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Genetic characterization and relationships of traditional grape cultivars from Transcaucasia and Anatolia

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Abstract

We present here the first large-scale genetic characterization of grape cultivars from Transcaucasia and Anatolia. These regions where wild grapes still grow in nature have been cultivating wine and table grapes for thousands of years and are considered the cradles of viticulture. Using 12 nuclear microsatellite markers, we genotyped 116 accessions of traditional grape cultivars from Armenia, Georgia and Turkey and we detected 17 identical genotypes and six homonymy cases, mainly within each national germplasm. Neighbour-joining analysis of genetic distance showed that each germplasm could have multiple origins and although they are now separated, they might have some common ancestors. In addition, four varieties from Western Europe included as outgroups turned out to be more related to Georgian cultivars than other germplasms, suggesting a possible ancient origin in Georgia. This work represents a first step towards germplasm management of this rich ampelographic heritage.

Keywords: Armenia; genetic relationship; Georgia; microsatellite; Turkey; *Vitis vinifera*

Introduction

Transcaucasia and Anatolia have long been regarded as likely homelands of viticulture and the earliest 'wine culture' (Vavilov, 1926; Negrul, 1938; Levadoux, 1956; Olmo, 1995; Zohary and Hopf, 2000; McGovern, 2003). The wild *Vitis vinifera* L. subsp. *silvestris* continues to thrive in these regions, where today hundreds of cultivars (*V. vinifera* L. subsp. *vinifera*) are grown for wine and table grapes. Based on recent archaeological and chemical evidence, a 'wine culture' had been established as early as 6000 BC in the upland region of the Taurus Mountains in Eastern Anatolia, the Caucasus Mountains (including Transcaucasia) and the northern Zagros Mountains of Iran (see McGovern, 2003 for discussion and references). Recent chemical analyses (P. McGovern, in preparation) of Neolithic pottery from Georgia (Shulaveris-Gora) and Eastern Anatolia (Cayönü), dating back to the early 6th millennium BC, corroborate that the same beverage was being produced over a broad area of the mountainous Near East.

The present work will focus on DNA typing of grape cultivars from these areas. In Georgia, more than 500 indigenous wine and table grape cultivars have been described

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(Ketskhoveli *et al.*, 1960), including centuries-old cultivars like 'Rkatsiteli', 'Mtsvane' or 'Khikhvi' (Chkhartishvili and Tsertsvadze, 2003). However, only half of these cultivars have been conserved in four national collections and today only a small number of local varieties are still cultivated (Chkhartishvili, 2003; Maghradze, 2003). The most important autochthonous cultivars for winemaking are 'Rkatsiteli' (white) and 'Saperavi' (red). In Armenia, the Merdzavan ampelographic collection used to contain more than 800 accessions of indigenous and introduced varieties (including various clones) until 1993, but it has been unfortunately destroyed after land privatization (Gasparyan and Melyan, 2003). Less than 100 accessions are now available from three national collections, of which very few are autochthonous cultivars. The most important indigenous wine varieties are the white 'Voskeat' and 'Mskhali' (used for brandy) and the red 'Areni Chernyi' and 'Kachet'. In Azerbaijan, more than 500 grape cultivars are kept in collection, half of them being considered local varieties (Musayev, 2003). The most important indigenous varieties are the white 'Bajac Shirei' and the red 'Shahani'. In Turkey, more than 1000 grape accessions exist in the National Germplasm Repository Vineyard at Tekirdağ Viticulture Research Institute in Thrace (Ağaoğlu and Celik, 1986; Ergül *et al.*, 2002), most of them being considered indigenous to Anatolia. The most important indigenous varieties are the white 'Sultani Çekirdeksiz' ('Sultanina' or 'Thompson Seedless', especially for table grape production), 'Emir', 'Narince' and 'Misket' and the red 'Öküzgözü' and 'Boğazkere'. The genetic relationships among and between these gene pools of grape cultivars were investigated here by DNA profiling.

Since their first application to grapevine (Thomas and Scott, 1993), microsatellites have been widely used for cultivar identification (Grando and Frisinghelli, 1998; Sefc *et al.*, 1998a; Meredith *et al.*, 1999) and analysis of genetic relationships (Lefort and Roubelakis-Angelakis, 2001; Aradhya *et al.*, 2003). However, only a fraction of the 8000–10,000 grape cultivars existing worldwide (Alleweldt, 1997) have been genotyped with microsatellites, most of them coming from occidental Europe. The greater part of the huge germplasm of grape cultivars from the Near and Middle East remains to be genotyped. To our knowledge, there are no microsatellite data available in the literature for cultivars from Armenia or Georgia, with the exception of the widespread 'Rkatsiteli' and 'Saperavi' in Lamboy and Alpha (1998). From Turkey, Aradhya *et al.* (2003) analysed five cultivars and Benjak *et al.* (2005) genotyped nine cultivars, of which three are analysed in the present paper ('Erik Kara'/'Kara Erik', 'Hatun Parmağı' and 'Kabarcık') with five loci overlapping. For each country, we selected the most ancient and traditional grape cultivars in order to obtain a representative sampling of the whole germplasm. We used 12 nuclear microsatellite markers to characterize 116 accessions of traditional grape cultivars from Armenia (13), Georgia (41) and Turkey (62) and searched for synonyms, homonyms and genetic relationships. This work represents the first microsatellite characterization of germplasms from Transcaucasia and Anatolia, and it is a first step towards germplasm management of this rich ampelographic heritage.

Materials and methods

Plant material

Genomic DNA was extracted with Qiagen DNeasy Plant Mini Kit or according to Lodhi *et al.* (1994) from dried leaves of 116 accessions sampled in vineyards or ampelographic collections and putatively corresponding to 98 grape cultivars (Table 1) from Georgia, Armenia and Turkey (Azerbaijan could unfortunately not be included in the sampling).

Microsatellite analysis

We analysed 12 nuclear microsatellite markers: VVMD5 and 7 (Bowers *et al.*, 1996), VVMD24, 28, 31 and 32 (Bowers *et al.*, 1999b), VrZAG62 and 79 (Sefc *et al.*, 1999), VVS2 (Thomas and Scott, 1993), and VMC2C3, 2H4 and 5A1 (Vitis Microsatellite Consortium, www.agrogene.com). Five of these markers belong to the 'core set' chosen by the international grape community (This *et al.*, 2004): this will allow comparison of our data with most other germplasms. PCR amplifications were performed in 10 μl reaction mixtures with Qiagen HotStarTaq Master Mix Kit. Microsatellite markers were labelled with three possible fluorescent dyes (6-FAM, HEX and NED, Applied Biosystems). PCR conditions were: 15 min at 95°C (initial activation step for HotStarTaq DNA Polymerase), 35 cycles comprised of 60 s at 94°C (denaturation), 30 s at 52 or 56°C according to literature (annealing), 90 s at 72°C (extension), followed by 10 min at 72°C (final extension). Every accession was amplified at least twice or more if necessary in order to avoid typing errors. PCR products were electrophoresed in an ABI PRISM 3100 DNA Sequencer (Applied Biosystems). Allele sizes were assigned against Genescan ROX 400 internal size standard and individuals were genotyped using Genescan analysis software and Genotyper software version 3.7 (Applied Biosystems). In each run, we have included four well-known cultivars from Western Europe ('Chasselas' and 'Pinot Noir' from Agroscope RAC Changins, Centre viticole du Caudoz, Pully,

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Table 1. Cultivars included in this study: the 116 cultivars are grouped by country of origin and numbered alphabetically

	Name[a]	Sampling[b]	Cultivation area[c]
Armenia			
1	Ak-kaltak (b,wt)	YR	Uzbekistan
2	Areni Chernyi (n,w)	N	Vajots Dzor (Armenia)
3	Areni Chernyi (n,w)	Areni†	Vajots Dzor (Armenia)
4	Chilar (b,w)	YR	Armenia
5	Garandmak (b,w)	YR	Armenia, Crimea and Caucasus
6	Kachet (n,w)	Areni†	Armenia
7	Karmir Kakhani (n,t)	YR	Armenia
8	Khatun Khardjzhi (b,w)	Areni†	Armenia
9	Mskhali (b,wt)	YR	Armenia
10	Mskhali (b,wt)	Areni†	Armenia
11	Tozot (n,w)	Areni†	Armenia
12	Vardagujn Jerevani (r,t)	YR	Erevan (Armenia)
13	Voskeat (b,w)	YR	Echmiadzin, Erevan (Armenia)
Georgia			
14	Alabeuri Chavi* (n,w)	Racha-Lechkumi†	Racha-Lechkumi and Crimea
15	Aladasturi (n,w)	TVI	Imereti and Crimea
16	Aleksandrouli (n,w)	TVI	Georgia and Crimea
17	Buera (b,wt)	TVI	Georgia and former USSR
18	Chavkapito (n,w)	Khartli†	Ossetia
19	Chinuri (b,w)	TVI	Georgia
20	Chitistvala Bodburi (b,w)	Khakheti†	Khakheti
21	Chkhaveri (n,w)	TVI	Mingrelia
22	Chkovra* (?,w)	Imereti†	Imereti
23	Dondglabi (b,w)	TVI	Imereti
24	Dondglabi Tetri* (n,w)	Imereti†	Imereti
25	Dzvelshavi Sachkheris (n,w)	TVI	Imereti and former USSR
26	Gorula (or Ananovra) (b,wt)	TVI	Khartli
27	Grdzelmtevana (b,w)	Gurdjani†	Khakheti, Imereti and former USSR
28	Kapistoni Imeretinskii (b,w)	Imereti†	Imereti
29	Kharistvala Tetri (b,wt)	TVI	Georgia
30	Khikhvi (b,w)	TVI	Khakheti, Moldavia, Crimea and Daghestan
31	Khounalige* (b,w)	TVI	Abkhazia
32	Khupishizh (n,w)	TVI	Abkhazia
33	Kichouri* (b,wt)	TVI	Khartli
34	Kisi (b,wt)	TVI	Khakheti
35	Krakhuna (b,wt)	TVI	Imereti and Crimea
36	Kundza (b,w)	TVI	Imereti, Khakheti
37	Kvira (r,w)	TVI	Racha-Lechkumi, Imereti
38	Maglari Tvrina (r,w)	TVI	Georgia
39	Mamukas Sapere (n,w)	TVI	Georgia
40	Meskhuri Chitiskvertskha* (n,w)	Khartli†	Khartli
41	Meskhuri Shavi (r,wt)	TVI	Khartli
42	Mudzhuretuli (n,w)	TVI	Georgia
43	Odzhaleshi (n,wt)	TVI	Samegrelo, Mingrelia, Imereti, Khakheti
44	Otskhanuri Sapere (n,w)	Imereti†	Imereti
45	Rkatsiteli (b,wt)	TVI	Khakheti and former USSR
46	Saperavi Mrgvalmarzvala* (n,w)	Khakheti†	Khakheti and former USSR
47	Saperavi Pachkha (n,w)	Khakheti†	Khakheti and former USSR
48	Skhilatubani (n,w)	TVI	Georgia
49	Tavkara (n,w)	Khakheti†	Khakheti
50	Tavkveri (n,wt)	TVI	Khakheti and Azerbaijan
51	Tkupkvirta (n,w)	Khakheti†	Khakheti, Imereti
52	Tsitska (b,wt)	Imereti†	Imereti
53	Tsolikouri (b,w)	Imereti†	Imereti
54	Uriatubanskii (n,w)	Vardisubani†	Russia
Turkey			
55	Abderi* (b,tr)	TNGRV	Çermik/Diyarbakır (SE Anatolia)
56	Aşeri (b,t)	TNGRV	Nevşehir (Cappadocia)
57	Azezi (b,wtr)	TNGRV	Adıyaman (SE Anatolia)

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Table 1. *Continued*

Name[a]		Sampling[b]	Cultivation area[c]
58	Ballıboz (b,t)	Adıyaman†	Adıyaman (SE Anatolia)
59	Belelük* (n,w)	Çüngüş/Diyarbakır†	Çüngüş/Diyarbakır (SE Anatolia)
60	Besni (b,tr)	TNGRV	SE and E Anatolia
61	Besni (b,tr)	AUKVRES	SE and E Anatolia
62	Boğazkere (n,wt)	TNGRV	Elazığ, Malatya, Gaziantep (SE Anatolia)
63	Boğazkere (n,w)	AUKVRES	Elazığ, Malatya, Gaziantep (SE Anatolia)
64	Burdur Dimriti (n,wt)	TNGRV	Eğridir/Isparta (Mediterranean)
65	Burdur Dimriti (b,wr)	TNGRV	Eğridir/Isparta (Mediterranean)
66	Dımışkı (b,t)	TNGRV	SE Anatolia
67	Dökülgen (b,wt)	Kahramanmaraş†	Gaziantep, Kahramanmaraş (SE Anatolia)
68	Dökülgen (b,w)	Konya†	Hadım/Konya (C Anatolia)
69	Dökülgen (b,w)	AUKVRES	E Turkey, Kalecik
70	Ekşi Kara (n,wtr)	TNGRV	Narlıdere/Karaman (C Anatolia)
71	Ekşi Kara (n,wtr)	TNGRV	Morcalı/Karaman (C Anatolia)
72	Emir (b,wt)	Nevşehir†	Nevşehir, Kayseri (C Anatolia)
73	Emir (b,wt)	AUKVRES	Cappadocia (C Anatolia)
74	Erik Kara (n,wt)	TNGRV	Sivas, Erzincan, Malatya (E Anatolia)
75	Gemre Siyah (n,t)	Isparta†	C/Isparta (Mediterranean)
76	Gemre Siyah (n,t)	Isparta†	C/Isparta (Mediterranean)
77	Gemre Siyah (n,t)	Isparta†	C/Isparta (Mediterranean)
78	Gök Üzüm (b,wt)	Morcalı†	Morcalı/Karaman (C Anatolia)
79	Hasandede Beyazı (b,wt)	AUKVRES	Ankara, Kırıkkale
80	Hasipali* (b,t)	Konya†	Çatalhöyük/Konya (C Anatolia)
81	Hatun Parmağı* (n,t)	Çermik†	Çermik/Diyarbakır (SE Anatolia)
82	Hönüsü (n,t)	AUKVRES	SE Anatolia
83	Hönüsü (n,w)	TNGRV	SE Anatolia
84	İri Beyaz (b,t)	Çatalhöyük†	Çatalhöyük/ Konya (C Anatolia)
85	İri Daneli Ak Üzüm (b,t)	Bozkır†	Bozkır/Konya (C Anatolia)
86	İri Kara (r,wtr)	Hadim†	Hadım/Konya (C Anatolia)
87	İri Siyah* (n,t)	Çatalhöyük†	Çatalhöyük/Konya (C Anatolia)
88	Kabarcık (b,wt)	TNGRV	E Turkey, Kalecik
89	Kabarcık (b,wt)	Kahramanmaraş†	Kahramanmaraş, Gaziantep, Malatya
90	Kayseri Karası (n,w)	Kayseri†	Kayseri (C Anatolia)
91	Kirkit (b,t)	Diyarbakır†	Diyarbakır (SE Anatolia)
92	Kırmızı Dimrit (n,w)	Nevşehir†	Nevşehir (Cappodochia)
93	Kızıl Üzüm (r,t)	TNGRV	Çatalhöyük/Konya (C Anatolia)
94	Künefi (n,t)	Gaziantep†	Gaziantep (SE Anatolia)
95	Luvanek* (b,tr)	Çermik†	Çermik/Diyarbakır (SE Anatolia)
96	Mor Üzüm* (b,t)	Uçhisar†	Uçhisar/Nevşehir (C Anatolia)
97	Morek* (n,t)	Ergani†	Ergani-Diyarbakır (SE Anatolia)
98	Muhammediye (b,wt)	TNGRV	Mardin (SE Anatolia)
99	Narince (b,w)	AUKVRES	C Turkey
100	Öküzgözü (n,w)	Elazığ†	Elazığ, Malatya, Gaziantep (SE Anatolia)
101	Öküzgözü (n,w)	AUKVRES	E Turkey
102	Parmak (b,t)	Nevşehir†	Nevşehir, Kayseri, Konya (C Anatolia)
103	Razakı (b,t)	Isparta†	C/Isparta (Mediterranean)
104	Şaraplık Siyah (n,w)	Çermik†	Çermik/Diyarbakır (SE Anatolia)
105	Şıralık (b,w)	Siverek†	Siverek/Urfa (SE Anatolia)
106	Şıralık (b,w)	Siverek†	Siverek/Urfa (SE Anatolia)
107	Şıralık (b,w)	Siverek†	Siverek/Urfa (SE Anatolia)
108	Şıralık (b,w)	Siverek†	Siverek/Urfa (SE Anatolia)
109	Şıralık (b,w)	Eğil†	Eğil/ Diyarbakır (SE Anatolia)
110	Siyah* (n,w)	Yalvaç†	Yalvaç/Isparta (Mediterranean)
111	Sungurlu (b,w)	AUKVRES	Kırıkkale, Çorum (C Anatolia)
112	Tahannebi (b,t)	AUKVRES	E Turkey
113	Tahannabi (b,t)	TNGRV	SE Anatolia
114	Timbo* (n,wt)	Adıyaman†	Adıyaman (SE Anatolia)
115	Vanki (b,wt)	Çermik†	Çermik-Diyarbakır (SE Anatolia)
116	Vilki* (n,t)	Çermik†	Çermik/Diyarbakır (SE Anatolia)

Switzerland and 'Syrah' and 'Nebbiolo' from Istituto Agrario di San Michele all'Adige, Italy). They served as standards in order to have consistent allele sizes over all runs and they allowed allele size comparison with other germplasms.

Identical genotypes and homonyms

The genotypes were compared to those of more than 1700 grape cultivars from all over the world put together and standardized from different databases (University of California, Davis; Grape Microsatellite Collection, IASMA, Italy, http://www.ismaa.it/areabioav/gmc.html; Greek Vitis Database, University of Crete, Heraklion, Greece, http://www.biology.uoc.gr/gvd/; Bulgarian Grape nSSR Database, http://bulgenom.abi.bg/Grape%20nSSR%20Database.html) and from various references in the literature. We checked for the presence of identical genotypes within the accessions with the program 'DNA-Data' (B. H. Prins, unpublished). This program offers the option of a user-defined level of discrepancy, in order to ascertain possible identities despite the presence of a few allelic mismatches. This is particularly useful with mutations or null alleles.

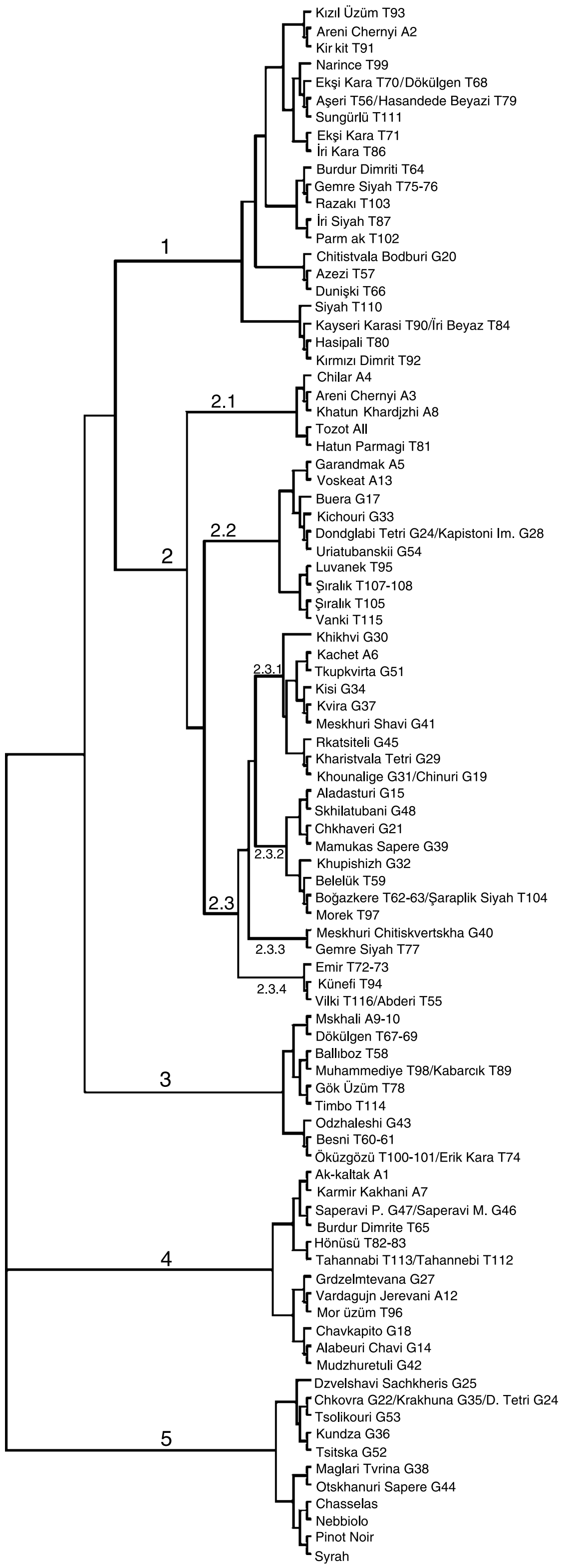
Genetic analysis

Standard genetic parameters were calculated using Microsat (Minch *et al.*, 1995). Probability of identity was estimated with the program Identity (Wagner and Sefc, 1999). Populations (version 1.2.28) (Langella, 2002) was used to calculate Nei *et al.*'s (1983) D_A pairwise genetic distance between individuals and construct the neighbour-joining tree of individuals presented in Fig. 1 and displayed with Treeview (Page, 1996). According to Takezaki and Nei (1996), the D_A genetic distance is more efficient than Nei's (1972) standard genetic distance (D_s), Nei's (1973) minimum genetic distance (D_m) and Rogers' (1972) distance (D_r) in obtaining the correct topology, either under the infinite-allele model (IAM) or the stepwise mutation model (SMM) of microsatellites evolution. The program Populations accepts input file in Genepop (Raymond and Rousset, 1995) format. Hence we used the software Genetix (Belkhir *et al.*, 1996–2002) to convert microsatellite allelic data computed in Microsoft Excel into Genepop format.

Results and discussion

The analysis of 116 accessions from Armenia (13), Georgia (41) and Turkey (62) at 12 microsatellite markers (Table 2) generated 138 alleles. The number of alleles per locus ranged from six (VVMD24) to 16 (VVMD28 and 32) with a mean number of 11.9 (Table 3), which is much higher than values previously reported for the same loci (Lopes *et al.*, 1999; Maletic *et al.*, 1999; Lefort and Roubelakis-Angelakis, 2001; Costantini *et al.*, 2005). Average observed heterozygosity was high at 0.796, slightly above Aradhya *et al.* (2003) who obtained 0.771 with 244 *Vitis vinifera* accessions analysed at eight microsatellite loci (of which five were analysed in the present work) and Sefc *et al.* (2000) who obtained 0.785 with 164 cultivars analysed at nine SSR markers (of which five were analysed in the present work). Such a high rate of heterozygosity is commonly observed among clonally propagated, outbreeding, perennial species (Aradhya *et al.*, 2003). Total probability of identity (PI) was very low at 1.67e-12. The most informative locus turned out to be VMC2H4 (12 alleles, PI = 0.054) and the least informative was VVMD24 (seven alleles, PI = 0.231). A few accessions exhibited three alleles at some loci (especially at VVS2 locus; see Table 2). Since one of the alleles usually had a weaker amplification signal, we suggest the presence of chimeric alleles at these loci. Chimerism has already been reported in grape cultivars (Franks *et al.*, 2002; Riaz *et al.*, 2002), especially for ancient cultivars (e.g. 'Pinot'). This suggests that cultivars showing chimeras in Table 2 ('Kachet' and 'Tozot' from Armenia; 'Dzvelshavi Sachkheris' from Georgia; 'Dımışkı',

Where possible, names are spelled according to the Vitis International Variety Catalogue (http://www.genres.de/idb/vitis/vitis.htm). The colour of the berries is indicated as n (noir, blue berries), b (blanc, white berries) or r (rose, pink berries), according to international usage. Grapes can be used for table (t), wine (w) or raisin (r). Accessions were sampled from grape collections or vineyards. Cultivation area gives an idea of the grape's distribution.
[a] Names not found in the Vitis International Variety Catalogue are marked with an asterisk (*).
[b] Accessions marked with a dagger (†) were sampled from vineyards. Abbreviations for ampelographic collections are: YR, Yeras Rahun collection, Scientific Centre of Agrochemistry and Farmer, Armenia; N, Nalbaldian collection, Armavir region, Armenia; TVI, Tbilisi Viticulture Institute collection; AUKVRES, Ankara University, Kalecik Viticultural Research and Experiment Station; TNGRV, Turkey National Germplasm Repository Vineyard.
[c] Particular areas within the country or areas other than sampling area, based on Galet (2000) or various personal communications.



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'Luvanek', 'Morek', 'Sungurlu' and 'Vilki' from Turkey) might be very old.

Identical genotypes and homonyms

The Anatolian and Transcaucasian genotypes were checked against a database of more than 1700 cultivars (mostly from Western Europe) and wild grapes (from Western Europe and Near East) at 6–12 microsatellite markers (depending on the data available). We found 17 cases of identical genotypes (Table 4) and six cases of homonymy (Table 5). Referring to Table 1, several identical genotypes occurred between accessions of different colours and/or different uses (Table 4, pairs in italic). In such cases, it has not been possible to determine whether the cause of identical genotypes was synonymy, misnaming or mutations, because this would require detailed ampelographic analysis with independent accessions when possible. Three cases of identical genotypes were found outside the study area:

- 'İri Daneli Ak Üzüm' and 'Italia': 'Italia' is an artificial cross between 'Bicane' and 'Muscat de Hambourg' obtained in 1911 (Galet, 2000). 'İri Daneli Ak Üzüm' literally means 'white grape with large berries'. It matched the genotype of 'Italia' from (i) IASMA collection at all loci; (ii) Crespan *et al.* (1999) at the six shared loci; (iii) Montpellier (Vassal, France) collection at the five shared loci; and (iv) Sanchez-Escribano *et al.* (1999) at the three shared loci. In addition, this genotype shares at least one allele at each available locus with 'Muscat de Hambourg' accessions from various sources (e.g. IASMA; University of California, Davis; Crespan, 2003). As a result, this genotype is most likely the true-to-type 'Italia'. Therefore, 'Italia' must have been introduced later to Turkey where it was given the name 'İri Daneli Ak Üzüm' after its berry colour and size.
- 'Parmak' and 'Jerusalem Bleu': 'Jerusalem Bleu' is a black-berried grape kept in a collection at Montpellier (Vassal, France) and supposedly introduced from Germany, but its origin is unknown (Galet, 2000). 'Parmak' is a white-berried grape cultivated in Central Anatolia. Careful ampelographic analysis would be required to determine whether mislabelling or colour mutation could explain their having identical genotypes.
- 'Mor Üzüm' and 'Tsaousi': according to Galet (2000), the Greek 'Tsaousi' is the same as 'Chaouch', a white table grape very widespread in the Near East. Indeed, we observed that the genotype of 'Tsaousi' in Lefort and Roubelakis-Angelakis' (2001) is identical to the genotype of 'Chaouchi Politico' in Bowers *et al.* (1996). Thus, 'Mor Üzüm', 'Tsaousi' and 'Chaouch' are synonyms, which is consistent with the suggestion of Lefort and Roubelakis-Angelakis (2001) that 'Tsaousi' might be of Eastern origin.

The other identical genotypes occurred within the studied areas: the genotype of 'Saperavi Mrgvalmarzvala' and 'Saperavi Pachkha' matched the 'Saperavi' accessions in Lamboy and Alpha (1998) and in the collection of the University of California at Davis. As a result, and although Galet (2000) considers them as distinct cultivars, our data provided evidence that 'Saperavi Mrgvalmarzvala' and 'Saperavi Pachkha' are clones of the same cultivar.

For most homonymy cases in Table 5, it has been for now impossible to determine which cultivar is true-to-type, because referring to ampelographic descriptions would be required, which is outside of the scope of this paper. The genotype of 'Areni Chernyi' (no. 2) sampled from a grape collection was different from the genotype of 'Areni Chernyi' (no. 3) that was sampled directly from the vineyards producing the nationally famous Areni wines; for that reason, we suggest that accession 3 is more likely the true-to-type 'Areni Chernyi', but analysing more independent samples and ampelographic descriptions would clear up this dilemma completely. Similarly, it has been impossible to determine the true-to-type accession of 'Burdur Dimriti' (Table 5). Since 'Dökülgen' 68 and 'Ekşi kara' 70 (Table 4) have the same genotype but different berry colours, 'Dökülgen' 68 is likely to be a misnaming and accessions 67 and 69 should be true-to-type 'Dökülgen'. However, because of identical genotypes with different names, we could not determine the true-to-type 'Ekşi kara' (see Genetic relationships). This would require careful study of ampelographic descriptions, etymology and local literature, which is out of the scope of the present

Fig. 1. Neighbour-joining tree of 89 distinct grape cultivars (identical genotypes were merged) from Anatolia and Transcaucasia and four Western European standards ('Chasselas', 'Nebbiolo', 'Pinot Noir' and 'Syrah') constructed from 12 microsatellite markers with Nei's D_A genetic distance. Every cultivar is shown with its country of origin (A, Armenia; G, Georgia; T, Turkey) and its accession number in Table 1. Five distinct clusters were isolated, and the main cluster (no. 2) was subdivided (see text for details). Germplasms from each country are well separated and might have multiple origins, although all three germplasms are likely to have common ancestors. The Western European standards turned out to be closer to Georgian cultivars than Turkish or Armenian, suggesting they could have some Georgian ancestors.

Table 2. Genotypes of 89 grape cultivars from Transcaucasia and Anatolia (identical genotypes were merged) and four standard varieties at 12 microsatellite markers (accession numbers corresponding to Table 1 are cited in parentheses); chimeric cultivars have three alleles

Cultivar	VVMD5	VVMD7	VVMD24	VVMD28	VVMD31	VVMD32	VVS2	VrZAG62	VrZAG79	VMC2C3	VMC2H4	VMC5A1
Ak-kaltak (1)	240–234	253–243	223–214	249–235	212–196	257–251	157–151	189–189	257–247	170–162	218–208	171–161
Areni Chernyi (2)	236–236	245–235	219–210	261–237	222–210	253–249	143–135	195–189	249–237	170–165	212–212	169–165
Areni Chernyi (3)	240–236	249–249	218–210	247–247	216–210	273–273	133–133	201–199	247–243	179–170	222–218	167–165
Chilar (4)	236–236	253–249	218–214	279–279	212–196	273–267	135–133	205–197	251–241	179–170	222–210	167–165
Garandmak (5)	236–234	249–247	212–210	281–279	212–212	267–265	143–125	195–191	251–239	170–165	210–206	167–161
Kachet (6)	240–238	253–239	219–210	239–239	216–212	273–251	157–143–135	203–201	249–237	195–165	212–210	171–161
Karmir Kakhani (7)	240–240	253–243	210–210	247–241	216–214	273–251	151–135	197–189	257–247	170–165	220–218	171–171
Khatun Khardjzhi (8)	246–240	249–239	218–218	247–247	216–210	273–273	133–125	197–189	247–239	179–170	218–208	171–165
Mskhali (9)/ Mskhali (10)	238–238	249–247	214–210	251–239	210–210	273–257	151–135	201–189	247–247	165–165	208–204	171–171
Tozot (11)	234–234	255–239	218–218	273–243	210–202	273–263	157–145–125	205–189	247–239	169–165	208–206	171–169
Vardagujn Jerevani (12)	234–228	247–239	219–208	279–219	224–212	273–251	151–143	205–189	259–251	170–162	208–206	171–161
Voskeat (13)	236–236	249–247	218–210	261–261	212–212	275–267	145–143	195–191	249–239	179–165	210–204	171–167
Alabeuri Chavi (14)	228–226	247–245	218–210	261–251	212–210	263–251	153–143	205–203	251–251	165–165	218–206	171–161
Aladasturi (15)	232–232	249–233	210–210	237–237	214–214	257–247	145–133	205–201	251–247	165–165	212–208	169–169
Aleksandrouli (16)	240–226	263–239	210–210	239–231	216–206	259–241	147–139	205–195	259–247	198–179	218–216	169–169
Buera (17)	238–236	259–247	210–210	247–247	212–196	251–247	145–137	197–191	251–251	170–165	218–210	169–165
Chavkapito (18)	240–228	247–239	210–208	261–237	210–196	273–251	145–135	201–191	251–251	195–165	218–212	171–161
Chitistvala Bodburi (20)	240–236	249–249	219–210	261–247	214–212	263–253	145–143	205–201	251–251	170–170	218–210	171–171
Chkhaveri (21)	240–232	263–247	210–210	237–229	216–214	263–251	133–133	205–203	253–239	200–165	208–206	169–165
Chkovra (22)/ Krakhuna (35)/ Dondglabi Tetri (24)	234–232	253–239	214–210	239–239	216–212	253–251	145–133	197–195	253–239	195–165	212–208	169–169
Dondglabi (23)/ Kapistoni Im. (28)/Gorula (26)/Tavkara (49)	236–234	253–247	210–210	247–237	216–196	273–251	143–141	201–191	251–237	165–165	210–210	175–169
Dzvelshavi Sachkheris (25)	240–226	251–247–239	214–210	239–239	214–212	273–251	145–143	201–195	261–255	192–165	208–204	171–171
Grdzelmtevana (27)	234–228	259–249	219–210	243–239	212–212	251–245	145–135	203–197	259–255	195–170	218–206	161–161
Kharistvala Tetri (29)	240–238	253–249	210–210	277–261	216–210	273–253	141–137	201–201	251–245	165–165	216–210	171–165
Khikhvi (30)	240–236	259–253	218–210	237–237	212–210	263–261	141–135	201–197	249–237	165–165	218–210	169–161
Khounalige (31)/ Chinuri (19)	240–238	253–249	210–210	261–239	216–210	273–263	141–137	201–201	251–249	170–156	224–210	165–161
Khupishizh (32)	238–232	251–249	210–210	237–237	212–210	263–253	155–151	201–195	255–237	170–170	222–200	167–161
Kichouri (33)	236–234	247–239	219–210	261–239	212–196	273–271	145–141	201–191	251–237	170–170	210–204	175–161
Kisi (34)	240–234	253–247	219–210	239–239	216–210	263–261	143–141	201–191	251–237	156–156	224–208	169–161
Kundza (36)	232–226	253–253	214–210	261–239	216–212	273–263	155–143	201–195	251–239	195–170	218–212	171–169
Kvira (37)	240–240	253–247	210–210	239–237	216–212	263–251	143–141	205–201	243–235	195–165	224–210	161–161

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Table 2. *Continued*

Cultivar	VVMD5	VVMD7	VVMD24	VVMD28	VVMD31	VVMD32	VVS2	VrZAG62	VrZAG79	VMC2C3	VMC2H4	VMC5A1
Maglari Tvrina (38)	232–228	249–239	214–210	261–239	216–212	273–241	143–137	197–195	251–251	170–165	224–210	169–161
Mamukas Sapere (39)	240–232	253–233	210–210	239–237	216–214	263–255	151–141	205–201	259–239	179–165	208–204	165–165
Meskhuri Chitiskvertskha (40)	246–234	253–249	210–208	261–237	212–210	259–251	141–133	201–201	251–237	170–156	224–202	171–169
Meskhuri Shavi (41)	240–240	253–247	218–210	251–239	216–216	263–251	145–141	205–201	249–243	165–165	224–210	169–161
Mudzhuretuli (42)	228–226	245–239	218–210	261–251	212–210	263–251	155–143	205–205	251–245	165–165	218–206	171–161
Odzhaleshi (43)	240–234	247–239	214–210	251–243	216–212	273–263	145–143	205–189	257–251	165–165	210–210	171–165
Otskhanuri Sapere (44)	232–228	263–247	214–210	261–239	216–212	273–241	139–133	205–195	247–245	170–165	224–210	169–161
Rkatsiteli (45)	240–234	253–247	210–210	247–239	210–210	273–263	141–133	201–191	259–249	170–165	210–210	165–161
Saperavi Pachkha (47)/Saperavi Mrgvalmarzvala (46)	240–224	239–239	219–214	247–237	212–212	251–245	145–133	201–189	259–243	165–165	224–208	171–167
Skhilatubani (48)	232–232	249–241	210–210	237–237	216–212	263–255	151–151	201–195	251–239	198–165	218–208	169–169
Tavkveri (50)	238–228	243–239	218–216	239–221	216–216	273–241	151–137	195–189	245–239	198–170	204–204	167–157
Tkupkvirta (51)	240–238	253–247	210–210	239–239	216–216	259–251	143–141	205–201	257–237	165–156	212–212	171–165
Tsitska (52)	234–226	253–239	210–210	261–239	216–212	273–263	145–143	197–195	251–251	179–165	212–212	171–169
Tsolikouri (53)	232–226	253–247	214–210	239–237	216–216	263–249	145–143	209–195	239–239	195–165	212–208	171–169
Uriatubanskii (54)	240–236	247–247	210–210	239–237	216–216	273–263	145–137	205–191	237–237	195–165	210–204	175–171
Aşeri (56)/ Hasandede Beyazı (79)	240–236	253–249	210–210	261–239	212–212	257–257	149–143	189–189	247–247	170–165	224–218	171–165
Azezi (57)	234–226	249–249	214–210	239–239	214–210	273–253	135–133	205–193	257–251	170–170	210–202	173–171
Ballıboz (58)	246–234	253–251	219–214	261–261	212–196	273–263	143–139	205–205	247–243	165–165	218–210	171–171
Belelük (59)	232–232	249–249	214–210	247–237	212–204	259–241	155–141	195–195	249–249	170–165	218–204	171–165
Besni (60)/ Besni (61)	238–232	247–247	219–210	237–237	216–210	273–263	151–141	205–193	257–257	179–165	210–204	171–157
Boğazkere (62 and 63)/ Şaraplık Siyah (104)	238–232	255–249	210–210	247–237	216–212	273–259	155–151	205–195	249–247	165–165	210–204	171–167
Burdur Dimriti (64)	236–236	249–247	210–210	247–237	216–210	257–257	143–137	205–201	255–247	195–170	222–218	171–169
Burdur Dimriti (65)	234–234	255–239	219–210	247–237	212–212	251–251	151–143	201–189	259–247	165–162	218–208	171–171
Dımışkı (66)	240–236–226	249–239	214–212	261–247	214–214	257–253	149–133	205–189	257–257	179–170	218–202	171–171
Dökülgen (67 and 69)	246–226	247–247	214–212	261–247	216–210	273–253	143–135	205–193	251–247	165–165	220–204	171–169
Ekşi Kara (70)/ Dökülgen (68)	236–228	249–239	210–208	261–251	212–212	273–253	139–137	189–189	251–247	170–165	222–202	165–161
Ekşi Kara (71)	240–236	249–243	219–210	261–237	212–210	273–273	143–137	201–189	251–247	170–165	222–202	169–165
Emir (72)/Emir (73)	246–236	249–247	210–208	251–243	214–196	263–251	133–133	205–197	249–243	170–165	218–208	171–167
Gemre Siyah (75)/ Gemre Siyah (76)	240–236	249–247	212–210	247–247	216–196	253–253	143–137	205–189	255–255	195–170	220–218	171–165
Gemre Siyah (77)	236–236	253–249	219–210	247–237	210–210	251–249	133–131	201–189	259–251	170–165	220–204	171–165
Gök Üzüm (78)	238–234	251–247	219–210	247–247	224–196	263–257	143–143	205–205	247–245	170–170	218–202	173–171

Table 2. *Continued*

Cultivar	VVMD5	VVMD7	VVMD24	VVMD28	VVMD31	VVMD32	VVS2	VrZAG62	VrZAG79	VMC2C3	VMC2H4	VMC5A1
Hasipali (80)	240–226	253–239	218–210	261–251	212–212	273–259	145–143	201–189	259–243	165–165	218–204	171–171
Hatun Parmağı (81)	246–236	247–239	218–210	237–237	210–196	273–257	145–141	205–189	247–247	179–170	222–206	171–169
Hönüsü (82)/ Hönüsü (83)	232–228	253–239	219–210	247–247	210–204	275–251	149–143	189–189	259–257	195–179	208–202	165–161
İri Daneli Ak Üzüm (85)	238–232	247–243	214–210	247–237	214–212	273–253	149–133	205–193	257–255	m.d.	m.d.	m.d.
İri Kara (86)	240–238	263–243	219–210	261–237	212–210	273–241	143–137	205–201	247–243	198–165	218–202	169–169
İri Siyah (87)	236–236	249–247	210–210	261–237	216–212	275–275	143–143	205–189	251–247	198–170	218–202	171–165
Kayseri Karası (90)/İri Beyaz (84)	240–236	247–239	218–208	251–247	214–212	273–259	145–137	205–189	259–251	165–165	218–204	171–171
Kirkit (91)	236–226	247–239	219–210	261–261	210–210	257–253	143–143	193–189	251–247	170–165	212–202	175–171
Kırmızı Dimrit (92)	240–236	253–249	218–210	261–261	212–210	273–259	145–137	201–201	259–243	198–165	224–204	171–171
Kızıl Üzüm (93)	236–236	249–243	210–210	261–261	216–210	257–257	143–133	205–201	251–251	170–165	218–202	167–165
Künefi (94)	236–234	247–243	214–210	247–237	216–212	263–241	135–133	193–189	249–249	170–165	216–204	171–171
Luvanek (95)	238–236	249–247	212–210	261–261	210–202	273–263	155–141–133	195–191	257–249	192–165	210–210	171–165
Mor Üzüm (96)	238–228	249–247	219–208	261–261	224–210	273–253	151–135	205–189	249–247	179–179	216–206	171–161
Morek (97)	238–232	255–247	210–210	247–247	216–212	259–259	155–151–135	205–195	249–247	165–165	210–204	171–171
Muhammediye (98)/Kabarcık (88 and 89)	234–234	253–247	219–210	261–261	212–210	263–251	143–133	205–193	247–247	165–165	218–206	173–171
Narince (99)	240–236	249–243	210–210	261–237	212–212	273–253	145–143	201–189	251–251	165–165	224–224	171–165
Öküzgözü (100)/ Öküzgözü (101)/ Erik Kara (74)	234–234	249–247	219–219	247–237	216–216	257–241	151–143	205–205	257–251	192–179	210–204	171–169
Parmak (102)	236–236	249–247	210–210	247–237	212–210	275–257	143–137	201–189	251–247	198–198	224–218	173–171
Razakı (103)	236–236	249–247	210–210	247–247	212–196	275–253	137–137	189–189	255–251	195–195	224–218	171–171
Şıralık (105)	240–236	249–243	210–210	247–237	210–196	273–263	143–133	191–189	249–247	170–165	210–210	171–169
Şıralık (107, 108 and 109)	236–236	249–247	212–210	261–261	210–202	273–263	133–133	205–201	249–247	192–165	210–208	167–165
Siyah (110)	236–226	249–239	214–210	257–247	210–204	273–257	145–145	201–187	251–243	165–165	218–218	171–171
Sungurlu (111)	240–236–232	253–249–239	210–210	261–239	212–204	273–257	149–143–135	189–189	247–243	165–165	224–218	165–161
Tahannebi (112)/ Tahannebi (113)	228–226	247–239	218–214	247–239	210–210	275–273	143–135	193–189	257–257	165–165	202–202	171–165
Timbo (114)	232–232	255–247	214–210	261–247	216–196	273–257	151–143	205–203	247–239	170–165	218–204	171–171
Vanki (115)	240–236	249–249	210–210	261–247	210–196	273–251	143–133	191–189	251–247	192–165	210–210	171–169
Vilki (116)/ Abderi (55)	236–234	247–243	214–210	237–237	210–210	263–241	155–135–133	193–189	249–249	170–165	222–208	171–169
Chasselas	236–228	247–239	214–210	271–221	216–212	241–241	143–133	205–195	259–251	198–192	218–204	167–167
Nebbiolo	236–232	249–247	214–210	271–239	212–212	263–241	155–133	201–195	251–243	192–170	218–218	167–167
Pinot Noir	238–228	243–239	218–216	239–221	216–216	273–241	151–137	195–189	245–239	198–170	204–204	167–157
Syrah	232–226	239–239	216–210	231–221	216–212	273–241	133–133	195–189	251–245	198–195	218–218	171–167

m.d., missing data.

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Table 3. Number of alleles (*N*), observed heterozygosity (*Ho*) and probability of identity (PI) of 89 cultivars analysed at 12 microsatellite markers

Loci	*N*	*Ho*	PI
VVMD5	9	0.8347	0.087
VVMD7	13	0.8123	0.109
VVMD24	6	0.5979	0.231
VVMD28	16	0.8118	0.114
VVMD31	9	0.7801	0.147
VVMD32	16	0.8531	0.067
VVS2	14	0.8607	0.061
VrZAG62	11	0.8246	0.099
VrZAG79	14	0.8587	0.723
VMC2C3	10	0.6955	0.204
VMC2H4	12	0.8732	0.054
VMC5A1	8	0.7457	0.161
Total	138		
Mean	11.5	0.7957	
Cumulative			1.666e-12

paper. The true-to-type 'Gemre Siyah' should be the one with two accessions (75 and 76). Similarly, the true-to-type 'Şıralık Beyaz' should be the one with three accessions (107, 108 and 109). The genotypes of 'Erik Kara', 'Hatun Parmağı' and 'Kabarcık' in Benjak *et al.* (2005) were difficult to harmonize with our data since they did not use any standard cultivar. However, the cultivar 'Bogdanuša' from Croatia was common to both Benjak *et al.* (2005) and Sefc *et al.* (2000), so that we were able to adjust the allele sizes of the Turkish accession. None matched our corresponding accessions at the five markers in common. In particular, Benjak *et al.* (2005) found that their 'Hatun Parmağı' was identical to 'Kişmiş'. According to Galet (2000), this is a synonym of 'Sultanina' (also called 'Thompson Seedless'). However, 'Kişmiş' genotype did not match any 'Sultanina'/'Thompson Seedless' accession (e.g. Sanchez-Escribano *et al.*, 1998; Sefc *et al.*, 1998b; Crespan *et al.*, 1999). In Benjak *et al.* (2005), 'Kabarcık' appeared to be a clonal mutation of 'Kişmiş', but our 'Kabarcık' (two independent accessions) had a different genotype identical to 'Muhammediye'. As a consequence, there is obviously a need to determine the true-to-type accessions for many cultivars in Turkey, Georgia or Armenia, by verifying ampelographic descriptions and/or by searching for additional accessions.

Table 4. Identical genotypes of grape cultivars from Georgia and Turkey uncovered by the analysis of 12 microsatellite markers: identical pairs with different colour and/or use are highlighted in *italic*

Identical pairs	
Georgia	
Dondglabi (23)	Gorula (26)
	Kapistoni Imeretinskii (28)
	Tavkara (49)
Khounalige (31)	Chinuri (19)
Saperavi Mrgvalmarzvala (46)	Saperavi Pachkha (47)
Chkovra (22)	Dondglabi Tetri (24)
	Krakhuna (35)
Turkey	
İri Daneli Ak Üzüm (85)	Italia (IASMA)
Parmak (102)	Jerusalem Bleu (UCD)
Mor Üzüm (96)	Tsaousi (GVD)
Aşeri (56)	Hasandede Beyazı (79)
Boğazkere (62 and 63)	Şaraplık Siyah (104)
Ekşi Kara (70)	*Dökülgen (68)*
Kayseri Karası (90)	*İri Beyaz (84)*
Muhammediye (98)	Kabarcık (89)
Öküzgözü (100)	Erik Kara (74)
Vilki (116)	*Abderi (55)*

Table 5. Homonyms of grape cultivars from Armenia and Turkey uncovered by the analysis of 12 microsatellite markers

Homonym pairs	
Armenia	
Areni Chernyi (2)	Areni Chernyi (3)
Turkey	
Burdur Dimriti (64)	Burdur Dimriti (65)
Dökülgen (67 and 69)	Dökülgen (68)
Ekşi kara (70)	Ekşi kara (71)
Gemre Siyah (75 and 76)	Gemre Siyah (77)
Şıralık (107, 108 and 109)	Şıralık (105)

Genetic relationships

Since 'İri Daneli Ak Üzüm' turned out to be identical to the cultivar 'Italia' which certainly belongs to other germplasms, it was discarded from the genetic analysis. However, the four standard cultivars ('Chasselas', 'Nebbiolo', 'Pinot Noir' and 'Syrah') were kept as outgroups. For chimeric genotypes (Table 2), we have discarded the alleles with the weakest signal. The cladogram in Fig. 1 represents the genetic relationships of the Anatolian and Transcaucasian cultivars. Five major groups of cultivars were detected.

Group 1

Group 1 appeared as predominantly Turkish (19 cultivars), with only one cultivar from Armenia ('Areni Chernyi' 2) and one from Georgia ('Chitistvala Bodburi'). As mentioned above, 'Areni Chernyi' 2 is not likely to be true-to-type, and this accession could represent a misnamed introduction from Turkish germplasm. 'Chitistvala Bodburi' is supposed to be exclusively cultivated in Georgia, but it may also represent an introduction from

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Turkey. Interestingly, the closely related pair 'Ekşi Kara' 71 and 'İri Kara' clustered with the homonym 'Ekşi Kara' 70/'Dökülgen' 68. We investigated their possible relationships and found that the genotype of 'Ekşi Kara' 71 was consistent with being the progeny of 'İri Kara' and 'Ekşi Kara' 70/'Dökülgen' 68. However, 12 microsatellite markers are not enough for parentage analysis, and according to other studies (Sefc *et al.*, 1998c; Bowers *et al.*, 1999a; Vouillamoz *et al.*, 2003) we would suggest analysing a minimum of *ca* 30 markers to verify this parentage. Similarly, our data suggested a possible parent–progeny relationship between 'Sungurlu' and 'Aşeri'/'Hasandede Beyazı' (Table 2), two cultivars that clustered together in Fig. 1. Interestingly, the Vitis International Variety Catalogue (VIVC) lists 'Sungurlu' as a synonym of 'Hasandede Beyazı'. This synonymy is not supported by our data (Table 2), but we suggest that they are closely related.

Group 2

Group 2 was the largest and contained accessions from all three countries. It was subdivided into three distinct sub-groups (2.1–2.3). Sub-group 2.1 was predominantly Armenian, with the exception of 'Hatun Parmağı' from South-Eastern Anatolia, not far from the Armenian border. The true-to-typeness of 'Hatun Parmağı' still has to be established, since our accession did not match the homonym in Benjak *et al.* (2005). However, the name similarity between 'Hatun Parmağı' and 'Khatun Khardjzhi' from Armenia and their clustering together let us suggest that our accession of 'Hatun Parmağı' could be an Armenian introduction to Turkey, even if their colours and use are different (Table 1). Moreover, 'Hatun Parmağı' is a local name that does not exist in VIVC or in Galet (2000). 'Areni Chernyi' 3 clustered with other Armenian cultivars: this supports our hypothesis that 'Areni Chernyi' 3 is true-to-type and 'Areni Chernyi' 2 is another cultivar, probably introduced from Turkey. Sub-group 2.2 can be separated into two distinct clusters, one comprised of Armenian and Georgian grapes and one made of Turkish grapes. All these grapes might have a common origin. Their genetic (and perhaps phenotypic) similarity probably explains why the 'Şıralık Beyaz' homonyms clustered together and share the same name. Sub-group 2.3 can be separated into four distinct clusters. Cluster 2.3.1 almost exclusively consisted of Georgian grapes with the exception of 'Kachet' from Armenia. However, as suggested by its etymology, 'Kachet' is supposed to have been introduced from Khakhetia in Georgia (G. Melyian, personal communication). Our results supported this hypothesis. According to VIVC, 'Kisi' is an artificial cross 'Mtsvane' × 'Rkatsiteli', and 'Mtsvane' is a synonym of 'Kundza' (VIVC; Galet, 2000). This parentage hypothesis was not supported here (Table 2). Our data suggested a possible parent–progeny relationship between 'Kvira' and 'Meskhuri Shavi' (Table 2) that clustered together in Fig. 1. Cluster 2.3.2 contained grapes from Georgia and Turkey that might have a common origin. All these Georgian cultivars are cultivated in western Georgia (Table 1). In particular, the Georgian 'Khupishizh' clustered with Turkish cultivars probably because it is cultivated in Abkhazia, a region bordering Turkey. The closely related pair 'Boğazkere' (identical to 'Şaraplık Siyah') and 'Morek' had genotypes consistent with a possible parent–progeny relationship (Table 2). Clusters 2.3.3 and 2.3.4 were mostly from Turkey and rather isolated. They might have different origins.

Group 3

Group 3 was comprised almost entirely of Turkish cultivars, with the exception of 'Mskhali' from Armenia and 'Odzhaleshi' from Georgia. 'Mskhali' is mainly used for brandy in Armenia. Since brandy production came later than wine production in Armenia, it is reasonable to suggest that 'Mskhali' was introduced from Turkey. 'Odzhaleshi', meaning 'grape to put on a tree', is one of the best red wine varieties and is mainly cultivated in Mingrelia in Western Georgia, near the Turkish border. Although it is considered an ancient Georgian variety, its position in Fig. 1 suggests an introduction from Turkey.

Group 4

Group 4 consisted of miscellaneous cultivars from all studied areas and was considerably separated from the other groups. Among those from Armenia, 'Ak-Kaltak' is mainly cultivated in Uzbekistan, 'Karmir Kakhani' is a dioecious traditional table grape and 'Vardagujn Jerevani' is a seedless cultivar probably obtained from a deliberate cross (G. Melyian, personal communication). These particularities could explain why they did not cluster with other Armenian varieties (sub-groups 2.1 and 2.2). 'Saperavi Mrgvalmarzvala/Pachkha' is the most praised red wine variety in Georgia. However, it was genetically isolated from many other Georgian varieties (sub-groups 2.2 and 2.3 and group 5). The Turkish 'Mor Üzüm' clustered with several Georgian grapes. We found (Table 4) that 'Mor Üzüm' was identical to the Greek 'Tsaousi', and Galet (2000) suggested it is one and the same as 'Chaouch'. 'Chaouch' is a table grape widespread all over the Near and Middle East. It is known in Turkey as 'Çavuş Chaouch', a name encompassing several distinct types. According to our data, this variety might originate from Georgia.

Group 5

Group 5 was also considerably separated from the other groups. Interestingly, it exclusively consisted of Georgian

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cultivars that clustered with all four Western European standards ('Chasselas', 'Nebbiolo', 'Pinot' and 'Syrah'). This suggests that these Western European cultivars, or more likely some of their ancestors, initially originated from Georgia. These four Western European cultivars are supposed to be quite divergent from each other, but they most likely clustered together because they are more related to each other than to any Eastern cultivars. In particular, close clustering between 'Pinot' and 'Syrah' can be explained by their recently proven genetic relationship (J. F. Vouillamoz and M. S. Grando, unpublished data). However, the scale of the cladogram is not linear, so that close clustering between e.g. 'Chasselas' and 'Nebbiolo' does not represent the same genetic similarity as e.g. 'Ekşi Kara' T71 and its putative parents.

On the lower part of the cladogram (Fig. 1), most of the Armenian, Georgian and Turkish germplasms were generally well separated. This suggests that very few recent grape exchanges occurred between these areas, with the exception of some clusters with cultivars from all three areas. On the whole, Armenian cultivars were usually closer to Georgian than Turkish cultivars. On the upper part of the cladogram (Fig. 1), groups 1 and 2 clustered together, suggesting some common ancestors, and they could represent recent evolution of these cultivars in Trancaucasia and Anatolia. Groups 3, 4 and 5 were very distinct and could represent three separate ancient origins. One of them (the Georgian group 5) might have common ancestors with Western European cultivars.

Conclusion

In the present work on Anatolian and Transcaucasian cultivars, we detected 17 identical genotypes and six homonymy cases among 116 accessions corresponding to 89 distinct grape cultivars according to our analyses, thus helping to improve the management of these germplasms. However, they need to be more deeply investigated, since we only genotyped here a fraction of the existing autochthonous cultivars. Special care should be taken to conserve these cultivars in ampelographic collections, especially in areas where old vineyards are rapidly disappearing (Gasparyan and Melyan, 2003). Additional studies on ampelography, origin, etymology and distribution of these cultivars should help in solving the true-to-typeness issues mentioned in this paper. Similarly, we suggested a few possible parentages within our sampling, but additional microsatellite markers would be undoubtedly necessary to test these hypotheses. The cladogram topology suggested that most of the Armenian, Georgian and Turkish germplasms were well separated and could have multiple origins, although they are likely to have common ancestors. A few examples of varieties having possibly been exchanged between these countries were discussed above. Since the four varieties from Western Europe were closely related to a group of Georgian cultivars, we propose that they could have some ancient Georgian ancestors. As a next objective, we will investigate the genetic relationships between the cultivars genotyped in this study and additional Western European cultivars as well as wild grapes from Transcaucasia and Anatolia in order to determine the origins of Western European cultivars and locate putative sites of primary domestication. For the present study, it has not been possible to expand the sampling area to neighbouring countries, but we plan to include Azerbaijan, Iran and Lebanon in the near future. Hopefully, an expansion of the database with the analyses of additional varieties will further elucidate the origins of grape cultivars.

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