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AUTOCHTHONOUS WINE GRAPE VARIETIES OF CENTRAL EUROPE — A REVIEW OF PARENTAGE ANALYSIS

Abstract: Central Europe is home to 198 autochtonous grape varieties that are commercially cultivated in seven countries: Germany (73), Switzerland (39), Hungary (34), Austria (19), Slovakia (12), Czech Republic (11) and Slovenia (7). Out of these varieties, 45 are hybrids, 93 are crossings and 60 are native varieties born from spontaneous pollination in the vineyards. The parentage of hybrids and crossings being generally not subject to speculation, the present article will focus on the DNA profiling studies of the origin and parentage of the most important native varieties. For each of the five countries that have spontaneous native varieties (Austria, Germany, Hungary, Slovenia and Switzerland), some controversial parentages and remarkable studies will be presented, along with cases yet to be solved. In Slovenia, 'Vitovska Grganja' has long been considered a variation of 'Vitovska', until DNA profiling showed that they are distinct. In Switzerland, 'Humagne Blanc' and 'Humagne Rouge' are, quite confusingly, not genetically related to each other, the former possibly originating from Southwestern France, the latter from Aosta Valley (Italy). In Germany, the origin of 'Orangetraube' has been long debated, and an unpublished possible parentage is suggested. In Austria, the parentages of 'Blaufränkisch' and 'Grüner Veltliner' have been recently debunked, showing the importance of safeguarding old and obscure varieties. In Hungary, the alleged discovery of 'Furmint's parents is currently the subject of controversy. Further studies will be needed for a better understanding of the origins and relationships of the grape varieties of Central Europe.

Key words: parentage analysis, SSR, genotyping, microsatellite

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INTRODUCTION

The delimitations of Central Europe vary according to the sources. For the purpose of this article, it will be adopted the list of countries mentioned in The World Factbook [1]: Austria, Czech Republic, Germany, Hungary, Poland, Slovakia, Slovenia, Switzerland (including Liechtenstein). In our reference book Wine Grapes [2], we have tallied a total of 1'368 grape varieties that were currently cultivated to make wine that was available on the market. Of these, 198 originate from seven countries of Central Europe [NB: Poland doesn't have any indigenous variety], of which 45 are hybrids (deliberate Vitis vinifera × Vitis spp. non-vinifera), 93 are crossings (deliberate Vitis vinifera × Vitis vinifera) and 60 are native varieties (spontaneous pollination of two Vitis vinifera) (Figure 1). Germany is the country with the highest number of cultivated varieties (76), followed by Switzerland (39) and Hungary (34) (see Table S1 in Supplementary Material). Thanks to the longtime breeding programs carried out in particular by the JKI Institute for Grapevine Breeding in Geilweilerhof [3], Germany is also the country with the highest number of cultivated hybrids (24) like 'Johanniter', 'Regent' or

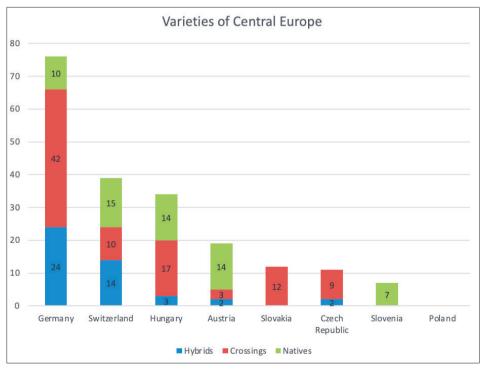


Figure 1. Central Europe is home to 45 hybrids, 93 crossings and 60 native varieties for a total of 198 wine grape varieties

'Solaris', and crossings (42) like 'Dornfelder', 'Kerner' or 'Scheurebe'. However, when it comes to the native varieties, Switzerland has the highest diversity (15) with varieties like 'Arvine', 'Chasselas' and 'Completer', whereas Slovakia and Czech Republic have none.

PARENTAGE OF NATIVE VARIETIES

Native varieties that spontaneously appeared in the vineyards by natural pollination only exist in five countries of Central Europe: Austria, Germany, Hungary, Slovenia and Switzerland. For each country, I present here an overview of the parentage of some important native grape varieties that were discovered by DNA profiling analysis.

AUSTRIA

With 13 cultivated native varieties, Austria has an important ampelographic heritage (Table 1). While 'Brauner Veltliner' and 'Roter Veltliner' are still "orphan" varieties, DNA parentage analysis allowed the discovery of one or both parents for the other 11 varieties. 'Roter Veltliner' is involved in four of them ('Frühroter Veltliner', 'Neuburger', 'Rotgipfler' and 'Zierfandler'), while 'Gouais Blanc' is involved in three of them ('Blauer Wildbacher', 'Blaufränkisch' and 'Österreichisch Weiss'), and so is 'Savagnin' ('Grüner Veltliner', 'Rotgipfler', 'Silvaner').

Maul *et al.* [4] discovered that 'Blauer Portugieser' is a 'Silvaner' × 'Blaue Zimmettraube', and that 'Blaufränkisch' is a 'Gouais Blanc' × 'Blaue

Variety	Parent 1	Parent 2	Reference
'Blauer Portugieser'	'Silvaner'	'Blaue Zimmettraube'	[4]
'Blauer Wildbacher'	'Gouais Blanc'	?	[5], [6]
'Blaufränkisch'	'Gouais Blanc'	'Blaue Zimmettraube'	[4]
'Brauner Veltliner'	?	?	
'Frühroter Veltliner'	'Roter Veltliner'	'Silvaner'	[7]
'Grüner Veltliner'	'Savagnin'	'St Georgener'	[8]
'Neuburger'	'Roter Veltliner'	'Silvaner'	[7]
'Österreichisch Weiss'	'Gouais Blanc'	?	[9]
'Roter Veltliner'	?	?	
'Rotgipfler'	'Savagnin'	'Roter Veltliner'	[7]
'Sankt Laurent'	'Pinot'	?	[10]
'Silvaner'	'Savagnin'	'Österreichisch Weiss'	[7]
'Zierfandler'	'Roter Veltliner'	?	[11]

Table 1. Parentage of Austrian wine grape varieties

Zimmettraube'. The surprise came from the missing link 'Blaue Zimmettraube', an old black-berried variety from Rheinhessen (Germany) with female flowers, also called Sbulz'na in Friuli (Italy). Together with 'Silvaner' and 'Gouais Blanc', 'Blaue Zimmettraube' used to be cultivated in Lower Styria, the most likely place of origin for both 'Blauer Portugieser' and 'Blaufränkisch', which should consequently be considered to originate from Slovenia instead of Austria.

Another missing link was fortuitously found for 'Grüner Veltliner': it is a 'Savagnin' × 'St Georgener' natural crossing [8]. 'St Georgener' is an obscure variety found in St Georgen am Leithagebirge near Eisenstadt (south of Vienna) that has survived as a single old vine growing in a thicket, possibly the location to an ancient vineyard. This single vine, shamefully vandalized in 2011, has been propagated and a St Goergener "Patenschaft" (sponsorship) has been created to protect and vinify this variety.

The parentage of 'Sankt Laurent' is still debated. One of the parents is most likely 'Pinot' [10]. Russel Poulter from Australia has proposed 'Savagnin' as the other parent (unpublished), but I have compared the DNA profiles in my database and this hypothesis can be ruled out.

GERMANY

Germany has eight cultivated native varieties, and 'Gouais Blanc' is involved in the parentage of five of them (Table 2).

'Affenthaler' is an old variety from Affental near Baden-Baden in Baden-Württemberg. Its parent-offspring relationship with 'Gouais Blanc' has been demonstrated [6, 12]. With 18 microsatellite markers only, Lacombe et al. [6] also suggested two possible parent-offspring relationships with 'Sainte-Marie de Biviers', an old variety from Isère (France), and with 'Hängling blau' (with one discrepancy). 'Hängling blau' is a synonym of 'Süßschwarz', an old variety that was considered extinct until it was rediscovered in 2007 by Jung

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Variety	Parent 1	Parent 2	Reference
'Affenthaler'	'Gouais Blanc'	'Süßschwarz'?	[6], [12]
'Elbling'	'Gouais Blanc'	?	[10], [12]
'Gänsfüsser'	?	;	
'Orangetraube'	'Pinot' ?	'Chasselas'?	[2]
'Orleans Gelb'	?	?	
'Räuschling'	'Gouais Blanc'	'Savagnin'	[2], [13]
'Riesling'	'Gouais Blanc'		[9]
'Tauberschwarz'	'Gouais Blanc'	'Süßschwarz'?	[14]

Table 2. Parentage of German wine grape varieties

[15] in old vineyards near Karsdorf and Steigerwald (Saxony-Anhalt, Germany). The Vitis International Variety Catalogue gives 'Gouais Blanc' and 'Süßschwarz' as the parents of 'Affenthaler', but this parentage still need to be confirmed with more markers. 'Süßschwarz' has also been proposed as the possible missing link in the parentage of 'Tauberschwarz', also an old variety from Baden-Württemberg, also via a spontaneous crossing with 'Gouais Blanc' [6], thus resulting in 'Affenthaler' and 'Tauberschwarz' being possible full-siblings. In addition, 'Süßschwarz' is also likely to be a progeny of 'Savagnin' [16]. All these relationships rely on too few markers and should be further investigated for confirmation.

'Gänsfüsser', also named 'Argant' in France, has given birth to 'César' in Northern France by a natural crossing with 'Pinot', and it has a parent-off-spring relationship with the omnipresent 'Blaue Zimmettraube' as well as, most surprisingly, 'Fetească Albă' from Romania [10].

'Orangetraube' is most likely a chance seedling found in a riverine forest along the Rhine River near Speyer (south of Mannheim in Rheinland-Pfalz). Based on a mere ten SSR markers, I have suggested that 'Orangetraube' could be a natural 'Pinot' × 'Chasselas' [2], which has been recently confirmed by SNPs genotyping [10].

HUNGARY

Hungary is the second most diverse Central European country with 14 native varieties that are cultivated, the parentage being unknown for most of them (Table 3).

Variety	Parent 1	Parent 2	Reference
'AranySárfehér'	?	;	
'Budai Zöld'	?	?	
'Csókaszőlő'	?	;	
'Ezerjó'	?	?	
'Furmint'	'Gouais Blanc'	'Alba Imputotato'	[6], [10]
'Hárslevelű'	'Furmint'	?	[10], [17]
'Juhfark'	?	?	
'Kadarka'	'Papazkarası'	?	[6], [10]
'Kéknyelű'	?	?	
'Királyleányka'	'Leányka'?	?	[2]
'Kövidinka'	?	?	
'Leányka'	?	?	
'Menoir'	?	?	
'Mézes Fehér'	?	?	

Table 3. Parentage of Hungarian wine grape varieties

The full parentage of 'Furmint', the pride of the Tokaji region, proposed by Lacombe *et al.* [6] is surprising. While the parent-offspring relationship with 'Gouais Blanc' was already proven [12], the proposed parentage 'Furmint' = 'Gouais Blanc' × 'Alba Imputotato' was only verified at 20 microsatellite markers, which has been shown to not be sufficient for parentage and kinship reconstruction [18, 19]. Yet, it has been recently confirmed by SNPs genotyping [10]. The white-berried 'Alba Imputotato' supposedly originates from Romania, where no historical record could be found. Interestingly, the DNA profile of 'Alba Imputotato' in Lacombe *et al.* [6] is identical to 'Bisetta' in the Italian Vitis Database [20], the latter being an old variety already mentioned near Modena (Reggio Emilia) in 1867. This identity could speak in favour of an Italian origin for 'Furmint', as reported by several legends [2], however this is highly doubtful because 'Furmint' has never been observed in Italy and has no genetic link with any other Italian varieties. The following parentages involving 'Alba Imputotato' have also been suggested:

- 'Alba Imputotato' = 'Sarfehér' × 'Hamvas' [6], two old and obscure Hungarian varieties that are not cultivated anymore;
- 'Frâncuşă' (from Romania) = 'Gouais Blanc' × 'Alba Imputotato', thus a full-sibling of 'Furmint' [6];
- 'Javor Gross' (from Romania) = 'Gouais Blanc' × 'Alba Imputotato', thus a full-sibling of 'Furmint' [6, 10];
- 'Köver Szölö faux' (from Hungary) = 'Gouais Blanc' × 'Alba Imputotato', thus a full-sibling of 'Furmint' [6];
- 'Goher' (from Hungary) = 'Alba Imputotato' × 'Lisztes Féher' [6, 10], the latter being an old non-cultivated variety from Hungary;
- 'Beala Debela' (from Romania) = 'Alba Imputotato' × 'Prokupac', thus a full-sibling of 'Papazkarası' [6], with 'Prokupac' being a major variety from Serbia;
- 'Papazkarası' (from Turkey) = 'Alba Imputotato' × 'Prokupac', thus a full-sibling of 'Beala Debela' [6, 10];
- 'Žilavka' (from Bosnia & Herzegovina) = 'Alba Imputotato' × 'Dobrogostina' [21], the latter being an obscure variety from Bosnia & Herzegovina.

In addition, 'Alba Imputotato' has been proposed by Lacombe et al. [6] as a genitor of 'Arvina di Petralia' (Italy), 'Sarfehér' (Hungary) and 'Sarpiros' (Hungary). Since limited data is available on 'Alba Imputotato' (or 'Bisetta'), possibly born from Hungarian parents but originating from Romania, it is difficult to understand how it could have had progenies as far as in Italy, Bosnia & Herzegovina and Turkey. More research is needed to understand the role of 'Alba Imputotato' in these numerous putative parentages on such a vast geographical scale.

'Kadarka' has a parent-offspring relationship with 'Papazkarası' from Turkey [6, 10]. Since 'Papazkarası' is most likely a natural 'Alba Imputotato' × 'Prokupac' from Serbia [6, 10], 'Kadarka' must be a progeny of 'Papazkarası', the other parent being unknown.

SLOVENIA

Slovenia has seven cultivated native varieties, the omnipresent 'Gouais Blanc' being involved involved in the parentage of two of them (Table 4).

Variety	Parent 1	Parent 2	Reference
'Bouvier'	'Pinot'	'Muscat Blanc à Petits Grains'	[6]
'Klarnica'	?	?	
'Ranfol'	'Gouais Blanc'	?	[22]
'Vitovska'	'Malvasia Bianca Lunga'	'Prosecco Tondo'	[23]
'Vitovska Grganja'	'Gouais Blanc'	'Vitovska'	[6], [22], [24]
'Žametovka'	?	?	
'Zelen'	?	?	

Table 4. Parentage of Slovenian wine grape varieties

The parentage 'Bouvier' = 'Pinot' × 'Muscat Blanc à Petits Grains' proposed by Lacombe *et al.* [6] with 20 microsatellite makers could explain the Muscat aromas of 'Bouvier', but more markers (30 to 40) are needed to confirm or infirm this parentage.

Contrary to popular belief, 'Vitovska', a natural 'Malvasia Bianca Lunga' × 'Prosecco Tondo' crossing [23], is not identical to 'Vitovska Grganja', which is most likely its progeny via a natural cross with 'Gouais Blanc' [22, 24].

SWITZERLAND

Despite its small size, Switzerland is the most diverse Central European country with 15 native varieties that are cultivated (Table 5).

Parent-offspring relationships have been identified by DNA profiling between 'Chasselas' and two French varieties: 'Béclan' from Jura and 'Mornen Noir' from Rhône-Alpes [6, 25, 26, 28]. One of these varieties could theoretically be a genitor of 'Chasselas'. However, 'Chasselas' is a very old variety that was already mentioned in 1612, so that it is logical to consider these three varieties as its progenies.

The white-berried 'Humagne' is an old variety that was already mentioned in Valais (Switzerland) in 1313 [28]. It has nothing to do with 'Humagne Rouge', the Valais synonym of 'Cornalin' from the Aosta Valley (Italy). 'Humagne' was found by DNA profiling in the Pyrénées-Atlantiques (France)

Variety	Parent 1	Parent 2	Reference
'Amigne'	?	;	
'Arvine'	?	;	
'Bondola'	?	;	
'Bondoletta'	'Bondola'	'Completer'	[24]
'Chasselas'	?	;	[25]
'Completer'	?	?	
'Eyholzer Rote'	?	;	
'Himbertscha'	'Humagne'	?	[26]
'Hitzkircher'	'Bondola'	'Completer'	[24]
'Humagne'	'Colombaud'	?	[24]
'Lafnetscha'	'Humagne'	'Completer'	[26]
'Plantscher'	'Furmint'	?	[26]
'Rèze'	?	?	
'Rouge de Fully'	?	?	
'Rouge du Pays'	Petit Rouge	Mayolet	[17]

Table 5. Parentage of Swiss wine grape varieties

under the name 'Miousat' [29]. A parent-offspring relationship with Colombaud from Provence (France) was later discovered, suggesting a very ancient origin in Southwestern France for 'Humagne' [25].

Parent-offspring relationships have been identified by DNA profiling between 'Rèze' and six Alpine varieties: 'Poulsard Noir' from Jura (France), 'Grosse Arvine' and 'Diolle' from Valais (Switzerland), 'Cascarolo Bianco' from Piedmont (Italy) as well as 'Nosiola' and 'Gropello di Revò' from Trentino (Italy) [6, 25, 28, 30]. One of these varieties could theoretically be a genitor of 'Rèze'. However, 'Rèze' is a very old variety that was already mentioned in 1313, so that it is logical to consider these six varieties as its progenies. This makes 'Rèze' the Alpine grape variety *par excellence*.

CONCLUSION

In addition to the 198 wine grape varieties that are cultivated in Central Europe, there are dozens of other indigenous varieties that are only maintained in germplasm collection. New breeding programs will undoubtedly add more varieties, as well as the recovery of ancient varieties, thus increasing the diversity.

Further studies will be needed for a better understanding of the origins and relationships of the grape varieties of Central Europe, but the results obtained so far let us emphasize on the importance of safeguarding old and obscure grape varieties.

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SUPPLEMENTARY MATERIAL

Table S1. List of the 198 cultivated indigenous wine grape varieties of Central Europe

	Hybrid	Crossing	Native
Austria			
Blauburger		1	
Blauer Portugieser			1
Blauer Wildbacher			1
Blaufränkisch			1
Brauner Veltliner			1
Frühroter Veltliner			1
Goldburger		1	
Grüner Veltliner			1
Jubiläumsrebe			1
Neuburger			1
Österreichisch Weiss			1
Ráthay	1		
Roesler	1		
Roter Veltliner			1
Rotgipfler			1
Sankt Laurent			1
Silvaner			1
Zierfandler			1
Zweigelt		1	
Sub-total	2	3	14
Czech Republic			
Agni		1	
André		1	
Aurelius		1	
Cabernet Moravia		1	
Laurot	1		
Malverina	1		
Muškát Moravský		1	
Neronet		1	
Pálava		1	

	Hybrid	Crossing	Native
Rubinet		1	
Veritas		1	
Sub-total	2	9	0
Germany			
Acolon		1	
Affenthaler			1
Albalonga		1	
Allegro	1		
Arnsburger		1	
Bacchus		1	
Blauer Urban			1
Breidecker	1		
Bronner	1		
Bukettraube		1	
Cabernet Carbon	1		
Cabernet Carol	1		
Cabernet Cortis	1		
Cabernet Cubin		1	
Cabernet Dorio		1	
Cabernet Dorsa		1	
Cabernet Mitos		1	
Calandro	1		
Dakapo		1	
Dalkauer		1	
Deckrot		1	
Domina		1	
Dornfelder		1	
Dunkelfelder		1	
Ehrenfelser		1	
Elbling			1
Faberrebe		1	
Freisamer		1	
Gänsfüsser			1
Geisenheim 318–57	1		

	Hybrid	Crossing	Native
Gf-Ga 48–12	1		
Gutenborner			1
Helfensteiner		1	
Helios	1		
Heroldrebe		1	
Hibernal	1		
Hölder		1	
Huxelrebe		1	
Johanniter	1		
Juwel		1	
Kanzler		1	
Kerner		1	
Madeleine × Angevine 7672		1	
Merzling	1		
Monarch	1		
Morio-Muskat		1	
Müller-Thurgau		1	
Nobling		1	
Optima		1	
Orangetraube			1
Oraniensteiner		1	
Orion	1		
Orleans Gelb			1
Ortega		1	
Osteiner		1	
Perle		1	
Phoenix	1		
Prinzipal	1		
Prior	1		
Räuschling			1
Reberger	1		
Regent	1		
Regner		1	
Reichensteiner		1	

	Hybrid	Crossing	Native
Rieslaner		1	
Riesling			1
Rondo	1		
Rosetta	1		
Rotberger		1	
Saphira	1		
Scheurebe		1	
Schönburger		1	
Siegerrebe		1	
Solaris	1		
Tauberschwarz			1
Würzer		1	
Sub-total	24	42	10
Hungary			
Arany Sárfehér			1
Bianca	1		
Bíborkadarka		1	
Budai Zöld			1
Csaba Gyöngye		1	
Cserszegi Fűszeres		1	
Csókaszőlő			1
Ezerfürtű		1	
Ezerjó			1
Furmint			1
Generosa (Hungary)		1	
Hárslevelű			1
Irsai Olivér		1	
Juhfark			1
Kabar		1	
Kadarka			1
Karát		1	
Kéknyelű			1
Királyleányka			1
Kövidinka			1

	Hybrid	Crossing	Native
Kunleány	1		
Leányka			1
Magyarfrankos		1	
Mátrai Muskotály		1	
Menoir			1
Mézes Fehér			1
Rubintos		1	
Turán		1	
Zalagyöngye	1		
Zefír		1	
Zengő		1	
Zenit		1	
Zéta		1	
Zeusz		1	
Sub-total	3	17	14
Poland			
Sub-total	0	0	0
Slovakia			
Breslava		1	
Devín		1	
Dunaj		1	
Hetera		1	
Hron		1	
Mília		1	
Nitranka		1	
Noria		1	
Rimava		1	
Rudava		1	
Torysa		1	
Váh		1	
Sub-total		12	
Slovenia			
Bouvier			1
Klarnica			1

	Hybrid	Crossing	Native
Ranfol			1
Vitovska			1
Vitovska Grganja			1
Žametovka			1
Zelen			1
Sub-total			7
Switzerland			
Amigne			1
Arvine			1
Birstaler Muskat	1		
Bondola			1
Bondoletta			1
Cabernet Blanc	1		
Cabernet Colonjes	1		
Cabernet Jura	1		
Cabertin	1		
Carminoir		1	
Charmont		1	
Chasselas			1
Completer			1
Diolinoir		1	
Doral		1	
Eyholzer Rote			1
Galotta		1	
Gamaret		1	
Garanoir		1	
Himbertscha			1
Hitzkircher			1
Humagne			1
Kalina	1		
Lafnetscha			1
Mara		1	
Mennas		1	
Millot-Foch	1		

	Hybrid	Crossing	Native
Muscat Bleu	1		
Pinotin	1		
Plantscher			1
RAC 3209		1	
Réselle	1		
Rèze			1
Riesel	1		
Rouge de Fully			1
Rouge du Pays			1
Siramé	1		
VB 32–7	1		
VB 91–26–4	1		
Sub-total	14	10	15
TOTAL	45	93	60

José VOUILLAMOZ

AUTOHTONE SORTE VINOVE LOZE U CENTRALNOJ EVROPI — PREGLED ANALIZE RODITELJSTVA

Sažetak

Centralna Evropa je centar porijekla za 198 autohtonih sorti vinove loze koje se komercijalno gaje u sedam zemalja: Njemačkoj (73), Švajcarskoj (39), Mađarskoj (34), Austriji (19), Slovačkoj (12), Češkoj (11) i Sloveniji (7). Od ovih sorti, 45 su hibridi, 93 su sorte nastale ukrštanjem i 60 su domaće sorte nastale spontanim oprašivanjem u vinogradima. Pošto roditeljstvo hibrida i ukrštanja generalno nijesu predmet ispitivanja, ovaj članak će se fokusirati na proučavanje DNK determinacije porijekla i roditeljstva najvažnijih domaćih sorti. Za svaku od pet zemalja koje imaju spontane domaće sorte (Austrija, Njemačka, Mađarska, Slovenija i Švajcarska), biće predstavljena neka kontroverzna istraživanja roditeljstva i specifične studije, uporedo sa slučajevima koji još uvijek nijesu razjašnjeni. U Sloveniji, vitovska grganja se dugo smatrala varijacijom vitovske, dok je profilisanje DNK pokazalo da su različite sorte. U Švajcarskoj humagne blanc i humagne rouge su, sasvim neočekivano, genetski nepovezane; prva vjerovatno potiče iz jugozapadne Francuske, a druga iz Doline Aosta (Italija). U Njemačkoj se dugo raspravljalo o porijeklu orangetraube i predlaže se moguće porijeklo (moguće porijeko je sugerisano i još uvijek neobjavljeno). U Austriji, roditelji blaufrankisch i gruner veltliner su nedavno otkriveni, ukazujući na važnost očuvanja starih i nepoznatih sorti. U Mađarskoj, navodno otkriće roditelja furmint sorte je trenutno predmet kontroverzi. Dalja istraživanja za bolje razumijevanje porijekla i odnosa sorti vinove loze u centralnoj Evropi razriješiće ove enigme.

Ključne riječi: analiza roditeljstva, SSR, genotipiziranje, mikrosateliti