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Clémence Pagnoux, Laurent Bouby, Soultana Maria Valamoti, Vincent Bonhomme, Sarah Ivorra, et al.. Local domestication or diffusion? Insights into viticulture in Greece from Neolithic to Archaic times, using geometric morphometric analyses of archaeological grape seeds. *Journal of Archaeological Science*, 2021, 125, pp.105263. 10.1016/j.jas.2020.105263 . hal-03040458

HAL Id: hal-03040458

<https://hal.science/hal-03040458>

Submitted on 4 Dec 2020

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Local domestication or diffusion? Insights into viticulture in Greece from Neolithic to Archaic times, using geometric morphometric analyses of archaeological grape seeds

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ARTICLE INFO

Keywords:

Domestication
Past diversity
Viticulture
Geometric morphometrics
Aegean

ABSTRACT

Grapevine (*Vitis vinifera* L.) is one of the emblematic crops of Greece. Despite evidence of early wine making in the Aegean since the Late Neolithic (ca 4500–4000 BC), the hypothesis of a local domestication of the grapevine in this area hasn't be thoroughly investigated. In order to date the first appearance of the domesticated grapevine and to explore the past cultivated diversity in the Aegean, morphometric analyses were performed on a large data set of 2223 archaeological grape pips from 11 sites located in various areas of Greece and dated to the Late Neolithic, Bronze Age and Archaic period (6th millennium BC - 7th century BC).

All the grape pips from the Late Neolithic are morphologically wild. The shift from wild to domesticated shape occurred during the Middle Bronze Age (1900–1700 BC). From the Late Bronze Age (1500–1100 BC) onwards, domesticated types dominate almost all the assemblages. Possible indication of a local domestication process is provided by pips dated to the Early Bronze Age. Also still in the range of modern wild specimens, their shape is an intermediate between the Neolithic pips and those dated to later periods. A high morphological diversity characterizes the Late Bronze Age and Archaic assemblages. These grape pips are mostly allocated to modern varieties from the Balkans, Caucasus and South-West Asia. The geographical origin of the identified varieties may reflect introduction of cultivars from the eastern Mediterranean, but may also testify to an early stage of local domestication and grapevine diversification.

1. Introduction

Due to the economic and symbolic importance of the grapevine (*Vitis vinifera* L.), its domestication has been the subject of numerous researches and works. The phenotypic changes that occurred in grapevine domestication and separate the wild subspecies (*V. vinifera* subsp. *sylvestris*) and the domesticated one (*V. vinifera* subsp. *vinifera*) are well-known, but the domestication origins and history remain largely unknown. According to the prevailing view based on extensive

archaeological, archaeobotanical and genetic data, the grapevine is considered to have been first domesticated in South-West Asia between 6000 and 3000 BC, where the most ancient evidence of grapevine cultivation was found (Zohary and Spiegel-Roy 1975; McGovern 2003; Arroyo-Garcia et al., 2006; Miller 2008; Myles et al., 2011; Bacilieri et al., 2013; Riaz et al., 2018; Fuller and Stevens 2019). However, the possible contribution of local wild grapevine to the process of domestication outside this primary domestication area, where grapevine is supposed to have been first domesticated, or parallel domestication

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<https://doi.org/10.1016/j.jas.2020.105263>

Received 20 May 2020; Received in revised form 14 October 2020; Accepted 14 October 2020

Available online 13 November 2020

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events in the wider area of natural distribution of the grapevine, are still debated. Genetic relationships between local wild grapevines and cultivars from various regions have been brought to light by several molecular studies. The results of these studies are either considered, in Central and Western Mediterranean, as evidence of introgression from wild grapevines into cultivars of Eastern origin (Myles et al., 2011), or as indications of secondary domestication events, involving both local wild grapevines and varieties introduced from the primary centre, at various places (Grassi et al., 2003; Arroyo-García et al., 2006). Secondary domestication events may have occurred anywhere in the area of natural distribution of the wild grapevine (*Vitis vinifera* subsp. *sylvestris*), ranging from western Europe to the Himalayas and around most of the Mediterranean Basin (Levadoux 1956; Arnold et al., 1998), including Greece (Logothetis 1970). Parallel domestication events may also have occurred in this area without any role of introduced cultivars, but adequate research on a large dataset is lacking.

It is worth noting that neither grapevine cultivation nor winemaking require domesticated varieties: wild grapevines may be cultivated and used to make wine, as has been suggested for Dikili Tash in northern Greece (Valamoti 2015; Valamoti et al., 2015; Miller 2008). “Cultivation” refers here to grapevine management, including pruning and planting for fruit production. Cultivation of the wild grapevine may be considered as one of the first steps in the domestication process. However, we don’t know the time-scale involved in the shift from wild to domesticated morphology of the pip. Grape pips could possibly look wild while being already at an incipient stage of domestication, as it has been suggested (Valamoti 2009; Valamoti et al., 2015). Domestication is a complex process, and the difference between “wild” and “cultivated” in terms of practices as well as between “wild” and “domesticated” in terms of seed morphology is far from being a simple dichotomy (e.g. Miller 1992; Zeder 2011; Bouby and Ruas 2014).

As regards Greece, the question of a local domestication of grapevine has not been examined in a systematic way, based on a large dataset. In several publications, the case of the Aegean is unclearly described (e.g. Fuller and Stevens 2019). The development of arboriculture and viticulture in Greece is supposed to be strongly related with the emergence of palatial civilization in Crete and in the Peloponnese during the Bronze Age (Renfrew, J.M., 1972). The significant role of wine in the Minoan and Mycenaean cultures and the possible exploitation of marginal land would have favoured viticulture (e.g., Renfrew, C., 1972; Halstead 1992).

On the other hand, grapevine management in northern Greece may be supposed as early as the 5th millennium BC, i.e. long before the emergence of the Mycenaean civilization in Southern Greece, according to the discovery of grape pips on several sites, in some places in large quantities and/or associated with grapevine charcoal (Renfrew 1995; Megaloudi 2006; Valamoti 2009, 2015; Valamoti et al., 2007, 2015; Pagnoux 2019). The first evidence of wine making comes from Dikili Tash in northern Greece, dated to the Neolithic 4500–4000 BC (Valamoti et al., 2007, 2015; Garnier and Valamoti 2016). Several lines of evidence raise therefore the question of the geographic origin of the domesticated grapevine in Greece and the question of the chronological origin and development of viticulture in relation to social, economic and cultural changes during prehistoric and historical times. Grape seed shape offers accurate criteria to distinguish wild and domesticated grapevine (wild grapevine bears small and roundish pips with short stalk, while pips from cultivars are more elongated with longer stalk) and allows the identification of modern varieties or groups of varieties among the domesticated compartment (Terral et al., 2010; Pagnoux et al., 2015; Bouby et al., 2018). The comparison of archaeological grape pips with the modern reference collection, based on the analysis of their shape, aims to identify morphotypes among the archaeological samples and to investigate the past diversity and its possible connection with the modern one, rather than to link archaeological grape pips to modern cultivars.

The morphometric analysis of archaeological grape pips from Late

Neolithic (4500–4000 BC), Bronze Age (ca. 3200–1100 BC) and Archaic (8th/7th c. BC) sites located in various regions of Greece aims to answer the following questions: when did the first domesticated grapevines appear in Greece? Were they locally domesticated or introduced from elsewhere? How can the varietal diversity of grapevines in Prehistoric and Archaic Greece be characterized? How can this diversity and its evolution be related to the development of trade and exchange networks? Did the increase in trade and exchange during the Bronze Age and the Archaic period bring new domesticated varieties to Greece?

2. Material and methods

2.1. Archaeological material

A total of 2223 pips from 11 archaeological sites from Greece, dated to the Neolithic, Bronze Age and Archaic periods (from the 5th millennium BC to the 7th century BC) are considered in this paper (Table 1; Fig. 1). Two thousand twenty-nine (2029) of the analysed grape pips are carbonized. Only one assemblage coming from a basin in the temple of Hera (Heraion) on the island of Samos consists of waterlogged pips.

All the grape pips analysed come from settlements, except those from Samos which belong to a religious context.

2.2. Morphometric analyses

The shape of the 2223 seeds was described with outline analysis using elliptic Fourier transforms (further abbreviated EFT). The method was developed and improved by previous studies (Terral et al., 2010; Pagnoux et al., 2015). All the analyses have been performed using Momocs v. 1.3.0 (<https://github.com/MomX/Momocs/>; Bonhomme et al., 2014) and package MASS (Venable and Ripley, 2002) in the R environment (v. 4.0.0) (R Development Core Team 2020).

The seeds were photographed in dorsal and lateral views. The pictures were converted into black masks on white background, and 360 equidistant points along the curvilinear abscissa were sampled on each outline. The outlines were normalized using their centroid size and the position of the first point was normalized.

The EFT consist of the decomposition of the outline of a series of trigonometric functions called harmonics. Each harmonic is associated with four coefficients, defining an ellipse on the plane. According to Terral et al. (2010), six harmonics per outline should be considered in order to optimize the trade-off between maximizing efficiency of shape reconstruction and minimizing the measurement error. EFT were calculated separately for each orthogonal view, then the coefficients were combined into the same matrix. Each seed was eventually described by 48 coefficients (24 for both dorsal and lateral view) which were used as quantitative variables in further analyses.

2.3. Statistical analyses

A Principal Component Analysis (PCA) was performed using the coefficients of the 2223 seeds to reduce dimensionality and further to compare the archaeological assemblages to one another.

Then, the archaeological pips were compared to a reference collection of modern grape pips. This reference collection consists of 281 varieties (see Pagnoux et al., 2015; Bouby et al. in press). Two hundred and thirty-eight varieties have been sampled in the INRA Domaine de Vassal Grape Germplasm Repository (<https://www6.montpellier.inra.fr/vassal/>) and 43 autochthonous varieties from Georgia were sampled from the Saguramo Grape Repository (Jighaura, Georgia). The selected varieties are typical examples from different regions where viticulture has a long history, including Greece, and most areas of the Mediterranean, South-West Asia and Europe (Lacombe 2012; Pagnoux et al., 2015). In addition, 82 wild individuals have been sampled in their natural environment in Greece, Turkey, Georgia, Italy, France and Spain. This reference collection aims to be representative of the modern

Table 1
List of samples analysed.

Site	Region	Chronology	Preservation	Number of samples	Number of pips	Reference
Makri	Macedonia	Late Neolithic	Carbonized	1	22	Valamoti (2004)
Makriyalos	Macedonia	Late Neolithic	Carbonized	1	17	Valamoti (2004)
Loggas	Macedonia	Late Neolithic	Carbonized	5	52	Kotsachristou unpublished
Dikili Tash	Macedonia	Late Neolithic	Carbonized	6	368	Valamoti (2004), 2015, Valamoti et al., 2007,2015
Romanou	Peloponnese	Early Bronze Age	Carbonized	12	831	Valamoti. (2019)
Aghia Paraskevi	Central Greece	Middle Bronze Age	Carbonized	13	77	Karathanou unpublished, Gkotsinas et al., (2014)
Dikili Tash	Macedonia	Late Bronze Age	Carbonized	3	152	Pagnoux unpublished
Mitrou	Central Greece	Late Bronze Age	Carbonized	6	89	Karathanou unpublished
Kastanas	Macedonia	Late Bronze Age	Carbonized	1	55	Kroll (1979), 1983
Thessaloniki Toumba	Macedonia	Late Bronze Age	Carbonized	4	13	Mangafa and Kotsakis (1996), Mangafa et al., (1998), 2001 Karathanou unpublished
Thessaloniki Toumba	Macedonia	Archaic period	Carbonized	20	171	Mangafa and Kotsakis (1996), Mangafa et al., (1998), 2001, Gkatzogia unpublished Valamoti et al.
Karaboumaki	Macedonia	Archaic period	Carbonized	1	182	2018, Gkatzogia unpublished
Samos Heraion	East Aegean	Archaic period	Waterlogged	7	194	Kučan (2000)



Fig. 1. Location of the investigated sites.

diversity of the grapevine. Furthermore, it is important to note that the comparison to modern varieties is used as an analytical tool to characterize and interpret past diversity in light of modern diversity, as part of a long evolutionary history. The archaeological grape pips are considered as similar to modern varieties on the basis of a similarity in pip

shape, but they should not be considered as specific matches between ancient and modern varieties. In fact, modern varieties could have been created later than the considered periods in this paper, and the varieties which were cultivated in Greece during Prehistory and Antiquity may have disappeared since. The approach used in the present study does not

intend to trace modern lineage back in time, but rather to investigate past diversity and its evolution through time, and to explore possible connections with modern regional diversity on the basis of morphological features.

Previous studies have revealed that morphometric analyses based on EFT allow discrimination of both compartments (wild and domesticated) as well as groups of varieties (parental and eco-geographical groups) (Terral et al., 2010; Pagnoux et al., 2015). As shown by previous studies, carbonization causes a distortion of the pips (Logothetis 1970, 1974; Smith and Jones 1990; Mangafa and Kotsakis 1996), but recent investigations on the effect of carbonization have shown that the experimentally charred grape pips, despite distortion, are well classified in their groups of origin (Ucchesu et al., 2016; Bouby et al., 2018). Whereas the analyses conducted by Bouby et al. (2018) reveal that experimentally charred grape pips are well classified not only at the scale of the wild and domesticated compartments, but also at the cultivar level, the authors recommend to apply the characterization at the cultivar level only using the largest and best preserved samples (Bouby et al., 2018).

In light of these results, carbonized and waterlogged grape pips are compared to the uncarbonized reference collection. Archaeological grape pips were first classified as wild or domesticated by using a predictive linear discriminant analysis (LDA), trained on balanced reference samples. For this analysis, we used all the available 2430 pips of wild grapevines while 2430 pips from domesticated grapes were randomly selected within domesticated grapevines. Then, the archaeological pips classified as domesticated by the first LDA were assigned to modern cultivars by using a predictive LDA on the whole domesticated part of the reference collection (Bouby et al. in press). We consider that pips from large assemblages underwent less deformation and are more suitable for a comparison on the cultivar level. Thus, the second LDA was performed on grape pips from samples with 30 or more seeds. Pips with a posterior probability of assignment ≤ 0.75 were filtered out. The classification by the LDA is a statistical allocation to a predefined group

(wild or domesticated compartment and cultivars), which allows interpreting past diversity on the basis of morphological similarity.

3. Results

3.1. Comparison of archaeological sites

The PC1-PC2 (67.6% of the total variance) biplot shows a clear chronological structuring along PC1: Neolithic assemblages are clustered apart on PC1, the dot corresponding to the Early Bronze Age site is in the middle of the plot, and assemblages from the Middle Bronze Age, Late Bronze Age and Archaic period are in the opposite part of PC1 (Fig. 2). Among the Late Bronze Age, Dikili Tash and Thessaloniki Toumba (in northern Greece) cluster in the central part of PC2, while Kastanas (also located in northern Greece) is apart. No clustering according to geographic location of the assemblages was observed.

Samos, which represents the only waterlogged material but also the only religious context, is clearly distinct from the other Archaic sites which cluster with the Late Bronze Age assemblages in the central part of PC2.

3.2. Comparison of archaeological pips with the modern reference collection: wild and domesticated morphotypes

Archaeological grape pips have been compared to modern ones belonging to the wild grapevine and to several cultivars through a discriminant analysis. One thousand five hundred seventy-eight (1578, 71%) of the archaeological pips are classified as wild, 447 (20.1%) as domesticated, and 198 (8.9%) could not be allocated to any compartment with $p \geq 0.75$. Regarding the carbonized material, 1532 pips (75.5%) are classified as wild and 332 (16.36%) as domesticated. The proportion of pips with a $p < 0.75$ is lower than 30% in all sites (except in the Bronze layers at Toumba), and lower than 5% among pips dated to the Neolithic and Early Bronze Age.

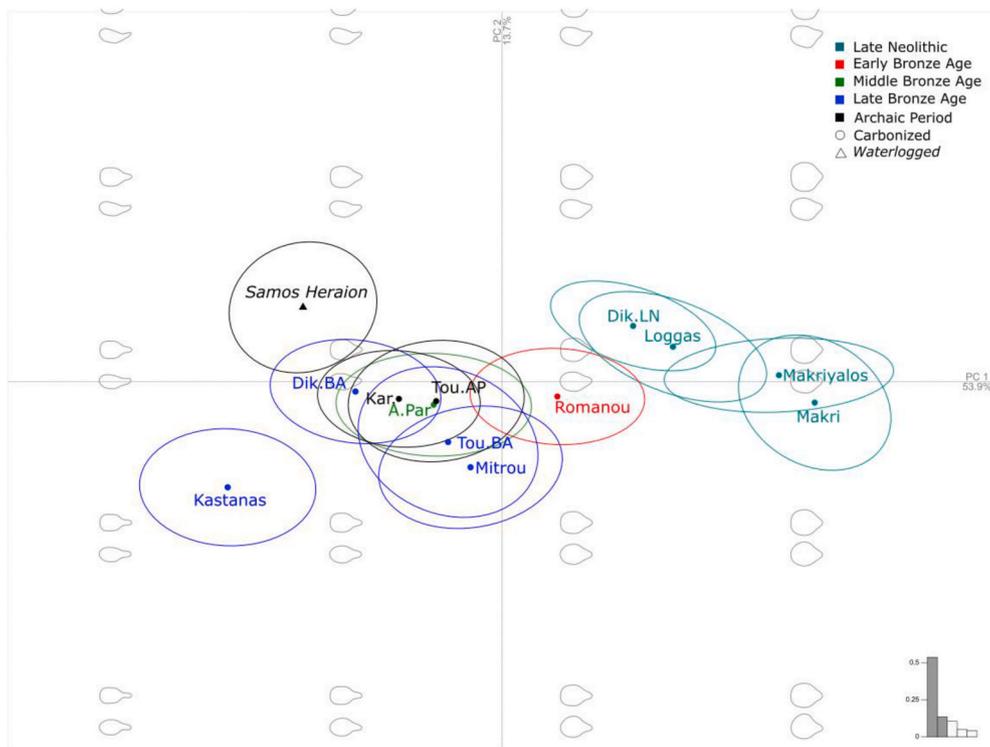


Fig. 2. Principal Component Analysis performed on the 48 coefficients of all the samples, biplot of axes 1 and 2. Each point represents the centroid of an assemblage, the ellipses represent confidence ellipse. A.Par = Platania-Agia Paraskevi, Dik.BA = Dikili Tash (Bronze Age), Dik.LN = Dikili Tash (Late Neolithic), Kar = Karabournaki, Tou.BA = Toumba (Bronze Age), Tou.AP = Toumba (Archaic period).

All the grape pips dated to the Neolithic are classified as wild, except two pips from Dikili Tash and one of the 22 pips from Makri (Fig. 3; Table 2).

The grape pips from Early Bronze Age P.O.T.A. Romanou are mostly (96.1%) classified as wild: only 3% (n = 28) of the assemblage is not classified and 0.5% (n = 4) is classified as domesticated.

For the Middle Bronze Age, only 77 pips from one site (Agia Paraskevi in Central Greece) have been analysed. The wild morphotype is dominant (64.9%), but quite a high proportion of the assemblage is classified as domesticated (22%).

The situation is very different concerning the Late Bronze Age. The same pattern is observed in all the sites: grape pips are mostly classified as domesticated. The proportion of pips classified as domesticated is the highest at Kastanas (95%). Of the assemblages of Mitrou and Dikili Tash, only 55% are classified as domesticated.

Assemblages dated to the Archaic period present a more contrasted pattern. While the grape pips from Toumba are mainly classified as wild (52%), those from Karabournaki are mostly classified as domesticated (40%) - although a significant proportion of the assemblage is classified as wild (36%).

Waterlogged grape pips from Samos are mostly allocated to the domesticated compartment (59%).

3.3. Comparison of domesticated-type pips with modern varieties

A second LDA was performed on the grape pips from assemblages of 30 or more seeds, including at least 20 seeds classified as domesticated by the first LDA with a posterior probability of assignment ≥ 0.75 . Several samples have therefore been excluded, and the second LDA was performed on 418 archaeological pips from six sites (Table 2: number of included pips are in bold).

A total of 251 (60.1%) pips were allocated by the LDA to 72 cultivars from various areas and 167 (39.9%) could not be classified with a significant probability (≥ 0.75) (Table 3, ESM1).

The archaeological carbonized pips are mostly similar to 'Heptakilo' (Greece) and 'Glycostaphyllo' (Turkey), especially at Mitrou, and to a lesser extent at Karabournaki, Toumba and Bronze Age Dikili Tash (Table 3).

Nine pips from Kastanas are classified as 'Marathefiko' (Cyprus). Pips from Bronze Age Dikili Tash are mainly allocated to 'Bzanavura' (Georgia), 'Muscat de Hambourg' (unknown origin) and 'Voudomato' (Greece). Few (less than 3%) or no grape seeds from other sites have been allocated to these varieties.

The waterlogged pips from the Heraion of Samos are morphologically similar to several varieties to which few or no carbonized pips from the other sites are allocated. Seeds from Samos are mostly classified as 'Bourboulenc' (France), 'Chaouch blanc' (Turkey), 'Chaani biely' (Azerbaijan), 'Haimka' (Bulgaria) and 'Agadaï' (Russia, Daghestan).

The identified varieties are considered to be originating mostly from the Balkans (especially Greece) and East Mediterranean/Caucasus (especially Turkey), and to a lesser extent from western Europe and the Middle East (Fig. 4). Grape pips from Bronze Age Dikili Tash, Kastanas and Mitrou are mainly allocated to varieties from Caucasus, while those from Archaic Toumba and Karabournaki are mainly classified as cultivars from Greece. Pips close to cultivars from the Middle East and Russia are rare except at Dikili Tash and Samos.

The assemblage from the Heraion of Samos includes more pips assigned to varieties regarded as typical of western Europe than the other assemblages. In addition, the proportion of grape pips classified as varieties from the Balkans and especially from Greece is less important in the Heraion than in the other sites.

4. Discussion

4.1. Early viticulture in Greece: the use of wild grapevine

The wild grapevine is undoubtedly part of the natural vegetation of Greece for millennia. Nowadays, it is still present in small and disconnected populations justifying its registration in the IUCN (International Union for Conservation of Nature) red list of threatened plants (Kyrtzidis et al., 2011). Pollen records indicate that the plant was growing in Greece during the Pleistocene and from the Early Holocene onwards. Most of the diagrams show *Vitis* pollen as early as the Neolithic (Bottema 1990; Jahns 1993; Bottema and Sarpaki 2003; Lawson et al., 2005; Lazarova et al., 2012). Pollen diagrams from both northern and southern Greece attest to its presence before the Neolithic (Avramidis et al., 2013; Wimjstra 1969; Bottema 1980, 1994).

According to seeds and fruit remains, grape was consumed from the Early Neolithic (7000–5200 BC) in the Peloponnese and Thessaly (Kroll 1981; Renfrew 1989; Hansen 1991; Valamoti 2009; Valamoti et al., 2015). Grape remains are present in eight of the 18 investigated sites for this period (Pagnoux 2016; Valamoti et al., 2018).

Grape remains are recorded more frequently on Late Neolithic sites (10 of the 17 sites investigated have yielded grape remains; Pagnoux 2016; Valamoti et al., 2018.). In Late Neolithic Makriyalos (first half of the 5th millennium BC) and Dimitra (second half of the 5th millennium

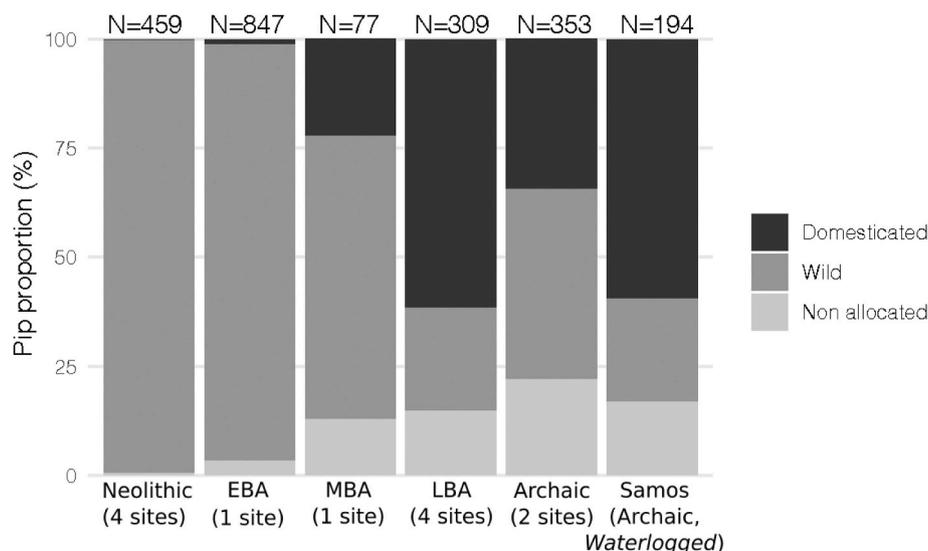


Fig. 3. Distribution of archaeological pips according to chronology and to the allocation to the wild or domesticated compartment.

Table 2

Number of pips allocated to the wild and domesticated compartment. In bold: number of pips considered in the second LDA.

	Chronology	Total number of seeds	Wild	Domesticated	Non allocated	% wild	% domesticated	% non alloc.
Makri	Late Neolithic	22	21	0	1	95,5%	0,00%	4,55%
Makriyalos	Late Neolithic	17	17	0	0	100,0%	0,00%	0,00%
Loggas	Late Neolithic	52	52	0	0	100,0%	0,00%	0,00%
Dikili Tash	Late Neolithic	368	366	0	2	99,5%	0,00%	0,54%
Romanou	Early Bronze Age	831	799	4	28	96,1%	0,48%	3,37%
Agia Paraskevi	Middle Bronze Age	77	50	17	10	64,9%	22,08%	12,99%
Dikili Tash (BA)	Late Bronze Age	152	37	84	31	24,3%	55,26%	20,39%
Mitrou	Late Bronze Age	89	32	49	8	36,0%	55,06%	8,99%
Kastanas	Late Bronze Age	55	2	52	1	3,6%	94,55%	1,82%
Toumba (BA)	Late Bronze Age	13	2	5	6	15,4%	38,46%	46,15%
Toumba (arch.)	Archaic period	171	89	48	34	52,0%	28,07%	19,88%
Karabournaki	Archaic period	182	65	73	44	35,7%	40,11%	24,18%
Samos Heraion	Archaic period	194	46	115	33	23,7%	59,28%	17,01%
Total		2223	1578	447	198	71,0%	20,11%	8,91%
Total carbonized		2029	1532	332	165	75,5%	16,36%	8,13%

Table 3

Allocation of archaeological grape pips to modern cultivars. Only cultivars represented by at least 3 pips are reported (see ESM1 for the exhaustive list).

Variety Tash	Dikili	Mitrou	Kastanas	Toumba	Karabournaki	Samos Heraion	Total	Geographical area
Heptakilo	3	11	0	4	4	2	21	Greece
Glycostaphyllo	2	10	2	0	5	1	18	Caucasus
Chaouch blanc	0	3	2	3	2	6	16	Caucasus
Marathefico	2	1	9	0	1	0	11	Balkans
Bourboulenc	0	0	1	2	0	7	10	Western- Central Europe
Muscat de Hambourg	5	0	2	2	0	0	4	ND
Sliva	1	1	1	1	2	1	6	Balkans
Chaaani biely	1	2	0	0	0	5	7	Caucasus
Bzvanura	6	0	0	0	1	0	1	Caucasus
Rhoditis	1	2	2	0	2	0	6	Greece Middle East
Agadai	3	0	0	0	0	4	4	Central Asia Russia
Voudomato	4	0	0	0	0	2	2	Greece
Listan	1	0	1	0	1	3	5	Iberian Peninsula
Haimka	0	0	0	0	0	5	5	Balkans
Adanasuri	0	0	3	1	0	1	5	Caucasus
Phraoula rose	0	0	0	3	0	2	5	Greece
Debina	1	0	0	2	1	0	3	Greece Middle East
Abjouch	2	0	0	1	0	1	2	Central Asia Russia Middle East
Kouldjinsky	0	0	0	1	0	3	4	Central Asia Russia
Chekobali	2	0	0	1	0	1	2	ND
Athiri	0	0	0	0	3	0	3	Greece
Manizi	3	0	0	0	0	0	0	Balkans
Peikani	0	0	0	0	0	3	3	Caucasus
Vertkvichalis tetri	0	0	0	0	0	3	3	Caucasus
Katsacoulias	0	0	1	0	1	1	3	Greece
Kypreiko	0	2	0	0	0	1	3	Greece
Mavrostypho	0	0	0	1	1	1	3	Greece
Merlot	0	0	0	0	0	3	3	Western- Central Europe
Total nb pips	81	49	52	48	73	115	418	
Nb of pips id p > 0.75	43	38	34	29	38	69	251	

BC), in northern Greece, grape pips are attested in most of the samples, and some samples have yielded relatively large (≥ 30) quantities of remains (Renfrew, 1997; Valamoti 2004; Valamoti 2009; Valamoti et al., 2015). At Makri and Dikili Tash, grape pips and grapevine charcoal have been discovered in the same contexts (Ntinou and Badal 2000; Ntinou 2002; Valamoti 1998; Valamoti et al., 2015) and interpreted as indications for early grapevine management (Valamoti 1998, 2015) as the joint discovery of seeds and charcoal is strong evidence of cultivation. As suggested by Miller (2008), charcoal recovered in domestic contexts may indicate the use of wood provided by pruning, which is a key operation of grapevine cultivation.

Besides these first indications for grapevine cultivation in northern Greece dated to the Late Neolithic, evidence for juice extraction and wine making is provided by the large concentration of grape pips from

Dikili Tash (Late Neolithic, 4500–4000 BC), where 2460 grape pips have been discovered, associated with other by-products of pressed grapes (pedicels and skin fragments) while tartaric and malic acids, present in grapes, as well as other acids characteristic of alcoholic fermentation were detected on sherds (Valamoti 2004, 2015; Valamoti et al. 2007, 2015; Garnier and Valamoti 2016). The joint discovery of these remains clearly testifies to wine making in Greece as early as the Late Neolithic. Yet, while some cultivation practices may have been applied to the grapevine in Late Neolithic northern Greece, along with wine making, the grape pips dated to this period are still morphologically wild (Mangafa and Kotsakis 1996; Pagnoux 2016).

Grape pips from the Late Neolithic, especially from Dikili Tash, may represent managed or cultivated grapevine, because of the large number of grapes that had been harvested for the production of wine (Valamoti

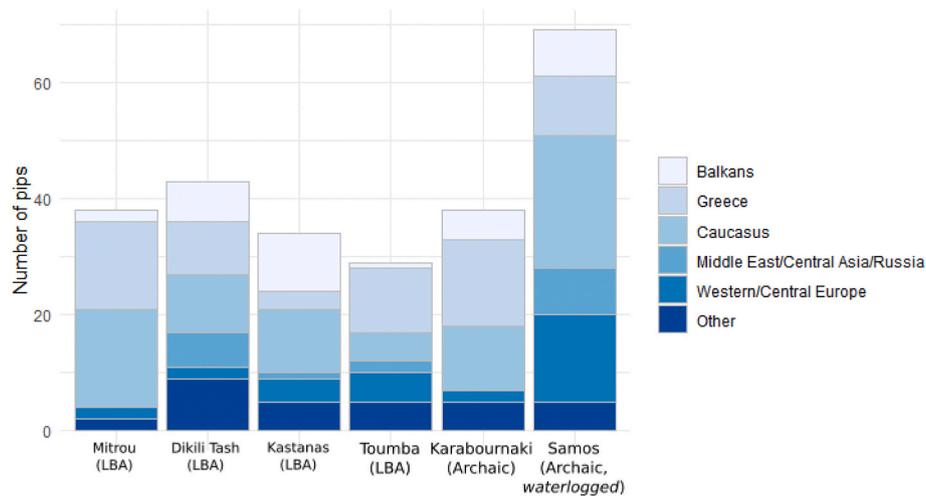


Fig. 4. Distribution of archaeological pips of each site according to the geographical group of identified cultivars.

et al., 2007; Valamoti 2015). Large quantities of grape pips are unlikely to represent the result of the gathering of berries from wild individuals: according to works on modern wild grape, the number of grapes per bunch, and consequently the yield of each plant may be variable and low (Ocete et al., 2011). The management of wild fruit plants in their natural environment, including pruning and clearing the surroundings to favour fruit production and/or to facilitate the harvest, may be at the heart of early arboriculture practices concerning grapevines and other fruit species, underway already in the Late Neolithic (Valamoti 2015). At this incipient stage of cultivation, it is unknown whether any human selection pressures were already applied to natural populations. In any case, seed shape does not bear the morphological signs of domestication.

4.2. A local domestication process? Evidence from early and middle Bronze Age contexts

During the Early Bronze Age (3200–2100 BC), grape remains are attested in the vast majority of sites investigated in Greece. Large concentrations have been discovered at Lerna (Peloponnese; more than 2000 pips; Hopf 1961, 1962) and at P.O.T.A. Romanou, where nearly 4000 grape pips have been found in association with grapevine charcoal (Valamoti et al., 2020). The discovery of grape pressing by-products along with grape seeds is reported at Myrtos, in Crete (Renfrew J.M. 1972), but the assemblages from Lerna and P.O.T.A. Romanou consist of pure seed concentrations. Due to the lack of grape pressing by-products, such as skin fragments and pedicels, evidence of wine making in these cases is harder to prove. However, archaeological samples with numerous grape seeds, few pedicels and no identifiable skin fragments could be considered as by-products of wine making, as shown by the experimental study done by Margaritis and Jones (2006): despite basket-sieving of the juice resulting from grape pressing before its transfer into a container for the fermentation process, numerous grape pips and lower quantities of pedicels and skin fragments were also present in the container; then, due to taphonomic processes (charring temperature but also flotation), skin fragments may be destroyed or broken to very small pieces which are hardly found, contrary to pips which are numerous in the experimental samples. Pure seed concentrations cannot be considered as a by-product of wine making *stricto sensu*, but these seeds may reflect the storage of wine making residues after a sieving or winnowing to separate the seeds from the other elements, for other purposes. Possible uses have been suggested in previous studies, such as production of oil or flour (Alonso and Rovira 2010).

Irrespective of the intended uses of the pips, these large numbers of seeds are evidence of grape management or incipient cultivation on a large scale, producing relatively large quantities of grapes and their use

for (possibly) various purposes, including wine making. The presence on several sites of these seed concentrations seems to reflect a change in grape cultivation and consumption practices between the Late Neolithic and the Bronze Age.

Although the increase in frequency and abundance of grape pip remains may indicate a development of grapevine cultivation during the Early Bronze Age, the shift from morphologically wild to domesticated type only occurred during the Middle Bronze Age (2100–1550 BC) on the basis of the results of the morphometric analyses presented above. In Early Bronze Age P.O.T.A. Romanou, the pips are mostly close to the wild morphotype (96%), but slightly different from the Neolithic pips. This morphological change from Neolithic to Early Bronze Age may reflect evolution under low or/and new and emerging selection pressures. Then, despite the low number of pips analysed, a large proportion of the assemblage from Middle Bronze Age Agia Paraskevi (1900–1700 BC) is classified as domesticated (22%), even if the wild morphological type is dominant (64%). This assemblage offers evidence of the cultivation of fully domesticated types as early as the beginning of the 2nd millennium BC, along with wild or “early selected” types.

In the end, our data bear evidence for a continuous trend from (1) widespread consumption, and probably already some sort of cultivation, of local wild grapevines during the Late Neolithic, to (2) an increased cultivation during the Early Bronze Age going together with incipient changes in pip morphology towards a more elongated shape and longer stalk typical of domesticated pips, and (3) the emergence of the fully domesticated morphotype of grape pips during the Middle Bronze Age. This could imply a local process of domestication, involving local wild grapevines, due to the continuous and increasing use of grapes. A recent study has shown that the change in fruit size under selective pressure led to a change in seed shape (Bonhomme et al. in press).

The influence of the Minoan civilization in Crete in the process of grapevine domestication during the Middle Bronze Age remains largely hypothetical. The discovery of large press equipment in contexts related to palaces or villas (Blitzer 1993; Platon and Kopaka 1993) may be considered as evidence of a change in social and economic practices of the Middle Bronze Age in Crete (Blitzer 1993; Hamilakis 1996). Evidence of juice extraction and possibly wine making comes from Monastiraki in Crete (Fiorentino and Solinas 2006; Sarpaki 2012), but morphometric data on grape pips from Crete are still lacking.

4.3. A wide range of varieties and practices from the late Bronze Age onwards

4.3.1. New types during the late Bronze Age and archaic period

The increase in domesticated types during the Late Bronze Age is

chronologically related to other evidence of viticulture: the increasing frequency of grape remains, which are recorded on most of the sites, and the increasing frequency of large concentrations of grape pips, reported from several sites from northern to southern Greece, sometimes associated with grape pressing by-products, as in the case of Late Bronze Age Thessaloniki Toumba in Macedonia (Mangafa et al., 1998; Valamoti 2009; Pagnoux 2016; Valamoti et al., 2018). Viticulture during the Late Bronze Age seems therefore well established in Greece. Domesticated types were known from Kastanas (Kroll 1979, 1983) and Toumba (Mangafa and Kotsakis 1996). Our morphometric analyses on a large body of data show that morphologically domesticated types are dominating most of the Late Bronze Age assemblages, at varying proportions between morphologically wild and domesticated within each assemblage.

In addition, the first written evidence of cultivated grapevines is dated to the Late Bronze Age: Linear B tablets from Knossos and Pylos record grapevine and fig trees. The word used to name the grapevine, *we-je-we*, means “married”: it could refer to an orchard where grapevines were grown on fig trees (Palmer 1994; see Pagnoux 2016, Valamoti and Stika 2019 and Valamoti et al., 2020 for recent discussion). It could also refer to grapevines and figs cultivated on the same plot. The economic and social role of wine and palatial control on its production may have led to new cultivation practices and possibly selection of new grapevine types.

The grape pips from the Late Bronze Age sites show morphological similarities with 52 modern varieties. These represent only 18% of the domesticated varieties of our set of reference: the archaeological grape pips analysed here are mainly assigned to varieties from Greece, the Balkans, Caucasus and to a lesser extent Western Europe. Conversely, some archaeological individuals could not be attributed to any modern reference varieties possibly due to seed shape distortion or/and the lack of modern reference. If the latter is the case, these pips may also correspond to extinct forms or varieties that are not included in our modern reference collection.

In addition to the continuous use of the grapevine from the Neolithic in Greece, the identified morphotypes within the Bronze Age assemblages may indicate a local domestication and selection process. In fact, some identified morphotypes may be considered as “low-selected” types on the basis of ampelographic research published by Negrul (1946) and Levadoux (1956). Archaeological pips from the Late Bronze Age and Archaic sites are mainly close to cultivars from Greece, the Balkans and the Caucasus. According to the geographical groups, named *proles*, defined by Negrul (1946) on the basis of ampelographic criteria, these cultivars belong to the *proles pontica*, which clusters cultivars from Caucasus and the Balkans (Negrul 1946; in Levadoux 1956). Varieties belonging to this group are considered as “low-selected” varieties, whose fruit may be used for wine making as well as for direct consumption (Levadoux 1956). Some traditional varieties from western Europe are supposed to have an eastern origin, thus sharing some features with the *pontica* cultivars, as is the case for ‘Bourboulenc’ (Levadoux 1956), to which ten pips are allocated. The presence of pips close to the supposed “ancestral” and low selected varieties from the Balkans and especially from Greece are also reported in Georgia during the Late Bronze Age (1110–940 BC) (Bouby et al. in press). These morphotypes may reflect an early domestication event and the emergence of new varieties at the first stage of plant breeding, in a geographical region far wider than previously thought.

Viticulture, like the cultivation of many perennial plants, is traditionally based on the use of vegetative propagation techniques. The adoption of these techniques is regarded as the keystone in the domestication of fruit trees (Zohary and Spiegel-Roy 1975, Zohary, 2004). It allows the fixation of desired phenotypic traits while offsprings from sexual crosses are often very different from their parents for such allogamic and highly heterozygous species. Sowing is consequently not regarded as an appropriate cultivation technique for grapevine and most fruit trees. The use of vegetative propagation techniques allow to

replicate varieties (clones) over very long periods, potentially centuries or millennia, without much change. On the other hand, the role of sexual crosses in traditional arboricultural systems is probably minimized in the modern scientific literature (Bouby and Ruas 2014). Sexual reproduction certainly played a major role in the early steps of grape domestication, for the spread of highly desirable traits, like hermaphroditism, or occasionally later for the production of new varieties. It is extremely challenging to gather any hints about the multiplication techniques used in the distant past. Since when has vegetative propagation been the key technique in viticulture? It is known from Latin writings that this was already the case in Roman antiquity (Columella, *On agriculture* V, 11; Cato, *On agriculture* 41, 1; Pliny the Elder, *Natural history* XVII, 23–26; Varro, *On agriculture* I, 40, 5). Palaeogenomic data confirm that clones could have been spread over hundreds of kilometres in Roman times and give evidence of direct parent-offspring relationships between some Roman grapes and modern varieties (Ramos-Madrugal et al., 2019). This implies a wide use of vegetative propagation to replicate nearly unchanged varieties for some two millennia. The wide and ancient use of vegetative propagation techniques could explain the dominant morphological proximity between Bronze Age pips and modern varieties from Greece, the Balkans and the Caucasus. Conversely, major changes in the morphological diversity of grape seeds could result from episodes of increased use of sexual propagation or of the introduction of allochthonous varieties. The emergence or introduction of new varieties during the Late Bronze Age probably also occurred. This period, and particularly the Mycenaean period (1650–1100 BC) in southern and central Greece, is characterized by intensification of exchange between the Aegean and surrounding regions. New varieties may therefore have been introduced, leading to an increase of new morphotypes from the Middle to the Late Bronze Age. The grape pips from Late Bronze Age Kastanas and Mitrou are partly classified as modern cultivars from Turkey, from the Levant and Caucasus: it may be consistent with an introduction of plant stock by means of contacts between Greece and the Levant. In addition, introduction of new varieties may have been followed by hybridization between these varieties and the local ones, leading to a range of phenotypic variability among the offspring plants.

While trade and exchanges between Greece and the rest of the Mediterranean basin increase during the Archaic period, no clear change in the cultivated diversity can be recognized from the domestic contexts of Greek sites examined here. On the other hand, the grape pips from the Heraion on the island of Samos, which is the most recent site investigated here, are different from the remaining assemblages, as they include more types from Caucasus and western Europe, and fewer pips close to Greek varieties. This particularity with the Heraion assemblage may be explained by several factors. It is the easternmost site of this study and clear evidence for contacts with the Levant are attested not only by the archaeobotanical material, including exotic species such as pomegranate or peach whose culture in Greece before the 4th century AD is uncertain, but also through pottery and other artefacts (Kučan 1995; Kyrieleis 1981). Consequently, importation of grape varieties along with other products from more eastern areas is highly probable (Pagnoux et al., 2015). The Heraion of Samos formed a major religious centre for archaic Greece and this may have affected the grapevine types recovered from it, in a way reflected in the wide range of imported foods and artefacts (see above). In addition, we cannot exclude the influence of the preservation mode on the results, although this possibility cannot be demonstrated (Bouby et al., 2018): grape pips from Samos represent the only waterlogged assemblage, while all the grape pips from the other sites are carbonized.

The introduction of new cultivars from the east Mediterranean is not inconsistent with the hypothesis of a local domestication. Diversity of cultivated forms probably increased during the Late Bronze Age and the Archaic period due to introduced new varieties in addition to locally selected grapevines, and possibly in relation to gene exchanges between introduced varieties and local wild and domesticated grapevines. To

explore this possibility, a large dataset of morphometric data from archaeological grape pips from Western Asia, the East Mediterranean and Caucasus is required.

4.3.2. Varietal diversity and cultivation practices

The grape pips dated to the Late Bronze Age and Archaic periods are mainly classified as domesticated, but a significant proportion of them belong to the wild type. This pattern is reported in other areas and until historical times, even until Hellenistic or Roman times, when specialized viticulture involved different varieties, landraces and specific cultivation practices in the wider Greek and Roman world, in Greece (Pagnoux 2016), Georgia (Bouby et al. in press) and France (Terral et al., 2010; Bouby et al., 2013). Gathering of wild berries and management of the grapevine in the wild cannot be excluded as stated above, but it seems less probable at the time when viticulture and cultivation of fully domesticated grapevine is fully established. This “wild” type reflects more probably grapevines which already underwent selection, but involving no change in seed morphology, as supposed in the case of large concentration of Neolithic and Early Bronze Age seeds. These seeds could reflect very long tradition inherited since the Late Neolithic.

Several practices could lead to the production of morphologically wild seeds, such as the use of individuals growing from seedlings, whose features may be closer to the wild grapevine (Levadoux 1956; Bouby et al., 2013; Bouby 2014). Agronomical practices including sexual propagation may also be responsible for the high variability and the dissimilarities from one sample to the other. Grape pips from every site dated to Late Bronze Age and Archaic period are allocated to various cultivars independent of the chronology, and several types are represented only on one site. The search for well-adapted varieties and the use of sexual propagation may lead to these site-specific assemblages. Clues to these practices could be found in Greek and Latin literature. Indeed, Cato (1st c. BC) refers to *miscellae* (Cato, *On agriculture* VI, 4), “mixed varieties” which may grow everywhere and whose fruit are acid-like those of the wild grapevine. It may refer to grapevine growing from seedlings (Bouby et al., 2013). In addition, Greek and Latin texts underline the strong link between a variety and the land where it is grown (Theophrastus, *Enquiry into plants* II, 5, 7; Pliny, *Natural history* 14, 70): it could reflect the selection of locally bred varieties, and may explain the site-level specificity we observed during the Late Bronze Age and the Archaic period.

5. Conclusion

The results presented here are based on morphometric analyses carried out on the largest dataset of grape pips dated to Neolithic and Bronze Age currently available. They suggest an early local grapevine domestication in prehistoric Greece. This process is rooted in the Neolithic and may consist of the management of wild grapevines or the cultivation of forms which underwent low and/or emerging selection pressure, corresponding to grape pips still morphology close to the wild form. The first indications of the domestication process date to the Early Bronze Age, with changes in grape pip morphology, still wild but already different from the seeds dated to the Neolithic. Then, the first cultivated types are dated to the Middle Bronze Age. Further studies and more assemblages from the 3rd and 2nd millennia BC are needed to lend further support to our hypothesis put forward here, that of a local domestication process.

During the Late Bronze Age, new domesticated types were perhaps introduced in the frame of increasing exchanges and trade between the Aegean and the Near East, new cultural habits and a new way to manage the grapevine under the palatial authority.

Viticulture during the Late Bronze Age and the Archaic period involved a wide range of varieties, including types close to the wild grapevine and cultivars which could reflect the early stage of plant breeding and diversification in the Mediterranean.

A local domestication process of the grapevine in prehistoric Greece,

as well as the introduction of varieties from the eastern Mediterranean during the Bronze Age, as a consequence of increased connectivity through exchange networks have been demonstrated on the basis of a robust dataset examined in this paper. Yet, further morphometric data is still required from the wider region of the grapevine’s natural distribution, south-eastern Europe, Western Asia and the East Mediterranean, in order to understand more robustly the processes of grapevine domestication in the Old World.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

This research has been funded by a doctoral fellowship from the University of Paris 1 Panthéon-Sorbonne and by the European Research Council, in the context of Project PLANTCULT “Identifying the Food Cultures of Ancient Europe”, conducted under the European Union’s Horizon 2020, Research and Innovation Program (Grant Agreement no. 682529), Consolidator Grant 2016–2021. This research also received funding from the French National Agency of Research (VINICULTURE project – ANR-16-CE27-0013) and the OSU-OREME (University of Montpellier).

We would like to thank the grapevine germplasm repositories of INRA-Domaine de Vassal (Marseillan-Plage, France) and Saguramo (Jighaura, Georgia) for their invaluable help in constituting our reference collection of modern grape seeds.

We would like to thank Felix Bitmann and the Lower Saxony Institute for coastal Research (NIhK, Wilhelmshaven, Germany) who gave access to the material from the Heraion of Samos, and all the archaeologists and archaeological projects and excavations who gave us access to the material: S. Andreou, P. Darcque, N. Efstathiou, G. Karamitrou, K. Kotsakis, E. Malapani, M.F. Papakonstantinou, S. Stocker, M. Tiverios, Z. Tsirtsoni and A. Van de Moortel.

The Institute for Aegean Prehistory (INSTAP) is acknowledged for funding S.M. Valamoti for the fieldwork conducted at P.O.T.A. Romanou.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jas.2020.105263>.

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