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Armenia: historical origin of domesticated grapevine

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Abstract. The Armenian Highlands are located on the northern border of Western Asia and stretch up to the Caucasus from the north. Throughout human history, the country has played an important role in connecting the civilizations of Europe and the Near East. A recent large-scale study about the dual domestication origin and evolution of grapes approved that in the Armenian Highlands human and grapevine stories are interlaced through centuries and roots of grapevine domestication are found deep in the Pleistocene, ending 11.5 thousand years ago. Until recently very little was known about the real magnitude of grape germplasm in Armenia. To address the gap in 2017, a nationwide program was launched to collect, conserve, and thoroughly characterize Armenian grapevine germplasm. Obtained results indicated that high genetic and morphological diversity as a source of novel alleles and genotypes is still safeguard in Armenia. A combination of genomic data, nuclear microsatellite markers and ampelography proved useful to determine the identity of collected samples recovered from old vineyards and home gardens, to analyze genetic relationships among two subspecies of *Vitis vinifera*, to demonstrated existence of gene flow between the wild and cultivated grapevines through overlaps and presence of admixed ancestry values.

1. The origin of viticulture and winemaking

To trace the history of grapevine (*Vitis vinifera* L.) domestication, multiple studies have consistently pointed that the process began in Western Asia and the Caucasus, leading to the development of distinct cultivated and wild subspecies with differing morphological characteristics [1-3]. A recent in-depth study has shed light on grapevine domestication history and baptized the legend of the "Noah hypothesis," which suggests that the first vine was planted on Mount Ararat. Armenia is considered an ancient origin of grapevine domestication and winemaking, as confirmed by the remains of wild and cultivated grapes, as well as wine-producing facilities found at archaeological sites in the country. A recent study by Dong and co-authors revealed that two distinct domestication events occurred concurrently around the advent of agriculture (~ 11000 years ago) in the two areas parallel. [4]. The geographic distribution of grapevine cultivars across Eurasia and North Africa, originating from the South Caucasus, reflects distinct human migration routes for the two primary grapevine groups. These cultivars were largely confined on both sides of the Caucasus Mountains, with only limited dispersal into the Carpathian Basin via the northern Black Sea. This finding challenges previous models, which suggested that cultivars from this region played a significant role in the development of European wine grapevines [4]. Instead, grapevines from the Armenian Highlands appear to represent a localized domestication process, exerting a relatively minor influence on overall grapevine diversification. Instead, grapes from the Armenian Highlands represent a local domestication effort that had a minor impact on grapevine diversification and serves as a unique gene pool with untapped potential.

Throughout millennia, grapevines have played a vital role in the religious and cultural traditions of Armenians. Cuneiform inscriptions from the era of the Van Kingdom provide valuable insights into historical practices of planting grapevines, constructing wine cellars, and engaging in other agronomic activities. The establishment of a powerful irrigation network and artificial reservoirs dates to this period in Armenian history. In the 8th century B.C., during the reign of King Argishti I, viticulture became one of the most essential branches of the country's economy. The ancient cities of Armenia - Van, Yervandashat, Armavir, Artashat, Tigranakert, Dvin, and

Vagharshapat were surrounded by agricultural lands, including vineyards with winepresses. The presence of agricultural areas was one of the most important features of Armenian cities, a characteristic typical of all societies in the region, especially during the Van Empire and the Hellenistic period, making it a key element of ethnic identity. Evidence of this can be found in the works of Herodotus, Xenophon, and Strabo [5,6]. The improvement of viticulture and winemaking traditions in Armenia recorded significant progress during the Middle Ages, as evidenced by archaeological excavations and bibliographic sources. Armenian historians and epigraphic inscriptions make numerous references to vineyards, wine presses and wine. The Armenian Church significantly contributed to the development of viticulture and winemaking as essential economic sectors. Almost all monasteries and famous churches had vineyards and wine presses and wine had an essential role in religious and spiritual life.

In the Armenian language, different names for vine plants exist: “vort,” “vortatunk,” “vaz,” “khaghogheni,” “movrashuk,” and “aghogh” (translated as grapevine or grape plant). The word “aygi,” in the modern sense, means a land plot planted with grapevines and fruit trees; however, the original meaning of the word specifically referred to a vineyard. Grapes were also an important source of food and medicine. The fruit of wild grapevines was harvested to make wine and juice, while the leaves and roots were used for various medicinal purposes. In the book "Haybusak," the author reports on the existence of wild grapes, describing them in detail as a liana growing in the mountains with small, sour, red berries [5].

Charred grape pips were recovered during excavations in 2001 (level I, UF87) at the ancient site of Aratashen in the Ararat Valley in a Neolithic settlement, suggesting the early use of grapevines in the region (Figure 1.) [7]. These seeds are the earliest related to human activity in Armenia. Most wild grapes have rounder pips with relatively short beaks, while cultivated varieties tend to have more elongated seeds with longer beaks. Based on the phenotype of the pips, they are morphologically closely related to wild grapes (*Vitis vinifera* L. subsp. *sylvestris*) rather than cultivated grapes, proving that 8,000 years ago, humans in this region had already begun domesticating wild grapes.

Figure 1. Charred grapevine seeds from the Late Neolithic settlement of Aratashen (after Harutyunyan *et al*., 2005).

In 2007, a significant archaeological discovery was made at the Areni-1 cave complex, located within the limestone formations of the Arpa River canyon in Vayots Dzor province. This site revealed an advanced, quasi-industrial wine production facility. The cave’s stable microclimate contributed to the exceptional preservation of organic materials, including grape seeds, which enabled detailed chemical analyses. These analyses confirmed continuous winemaking activity at the site, dating back to 4230-3790 BCE. The production complex included specialized infrastructure, such as a clay platform for grape crushing, a juice collection system, and pithoi (large earthenware vessels) used for wine fermentation and storage. One unique feature of the facility was the "aragast," or "sail," a distinctive design that has no known parallels in other ancient winemaking sites. This discovery represents the oldest well-preserved evidence of winemaking in the Armenian Highlands, documenting a 6,000-year tradition of viticulture in the region [8].

Domestication is an evolutionary process that involves intense selection for desired traits, often coupled with population bottlenecks, which significantly impact the genetic composition and phenotypic characteristics of a species [9]. In grapevine domestication, key morphological changes occurred, such as increased berry and cluster size, higher sugar concentrations, and modified seed morphology. One of the most profound effects of domestication was on the grapevine’s reproductive system. The shift from sexual reproduction to vegetative propagation, along with the transition from a dioecious (separate male and female plants) to a hermaphroditic species, enabled self-pollination, eliminating the need for cross-pollination [10]. This shift contributed to genetic bottlenecks, reducing genetic diversity. In contrast, wild grapevines (*V. vinifera* subsp. *sylvestris*), which remained dioecious, preserved higher levels of genetic polymorphism, exhibiting significant variation in traits such as berry size, shape, color, sweetness, and overall palatability. The recent study of genetic diversity conducted for Armenian wild grapes and indigenous cultivars unfolded the allelic richness of wild and cultivated gene pools and surprisingly revealed the absence of significant differences for all genetic parameters between the two subspecies. According to molecular fingerprinting data, the Armenian *V. sylvestris* population conserves a high genetic diversity and a low inbreeding level [11].

2. Karases (clay amphorae) in Armenian winemaking culture. A brief overview

Karases, traditional clay amphorae, have been a central element in Armenian winemaking since the third millennium BC and continue to be utilized successfully today. For winemaking in the Caucasus, the standard technology used is the fermentation of wine in clay vessels. In Georgia they are called qvevri, and in Armenia karas. However, making wine in a qvevri is quite different from similar processes involving karas. The technologies and vessels differ in terms of shape, volume, and type of clay.

Four types of karases have been employed in winemaking, distinguished by their placement in the production environment: above-ground, half-buried in the soil, buried up to the mouth, and fully buried. Due to the

technological approaches, these directions basically dictated the most important technical standards for the structure of the karas itself. Larger karases showcased the intricate relationship between winemaking and the potter's technological tricks [12]. Half-buried karases, widely used since Urartian times, are particularly noteworthy. Their partial underground placement allowed for thicker walls due to stable underground temperatures, reducing moisture infiltration and minimizing wine leakage. The above-ground section often featured triangular indentations to mitigate structural stress from temperature fluctuations. These adaptations were crucial in regions with extreme seasonal temperatures, where open platforms were used to concentrate wine by freezing in winter or exposing it to solar heat in summer [13]. Decorative elements, such as separating strips between the above- and below-ground portions of the karas, provided both structural support and aesthetic appeal. Fully buried karases were typically thick-walled with minimal surface decorations, while karases buried deeper, often exceeding one meter, exhibited asymmetric structures. In regions such as Paytakaran and the southern Caspian Sea coast, these karases were buried so deep that people and carts could pass over them.

Above-ground karases, commonly found in regions like the Ararat Valley, Vaspurakan, Nakhijevan, Vayots Dzor, and Syunik, had thinner walls to accommodate temperature fluctuations and reduce weight, allowing for mobility. Semi-buried karases, used for aging wines, offered better temperature stability, allowing wines to be stored for up to three years [13]. In contrast, wine stored in above-ground vats was consumed before the next harvest due to the high summer temperatures that prevented long-term storage.

Innovative approaches were used to control fermentation temperatures, such as the "vat-in-vat" method, where a smaller karas was placed inside a larger one with space for cold water circulation to cool the fermenting liquid. In regions with late harvests or sharp temperature drops, vats were placed near tandoors to maintain fermentation temperature, with bread baking adapted to regulate heat.

Karases varied in color depending on the source of the clay, with those from Shahumyan in Ararat being light-colored and those from Nork and Kanaker being reddish. Technological differences, such as the addition of hair, straw, or plant fibers to the clay, helped create microbubbles in the walls to reduce stress during firing. Preparing the karases for winemaking involved treating both the inner and outer surfaces. Semi-buried and fully buried karases were lined with dried herbs and antiseptic materials to create an aseptic environment and protect against moisture. Karases were meticulously prepared for winemaking, with the interior treated with mixtures of animal fat, beeswax, or herbs to create an aseptic environment. Before filling the wine, or after emptying, the karases were exposed to burning sulfur gas. In some cases, the jars were anointed with frankincense in parallel or sequentially with sulfur dioxide. By the way, these two substances were used not only before filling the container, but throughout the entire process of wine preparation and storage. Sulfur gas or frankincense was also applied for sterilization, and sealed jars were tied with waxed cloth and sometimes coated with clay or mazut. These practices, deeply rooted in Armenian tradition, demonstrate the sophistication of ancient winemaking techniques that continue to influence modern production.

3. Grapevine diversity and grapevine *ex-situ* collection of Armenia

The diverse altitudinal gradients and climatic zones of Armenia serve as key factors contributing to the country's exceptionally rich plant biodiversity, which includes numerous regionally endemic, relict, and rare species. Armenia is recognized as a significant center of endemism for wild relatives of economically important crops, notably the grapevine, which stands as one of the most emblematic species. Positioned at a strategic crossroads, Armenia has played a crucial role in the dissemination of grapevine cultivation, viticulture, and winemaking practices over the centuries.

There are five main viticulture regions in Armenia encompassing 16 000 ha of vineyards. Vineyards span a wide altitudinal range, from as low as 420 meters above sea level in Tavush Province to as high as 1800-2000 meters in Vayots Dzor Province. While vineyards in the country are oriented in various directions, the majority are situated on southern, southeastern, and occasionally eastern slopes, which provide the optimal sunlight and warmth needed for proper ripening in alpine conditions. Armenia's landscape is predominantly composed of volcanic soil, as well as sedimentary and sandy rocks. The high elevation of the vineyards, which ensures well-balanced and consistently ripened grapes, is essential for producing refined and elegant wines. On the map of Armenia, viticultural regions and their unique indigenous grapevine varieties native to each area are presented in Figure 2.

The study of genetic diversity within *Vitis vinifera* germplasm has been the focus of numerous investigations, initially utilizing ampelographic descriptors and incorporating genetic markers, as simple sequence repeats, SSRs and single nucleotide polymorphisms, SNPs. The integration of traditional ampelographic methods with molecular profiling has revealed the presence of 6,000 to 10,000 distinct *V. vinifera* cultivars, though this estimate is challenging due to the prevalence of homonyms and synonyms [14, 15]. Population genetic studies suggest that the vast diversity of vines is highly structured, influenced by factors such as the primary use cultivar and its geographical origin. This genetic variation is also reflected in phenotypic diversity observed in traits related to reproduction and quality, many of which are of significant interest for grape breeding programs [16]. Studies in association genetics have identified a strong correlation between genetic structure and phenotypic traits, driven by the preferential selection of alleles within genetic subgroups, resulting from processes such as diversifying selection or genetic drift. Despite this extensive diversity, only a small fraction of these cultivars is commercially

utilized, with most of the genetic variation preserved in germplasm collections. These collections play a crucial role in the establishment of core collections that aim to capture the global genetic and phenotypic diversity of grapevines, providing valuable resources for conservation and breeding efforts.

The first Armenian National Grapevine Collection, established in 1950 at the Institute of Viticulture, Fruit-Growing, and Wine-Making, encompassed around 850 varieties over 22 hectares. However, this collection was entirely lost following the collapse of the USSR in the early 1990s [3, 17]. In the years that followed, three new ampelographic collections were created, preserving almost hundred accessions, of which only seventy were autochthonous varieties. Despite these efforts, the preservation of Armenian grapevine germplasm in these collections was eventually discontinued, increasing the risk of losing valuable and endangered genetic diversity. Given this situation, the establishment of a new grapevine collection became essential [3]. To prevent genetic grapevine genotypes as a reservoir for future crop improvement. In 2016, the new *ex-situ* collection was established preserving up to 70% of the country's indigenous varieties.

The conservation and sustainable use of grapevine genetic resources depend on efficient management of germplasm collections and the precise description of the maintained accessions. Application of rules and adapted procedures are needed to ensure their survival and to make the material available to breeders, researchers and farmers. A general strategy for Armenian grapevine germplasm conservation encompasses the collection of the still existing diversity and the use of protection techniques to minimize the losses over time. Being studied mainly by ampelography, the genetic diversity of Armenian grapevines was re-investigated in accordance with modern requirements and international scales. The multidisciplinary study of Armenian grape cultivars and its wild ancestor, the subspecies *Vitis sylvestris*, by standard ampelographic and molecular methods, permit to estimate their breeding potential which is of great practical importance. For the recent years, the activities were forwarded to the comprehensive characterization of Armenian grapevine genetic diversity, based on its ampelographic, eno-carpological, genetic and genomic characteristics. With this purpose, Armenian-German cooperation highly supports the management of Armenian grapevine genetic resources. Several bilateral projects help to identify endangered, rare and unique genotypes and to promote their duplicates preservation in the grapevine collection at the Institute for Grapevine Breeding Geilweilerhof. The duplicate preservation is done in accordance with the objectives in the initiative of "European Genebank Integrated System" (AEGIS), implemented by the European Cooperative Programme for Plant Genetic Resources (ECPGR). The project permits to optimize and ensure duplication of autochthonous varieties in further Armenian grapevine collections as well. The available genetic diversity and its multidisciplinary study still allow us to identify valuable grape genetic resources, with possible resistance to pathogens and abiotic stresses and high wine and table grape quality.

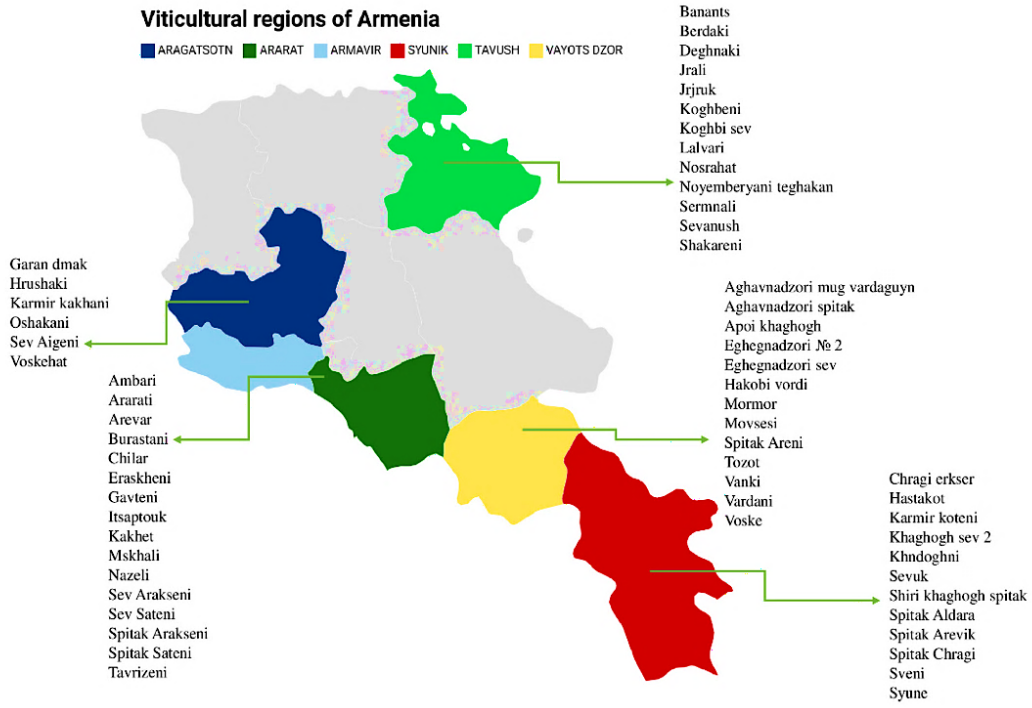

Figure 2. Some of the autochthonous grapevine varieties of the viticulture regions of Armenia.

Political shifts and economic decisions have posed significant threats to both the wild habitat of *Vitis sylvestris* and existing germplasm collections. A notable instance of such loss occurred with the collapse of the Soviet Union, which led to reduced funding for vital grapevine and perennial fruit collections. Despite these challenges, Armenia remains home to substantial populations of wild grapevines and for broad spectrum of autochthonous cultivars. However, the intensive cultivation of a limited number of commercial grapevine varieties has caused a concerning reduction in genetic diversity, with many traditional cultivars remaining underutilized and of only local importance within distinct wine-growing regions. To safeguard this genetic heritage, comprehensive surveys of old vineyards by skilled experts, combined with the preservation of germplasm in repositories, are essential.

This must be followed by the characterization, identification, and evaluation of agronomic traits, which are critical for breeding new cultivars and sustaining future generations of viticulture. Understanding the genetic diversity and relationships among grapevine cultivars is crucial for identifying gene pools and implementing effective conservation strategies. The management of germplasm collections is a complex and resource-intensive task, requiring technical, agronomic, and scientific efforts. The primary objectives are to maintain the accessions in optimal vegetative and productive conditions to ensure their long-term preservation and to verify the authenticity of the varieties, thus providing reliable material for research, breeding, viticulture, and germplasm exchange. Key initial steps in managing a collection involve meticulous documentation and characterization of each accession, following the "Multi Crop Passport Descriptors" (MCPD) standards set by Bioversity International. MCPD data provide essential information, such as the accession name, unique code assigned by the curator of the collection, berry color, provenance, and donor. Traditionally, grapevine cultivar identification has relied on ampelography, which involves describing and comparing morphological traits like shoot tips, shoots, leaves, and bunches. While highly accurate and reliable, this method demands experienced personnel. For many years, ampelography was the sole method for identifying cultivars in Armenia. However, DNA-based technologies are now being employed, particularly the use of microsatellite markers and whole genome sequencing data, which allows for effective comparison of allelic and genomic data with international collections.

Extensive efforts were undertaken for the last ten years to recover and identify local minor grapevine germplasm and wild grape populations in Armenia's traditional viticulture regions, including Ararat, Aragatsotn, Vayots Dzor, Tavush, Syunik, and Artsakh, during the vegetation and harvest seasons. The nationwide survey focused primarily on vineyards established in the early 20th century and earlier, many of which had been out of cultivation for extended periods. Family gardens were included in the survey, along with a few small private collections located in the Ararat Depression and Tavush. Some of the neglected autochthonous varieties discovered recent years are presented on Figure 3. The collection process was facilitated by local farmers and industry members, who provided essential support. Accession designations and MCPD data were recorded for each sample. In cases where grapevines lacked an official varietal name, generic names were assigned based on morphological traits, such as grape color or shape, or named after the farmer or locality where they were found. GPS coordinates and elevation data were also registered for each accession. Wild *Vitis sylvestris* plants were collected from their natural habitats, including riverbanks, rocky slopes, and trees. Each putative wild candidate underwent morphological analysis, and only those exhibiting key phenotypic characteristics of wild grapevines were selected for further genetic analysis. On the basis of realized in-depth investigation, a true-to-type inventory of Armenian grape germplasm was carried out and for nowthe data of 363 different Armenian varieties is documented in *Vitis* International Variety Catalogue (www.vitis.de).

Figure 2. Autochthonous grapevine diversity of Armenia.

4. Conclusion and perspectives

Surveys in traditional viticulture regions across Armenia revealed the huge grapevine genetic diversity existing in the country. More than 3000 different grape genotypes including neglected cultivars, clones, mutant forms and wild grapes are inventoried, characterized and documented. A combination of microsatellites and ampelography has been valuable in identifying collected samples recovered from old vineyards and home gardens. Synonyms, homonyms, alternative spellings, and misnomers were clarified. Well-identified and referenced grape genetic resourceswith controlled phytosanitary status are a prerequisite for its utilization and the management of germplasm repositories. However, the assignment of variety names was challenging. More than 130 genotypes could not be identified, due to missing genetic profiles in SSR databases or lack of names. Further bibliographical studies and cooperation with national germplasm repositories, preserving Armenian varieties is envisaged. First-degree genetic relationships between autochthonous varieties were uncovered. Missing parents might still exist in old vineyards but were not sampled yet or might have disappeared over time. Continuation of prospections to fill that gap is planned. The high number of new bred varieties included in the study reflects the enormous breeding activity in Armenia. Twenty-five non-determined genotypes were identified as new crosses due to the inferred parents involved in the cross. The high number of alleles, high observed and effective heterozygosity values, illustrate the huge diversity of Armenian germplasm. Presumably, these findings are related to recurrent introgression of *Vitis sylvestris* into the cultivated compartment during domestication events. Instability of grapevine cultivars was detected, showing three and in rare cases also four alleles at one locus. A deeper study of this quite frequent phenomenon will be carried out. So far, the most representative and comprehensive analysis of Armenian grape germplasm has been done.

The recent study forwarded on precise analysis of wild grapes growing in Armenia indicated that high genetic and morphological diversity as a source of novel alleles and genotypes is still preserved in the wild populations. An in-depth study to understand the resistant potential of Armenian wild grapes against powdery mildew is ongoing. Previous studies highlighted the importance of *V. sylvestris* germplasm conservation as the unique genetic resource, which can contribute to the development of improved cultivars with enhanced disease resistance, adaptability, and quality traits, and mirror the existence of significant diversity both within and between the subspecies suggesting that Armenia is an important origin of grape biodiversity.

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