species mentioned above, grapevine and date palm [44,60].

Unlike oleasters, any morphological deviation from the genuine wild morphotype may be considered as the result of human selection pressures, although stone geometry was certainly not the target of domestication. The morphological deviation from the wild rounded morphotype may be considered as a tenuous, but real domestication syndrome.

Numerous morphotypes have been found and distinguished, ranging from elliptical with rounded extremities to more tapered, apex-pointed and asymmetrical shapes (Figure 4; Table S4). They result from a complex history and evolution processes related to human-associated migration and spread of olive forms in the Mediterranean Basin over millennia. Moreover, it is important to notice that morphotypes characterized by a very pronounced domestication syndrome such as MT5, 6, 7, 8, 9, are discriminated at a low level of aggregation in the clustering. On the other hand, the other morphotypes whose morphological divergence from MT1 is lower, are distinguished at a higher level of aggregation. This is the case for MT10, 11 and 12.

The results of the identifications of the archaeological stones clearly show that oleasters (probably genuine wild olive) have long been exploited for fruit to be, as in the context of Hishuley Carmel site, treated (dry salting, debittering and pickling) for human consumption [33] or to be used to produce oil as recently demonstrated in Roman Andalusia (Spain) [63]. In the middle of the 7th millennium BP on the Carmel coast, the olive tree is probably at an early stage of domestication. This may explain why only stones characterized by a weak (low morphological deviation from the wild morphotype) but real domestication syndrome (MT2, 3, 4, 10, 11, 12) were identified in the archaeological material (Figure 7).

Thus, it is not surprising that we find the wild morphotype associated with domesticated forms, morphologically different such as stones of morphotypes 2, 10 and 11, for the most numerous. These distinct morphotypes evidenced in the archaeological material seem to characterize two different stages of domestication. MT2 appears to be relatively close to MT1 given the results of the cluster analysis (Figure 4). However, it is defined by table olive varieties of eastern origin from both geographical and genetic points of view (Table S4). These results agree with the geographical (Israel) and archaeological contexts (devices for table olive production) of the site. The MT11 shows a more accentuated morphological divergence (domestication syndrome), suggesting that varieties of this group from mainly Eastern Mediterranean areas, are at a more advanced stage of domestication. Although the following features have deliberately not been the focus of our investigations for reasons mentioned above, fruits of this group are bigger and offer the consumer a larger pulp but not necessarily higher oil content. Fruit size, fruit production and oil content are certainly traits that, originally and empirically, were selected (for the first time in the Levant) from wild morphological variants and then maintained by vegetative means (cuttings and grafting). However, the archaeological stones are mostly affiliated to groups of varieties whose vocation is the production of oil or/and used for table olive (Table S4). Thus, we suggest that the olive tree was first domesticated for oil production. Indeed, the treatment of the fruit to remove bitterness and lead the initiation of the fermentation process, required to reduce the pH and to allow the preservation of olive for long time, involves a more complex process. Later, fruit were used for different purposes and variants with larger fruit selected for the production of table olives.

Anyway, these morphotypes did not remain confined to the Mount Carmel area but contributed to the spread of the olive tree in the Mediterranean basin. Indeed, the morphotypes recognized in the archaeological material are constituted by varieties regarded today as of various origins even if the Eastern of admixed lineages dominates (Table S2; Figure S1), testifying to the complexity of exchanges and agrobiodiversity around the Mediterranean Basin. In the current state of research, MT2 was recognized in Egypt during the 7th century BC (Persian period) [32]. MT10 and 11 were evidenced for the first time, in continental Greece at the transition 2nd/1st millennium BC (Iron Age) [70], in Northwestern and Southern Spain, in the 5th century BC (Iberic period) [40] and since the 1st century BC (Roman period) [63], respectively.



Figure 7. Photographs of archaeological stones from Hishuley Carmel site allocated to modern olive morphotypes of which a representative is presented by means of a photographed, trimmed and masked stone before the extraction of open outlines coordinates (photos taken by Sarah Ivorra and Clémence Pagnoux).

5. Conclusions

This study provides new insights and knowledge on the history of olive exploitation and domestication from archaeological and evolutionary perspectives. Based on geometrical descriptors of stone outlines, traits weakly influenced by environmental parameters, especially climatic and cultivation practices, it allows to characterize the phenotypic features of exceptionally preserved stones of the oldest table olives uncovered so far. Using a reference model of stone shape diversity and divergence based on a modern collection of stones of supposed wild populations and varieties, originating from different regions of the Mediterranean, the analysis of archaeological stones reveals a surprising shape diversity. They range from a round morphotype, considered as ancestral and typical of genuine wild forms, to more complex morphologies, testifying to strong selection pressures (asymmetrical, tapered stones that can be pointed at the apex). The main morphotypes found at Hishuley Carmel illustrated in Figure 7, show how close the shape of the stones is to some modern varieties. Since the emergence of olive domestication, some selected shapes would not have changed significantly over time, considering that for some varieties today represented by heritage trees, several centuries or even millennia old, few generations have succeeded one another until today.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/agronomy11112187/s1>, Figure S1. Clustering of the morphotypes obtained, with cross-validation values on branches. For varieties, the panels represent the same tree with tips colored according to the different biogeographical origin (A), use (B), origin inferred by DNA nuclear markers (C) and maternal lineage (D). Table S1. Supposed wild olive (oleaster) populations. Table S2. Studied cultivated varieties. Table S3: Mean of geometrical parameters (*bi*) for each supposed wild population and variety from morphometric analysis of modern reference olive stones. These parameters were calculated using 20 landmarks per outline. A: dorsal view; B: lateral view. Table S4. Morphotypes differentiated by cluster analysis, constituted by modern supposed wild populations and varieties whose area of cultivation and belonging to a gene pool according to genetic data [21,54,55] are presented. Table S5. Geometrical parameters (*bi*) from morphometric analysis performed on archaeological pits from Hishuley Carmel site.

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