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The Muscats: A molecular analysis of synonyms, homonyms and genetic relationships within a large family of grapevine cultivars

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Summary

The Muscats are a large, wide-spread family of grapevines, having in common besides the name the typical Muscat flavour. A huge number of synonyms and homonyms makes it difficult to identify them. Sixty-four accessions were analysed in the present work; they are representatives of the huge variability of this family as far as morphological aspects, berry colour and size, time of ripening and aptitude for wine and/or table grape production are considered. An analysis was performed at two isozymes and 25 microsatellite loci. The 64 accessions were reduced to 20, which were easily distinguishable from each other at the molecular level by as few as two microsatellite loci. The remaining 44 were found to be synonyms. Three mutants with red and pink coloured berries were identified in the Moscato bianco group. Moscato nero encompasses at least two, Moscato rosa three different varieties. It seems that only two of the analysed Muscats are the main progenitors of the Muscat family: Moscato bianco and Muscat of Alexandria, which in turn are joined by a direct parent-offspring link. We were unable to discriminate biotypes belonging to the same cultivar by microsatellite markers.

K e y w o r d s : Muscat grapevines, synonyms, homonyms, discrimination, pedigree, microsatellites.

Introduction

The large family of Muscat vines is extensively spread all over the world; they have in common the characteristic Muscat flavour, from which their name is derived. The centre of origin has been assumed to be Greece, but DALMASSO *et al.* (1964) referred more prudently and generically to the Eastern Mediterranean basin. Almost all ampelographers agree that Muscat grapevines are known and appreciated since ancient times (SCIENZA *et al.* 1989). The Muscat germplasm has been used extensively by grape breeders; numerous crosses can be found in botanical gardens and ampelographic collections while others became popular either for winemaking, such as Muscat Ottonel, or for table grape production, *e.g.* Italia. Nowadays ampelography uses new tools to describe and identify varieties, among them are molecular markers. In recent years there has been an increasing development of microsatellite markers for grapevine. They were first isolated by THOMAS and SCOTT (1993), then by BOWERS *et al.* (1996) and by REGNER and coll. (pers. comm.). In 1999 the search for new microsatellites in grape was pushed forward by the "Vitis Microsatellite Consortium", established with the aim to isolate a large number of these markers in the frame of an international cooperation.

Microsatellite markers are very polymorphic; they give information at a single locus level and have a codominant Mendelian inheritance. Therefore they are very powerful for parentage analyses: THOMAS and SCOTT (1993) reported a pedigree analysis for Marroo Seedless, BOWERS and MEREDITH (1997) identified the parents of Cabernet Sauvignon and MEREDITH *et al.* (1999) those of Petit Sirah. SEFC *et al.* (1997 a) suggested a pedigree for 9 European varieties, REGNER *et al.* (2000) proposed a pedigree for Pinots.

In the present study a molecular analysis based on microsatellite markers was carried out for 64 Muscat accessions with different aims: firstly to clarify homonyms and synonyms; secondly, to investigate the genetic relationship among these accessions and to establish a hypothesis about their origin and finally to test the discrimination power of microsatellite markers among clones/biotypes belonging to the same variety. For this last goal 24 accessions of Moscato bianco collected from different sites were typed.

In addition the 64 Muscat accessions were analysed by two isoenzymatic systems: GPI (Glucose Phosphate Isomerase, EC 5.3.1.9) and PGM (Phosphogluco Mutase, EC 5.4.2.2) (CALÒ *et al.* 1989).

Material and Methods

P l a n t m a t e r i a l : Leaf samples were collected from 64 Muscat accessions (see Tab. 1) cultivated in the field collection of the Istituto Sperimentale per la Viticoltura of Conegliano. A few accessions were kindly supplied by the Istituto Agrario di S. Michele all'Adige (Trento, Italy) or were obtained from private vineyards. Leaf samples of 5 varieties chosen as outgroup were also collected to complete the sample set.

I s o z y m e a n a l y s i s : This analysis was performed with freshly collected leaves for GPI and PGM systems, following the method previously described by CRESPAN *et al.* (1998). The leaf extract was electrophoresed in a potato starch gel and stained by dipping the gel slices into solutions containing, besides other reagents, the appropriate substrate for isozyme reaction; the patterns were recorded as allele combinations, referring to the codes published by CALÒ *et al.* (1989).

M i c r o s a t e l l i t e D N A a n a l y s i s : The DNA was extracted according to the method described by CRESPAN *et al.* (1999). Twenty-five loci were analysed: VVS1 and VVS2

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Table 1

List of the 64 analysed accessions of Muscats, grouped by synonyms and in alphabetical order

The representative variety of a group is written in bold. At the bottom: the list of the outgroup varieties

DNA-No	Muscat accessions	Col*.	Source	Collection
42	**Moscadoul**	B	Dr. Bruni	ISV Susegana
54	**Moscatellone bianco**	W	Ist. Colt. Arb. Univ. Bari	ISV Susegana
49	**Moscatello nero**	B	Ist. Colt. Arb. Univ. Firenze	ISV Susegana
56	Moscatello nero	B	Crispiano (Taranto)	ISV Spresiano
79	Moscatello nero	B	Ist. Colt. Arb. Univ. Bologna	ISV Susegana
60	**Moscatello selvatico**	W	Az. Agr. Jatta, Ruvo di Puglia (Bari)	ISV Spresiano
46	Moscato selvatico	W	Ist. Colt. Arb. Univ. Bari	ISV Susegana
11	**Moscatel ruso**	W	Jerez de la Fronteira (Spain)	ISV Susegana
53	**Moscato**	B	Provincia di Padova	ISV Susegana
123	**Moscato bianco**	W	CNR Torino	
32	Moscatel fino	W	Jerez de la Fronteira (Spain)	ISV Susegana
120	Moscatello	W	Az. Ricci (Toscana)	Dr. Storchi
121	Moscatello	W	Az. Banfi (Toscana)	Dr. Storchi
122	Moscatello	W	Az. Poggione (Toscana)	Dr. Storchi
48	Moscatello bianco	W	Ist. Colt. Arb. Univ. Firenze	ISV Susegana
66	Moscatello bianco	W	Az. Bello, Crispiano (Taranto)	ISV Spresiano
50	Moscatello bianco	W	Ist. Colt. Arb. Univ. Bologna	ISV Susegana
64	Moscatello bianco di Basilicata	W	Az. Gaudiano, Potenza	ISV Spresiano
119	Moscato bianco	W	Toscana	
114	Moscato bianco	W	Parenzo (Croatia)	
65	Moscato bianco	W	Università degli studi di Firenze	ISV Spresiano
61	Moscato bianco	W	C.N.R. Centro Migl. Gen.Torino	ISV Spresiano
62	Moscato bianco di Basilicata	W	Az. Gaudiano, Potenza	ISV Spresiano
33	Moscato Chambave	W	Raccolta Di Rovasenda, Alba (Piemonte)	ISV Susegana
39	Moscato dei Colli Euganei	W	Conte Emo, Arquà (Padova)	ISV Susegana
115	Moscato di Momiano	W	Momiano (Croatia)	
16	Moscato di Montalcino	W	**	ISV Susegana
55	Moscato di Montalcino	W	Università degli studi di Firenze	ISV Spresiano
22	Moscato di Tempio	W	**	ISV Susegana
51	Moscato reale	W	Ist. Colt. Arb. Univ. Bari	ISV Susegana
38	Moscato rosa	Rs	Università di Belgrado	ISV Susegana
25	Moscato rosso	B	Raccolta Di Rovasenda Alba (Piemonte)	ISV Susegana
45	Muscat blanc à petites grains	W	E.N.S.A.M. Montpellier (France)	ISV Susegana
12	Muscat d'Alsace blanc	W	Colmar (France)	ISV Susegana
9	Muscat d'Alsace rouge	B	Colmar (France)	ISV Susegana
43	Muscat de Frontignan	W	Maclet Botton Villefranche (France)	ISV Susegana
24	**Moscato bianco casalese**	W	Prof. Zarattaro, Casale Monferrato (Piemonte)	ISV Susegana
63	**Moscato di Scanzo**	B	Ist. Colt. Arb. Univ. Milano	ISV Spresiano
19	**Moscato giallo**	W	Raccolta Di Rovasenda, Alba (Piemonte)	ISV Susegana
37	Moscato armeno	W	Prof. Musci (Bari)	ISV Susegana
20	Moscato fior d'arancio	W	Padova	ISV Susegana
128	Moscato giallo	W	Istituto Agrario di S.Michele all'Adige, Trento	
47	Moscato saraceno	W	Ist. Colt. Arb. Univ. Bari	ISV Susegana
21	Moscato sirio	W	Conte Emo, Arquà (Padova)	ISV Susegana
127	**Moscato fior d'arancio**	W	Istituto Agrario di S.Michele all'Adige, Trento	
23	Moscato bianco grosso	W	Università di Belgrado	ISV Susegana
29	Moscato Jesus	W	Prof. Musci (Bari)	ISV Susegana
116	**Moscato nero**	B	Breganze (Vicenza)	
27	Moscato nero	B	Raccolta Di Rovasenda, Alba (Piemonte)	ISV Susegana
75	**Moscato rosa**	Rs	Breganze (Vicenza)	
124	**Moscato rosa**	B	Istituto Agrario di S.Michele all'Adige, Trento	

Tab. 1 (continued)

DNA-No	Muscat accessions	Col*.	Source	Collection
26	**Moscato violetto**	B	Staz. Sperim. Agr. e For. S. Michele all'Adige, Trento	ISV Susegana
41	**Muscat of Alexandria**	W	**	ISV Susegana
35	Moscatel blanco	W	Jerez de la Fronteira (Spain)	ISV Susegana
34	Moscatel de Malaga	W	Jerez de la Fronteira (Spain)	ISV Susegana
67	Moscato francese	W	Vecchie varietà di Velletri (Lazio)	ISV Susegana
13	**Muscat of Hamburg**	B	ISV S.O.P. Bari	ISV Susegana
40	Moscatellone	B	**	ISV Susegana
14	Moscatel negro	B	Jerez de la Fronteira (Spain)	ISV Susegana
7	Muscat Madresfield Court	B	**	ISV Susegana
8	Muscat noir de H. Marsel	B	Jerez de la Fronteira (Spain)	ISV Susegana
10	**Muscat Ottonel**	W	Hungary	ISV Susegana
31	Muscat Ottonel	W	Trier (Germany)	ISV Susegana
44	**Thomuscat**	W	Davis (California)	ISV Susegana
Outgroup varieties				
129	Corvina veronese	B		ISV Susegana
80	Sangiovese	B		ISV Susegana
68	Pinot nero	B		ISV Susegana
18	Riesling renano	W		ISV Susegana
98	Sultanina	W		ISV Susegana

ISV = Istituto Sperimentale per la Viticoltura.
Col* = colour: W = white, B = black, Rs = pink.
** In some cases it was not possible to go back to the source of the material present in the collection for a very long time.

(Thomas and Scott 1993), VVS29 (Thomas, pers. comm.; CSIRO Plant Industry, Adelaide, Australia), VVMD5, VVMD7, VVMD8 (Bowers *et al.* 1996), VVMD14, VVMD17, VVMD21, VVMD24, VVMD25, VVMD26, VVMD28, VVMD31, VVMD32, VVMD34, VVMD36 (Bowers *et al.* 1999), VRZAG21, VRZAG47, VRZAG62, VRZAG64, VRZAG79 (Regner, pers. comm.), IVS2, ISV3 and ISV4 isolated in our institute which is a member of the VMC.

The PCR reaction mixture (25 µl final volume) contained: 10 ng total DNA, 0.5 U Taq DNA polymerase (Polymed, Firenze) and 1x relative buffer (Polymed, Firenze), 1.5 mM $MgCl_2$, 200 µM of each dNTP, 20 pmol of each primer. The PCR was performed in a PTC-100 thermal cycler (MJ Research, Massachussetts, USA) with a two-step protocol (Sefc *et al.* 1997 b): 5 min at 95 °C, 10 cycles of 50 °C for 15 s, 94 °C for 15 s, followed by 23 cycles of 50 °C for 15 s and 89 °C for 15 s, and a final step of 8 °C for at least 10 min to stop the reaction.

5 µl of the PCR product were tested on a 2 % agarose gel. On the basis of the signal intensity, 1-2 µl of amplified DNA was used for electrophoresis. Samples were denatured at 94 °C for 3 min in a buffer containing formamide and loaded onto a sequencing gel (5 % polyacrylamide, TBE 1 x, urea 7 M). Amplification products of cultivars carrying alleles of known molecular size were used as a reference for allele sizing. Bands on the gel were revealed by silver staining (Bassam *et al.* 1991, Tixier *et al.* 1997) immediately after run; the glass plate with the gel was dipped in different solutions as follows: 20 min in 10 % acetic acid; 4 rinses of 5 min each with distilled water; 30 min in 0.2 % $AgNO_3$ and 0.05 % formaldehyde; a brief rinse of 10 s with distilled water and finally 5-10 min in 3 % NaOH and 0.05 % formaldehyde, until bands appeared. The gels were manually scored at least twice and the images were recorded by a scanning apparatus (Epson GT-6500, Seiko Epson Corporation, Japan).

Data management: Two indices, δ_t and PD, were calculated to evaluate the allelic variability and the informative power of microsatellite loci: δ_t is a measure of H (expected heterozygosity), corrected on the sample size (Morgante *et al.* 1994), whereas PD estimates the discrimination power of loci as a function of genotype frequencies (Testolin *et al.* 2000). The formula to calculate δ_t is:

$$\delta_t = (1 - \Sigma p_i^2)\, N/(N-1)$$

where p_i is the frequence of the i^{th} allele, $1 - \Sigma p_i^2 = H$ and N the sample size. The formula to calculate PD is:

$$PD = 1 - \Sigma G_i^2$$

where G_i is the frequency of the i^{th} genotype.
A matrix of genetic similarity was generated by calculating the Dice coefficient (Dice 1945) for all pairs of cultivars. Then a similarity dendrogram was obtained by applying the UPGA (Unweighed Pair-Group Analysis) procedure, using the STATISTICA software (StatSoft Inc. 1993). All pairs of cultivars were finally compared with each other at all loci to find the parent-offspring putative relationships.

Results

As a result of the analysis carried out at 25 microsatellite and two isozyme loci, only 20 different molecular fingerprints were found, which are therefore referable only to 20 different Muscat varieties; they are listed in Tab. 2. The same profiles of these 20 varieties were found in the other 44 Muscat accessions at all examined loci: varieties with the same pat-

Table 2

Isozyme and molecular data of the 20 identified Muscat genotypes and of the 5 varieties chosen as outgroup, listed in alphabetical order (the alleles are in bp)

DNA-No	Muscat varieties	Col.	GPI*	PGM*	VVS1	VVS2	VVS29	VVMD5	VVMD7	VVMD8	VVMD14	VVMD17	VVMD21	VVMD24	VVMD25
42	Moscadoul	B	ab	aa	190 181	143 135	179 175	236 232	247 237	157 -	232 222	222 220	256 235	214 210	259 245
54	Moscatellone bianco	W	ab	aa	190 181	133 133	171 171	246 232	249 239	157 141	232 228	222 221	266 249	219 210	245 243
79	Moscatello nero	B	bb	aa	181 181	135 133	171 171	228 226	249 239	143 141	241 227	221 220	266 249	214 210	267 253
60	Moscatello selvatico	W	ab	aa	181 181	151 149	171 171	232 232	253 249	141 -	241 235	221 220	266 249	214 210	267 253
11	Moscatel ruso	W	ab	aa	187 181	155 133	179 171	240 232	253 251	141 -	232 227	220 220	266 249	214 214	253 249
53	Moscato	B	ab	aa	181 181	135 133	171 171	236 228	249 245	143 141	241 241	222 212	256 249	214 214	259 245
123	Moscato bianco	W	ab	aa	181 181	133 133	171 171	236 228	249 233	141 -	241 222	222 220	266 249	219 214	253 245
24	Moscato bianco casalese	W	aa	aa	190 181	133 133	181 171	228 226	239 233	143 -	241 222	222 220	249 249	219 210	253 245
63	Moscato di Scanzo	B	aa	aa	183 181	135 133	171 171	240 236	249 239	143 141	222 222	222 221	266 249	219 218	259 245
19	Moscato giallo	W	aa	aa	187 181	143 133	171 171	240 228	249 239	143 141	259 241	222 212	266 256	219 214	259 245
127	Moscato fior d'arancio	W	aa	aa	190 181	133 133	179 171	236 228	249 247	143 141	227 222	222 212	266 249	214 210	253 245
116	Moscato nero	B	ab	aa	181 181	133 133	179 171	228 226	251 247	143 141	241 222	221 220	266 256	219 214	253 245
27	Moscato nero	B	aa	aa	181 180	143 135	179 171	240 236	253 233	147 141	241 241	222 220	266 249	219 210	259 259
75	Moscato rosa	Rs	ab	aa	183 180	133 133	181 179	232 228	249 239	143 -	232 227	222 220	266 266	214 214	253 245
124	Moscato rosa	B	ab	aa	181 181	135 133	171 171	240 236	249 239	141 -	m.d.	222 222	266 243	219 210	259 245
26	Moscato violetto	B	aa	aa	181 181	133 133	181 171	228 226	249 247	143 141	230 222	222 222	266 256	219 210	253 245
41	Muscat of Alexandria	W	aa	ad	181 180	149 133	179 171	232 228	251 249	141 -	241 232	220 220	266 256	214 214	253 253
13	Muscat of Hamburg	B	aa	ad	190 181	149 135	179 171	238 232	249 247	157 141	241 232	222 220	256 249	214 214	259 253
10	Muscat Ottonel	W	aa	aa	190 181	143 133	179 171	228 226	243 239	143 141	235 227	222 212	266 266	214 214	259 253
44	Thomuscat	W	ab	ad	188 181	151 149	171 171	234 232	253 249	145 -	238 232	222 220	266 256	219 214	253 243
Outgroup varieties															
129	Corvina veronese	B	ad	ac	188 162	155 151	181 179	240 232	239 239	167 141	241 230	224 212	249 249	218 210	267 245
68	Pinot nero	B	bc	ab	190 183	151 137	179 171	238 228	243 239	143 141	241 222	220 212	249 249	218 216	253 243
18	Riesling renano	W	cc	ab	190 190	151 143	179 171	234 226	257 249	147 143	234 232	221 220	249 249	218 210	259 253
80	Sangiovese	B	ab	aa	181 181	133 133	171 171	236 226	263 239	147 143	235 232	221 21	249 243	216 210	245 245
98	Sultanina	W	ab	ad	188 181	151 145	179 171	234 234	253 239	157 145	238 228	222 222	256 249	219 210	253 243

*The letters correspond to the alleles described in CALÒ *et al.* (1989) as follows: a = 1, b = 3, c = 4, d = 5.
m.d. = missing data
Col.: see Tab. 1

Tab. 2 (continued)

DNA-No	VVMD26	VVMD28	VVMD31	VVMD32	VVMD34	VVMD36	VRZAG21	VRZAG47	VRZAG62	VRZAG64	VRZAG79	ISV2	ISV3	ISV4
42	251 251	239 237	214 212	273 257	240 240	295 240	206 200	159 157	191 179	191 137	254 254	143 141	139 139	197 187
54	251 249	261 251	212 212	273 257	242 240	270 254	206 206	169 163	199 195	159 143	250 246	165 141	139 133	177 169
79	251 251	251 247	216 213	273 265	240 240	266 254	206 190	172 157	195 185	159 139	254 248	143 143	139 131	169 169
60	251 251	251 247	216 213	273 265	240 240	266 254	206 190	172 157	199 185	141 137	254 250	165 143	139 139	195 191
11	249 249	247 237	216 214	265 257	248 240	288 254	206 200	157 157	187 185	141 139	254 246	143 141	145 139	177 169
53	263 251	261 249	216 212	273 265	248 240	266 244	206 206	163 157	201 185	141 137	254 238	143 143	139 133	187 177
123	251 251	271 249	216 212	273 265	240 240	264 244	206 206	172 157	195 185	159 141	254 250	143 141	139 133	187 169
24	251 249	261 247	212 212	265 253	242 240	264 254	214 206	159 157	195 187	159 159	258 254	169 151	139 133	169 169
63	255 251	249 237	216 216	271 241	240 240	295 244	206 190	172 157	193 185	163 159	254 250	159 141	139 133	187 169
19	251 249	249 239	212 210	273 259	240 240	295 264	206 190	157 157	187 185	159 141	254 248	167 141	139 133	191 169
127	251 249	271 249	216 212	273 241	240 240	264 244	206 200	163 157	203 185	159 137	254 250	165 143	139 133	169 169
116	251 249	271 271	224 196	265 263	240 240	264 264	190 190	163 157	203 191	143 139	254 250	143 141	139 133	177 169
27	251 249	261 231	224 212	273 241	242 240	254 252	206 190	172 157	199 195	157 141	254 250	151 141	133 131	197 169
75	249 249	271 247	224 216	265 241	240 240	264 254	206 200	167 157	193 185	139 139	254 248	141 141	139 133	195 169
124	251 251	271 251	216 212	273 265	248 240	264 254	206 200	172 157	187 185	159 141	254 248	165 143	133 133	187 187
26	251 249	261 249	216 216	273 251	240 240	270 244	206 190	161 157	203 185	159 141	254 244	161 141	133 133	177 169
41	251 249	271 247	224 216	273 265	240 240	264 254	206 190	172 157	203 185	141 139	254 246	143 141	139 133	195 169
13	251 249	247 239	216 212	273 273	240 240	295 254	206 190	163 157	191 185	191 139	254 238	161 141	139 139	187 169
10	251 249	271 261	216 212	265 241	240 240	276 264	206 206	167 157	193 187	159 137	258 254	143 141	139 133	177 169
44	249 249	247 211	224 212	273 251	240 240	254 250	202 190	172 157	187 185	143 139	258 254	143 143	139 133	195 191
Outgroup varieties														
129	251 251	261 261	216 212	273 241	248 240	276 254	206 190	167 157	193 187	143 137	250 250	165 151	139 133	187 169
68	255 249	239 221	216 216	273 241	240 240	254 254	206 200	167 163	193 187	163 139	244 238	165 151	145 133	177 169
18	251 251	237 231	214 204	273 253	240 240	264 254	206 202	167 159	203 193	159 137	244 242	151 143	145 139	197 169
80	249 249	247 237	212 212	257 253	240 240	264 264	204 202	163 157	195 193	139 137	258 242	165 143	139 139	197 177
98	251 249	247 221	212 212	251 251	248 240	268 250	202 190	172 159	187 187	159 143	258 246	143 143	139 133	193 191

terns were considered as synonyms and were grouped together in Tab. 1; the best known or the most ancient representative of that group is given in **bold**. Most of these groups are small, whereas the Moscato bianco group is very large, including 27 accessions.

Microsatellite markers showed a high polymorphism, the number of alleles found in the 20 unique genotypes of Muscats ranging from three at the locus VVMD34 to 11 at VVMD36, with an average of 6.58 (Tab. 2).

Both indices of genetic diversity, δ_t and PD, were high and followed the same trend, with an average of 0.719 and 0.793 respectively; VVMD14, VVMD28 and VVMD36 were the most discriminating loci (Fig. 1).

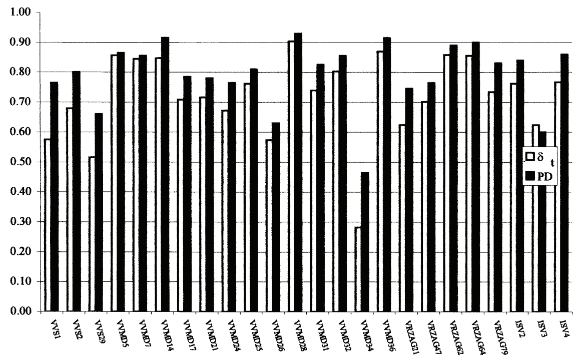

Fig. 1: δ_t and PD values calculated for each locus from the analysis of the 20 Muscat genotypes.

In many cases the polymorphism at a single locus was able to discriminate among most genotypes (Tab. 2): we frequently found unique profiles for single varieties due to the presence of an allele or a combination of alleles absent in all other varieties; *e.g.*, the locus VVMD36 gave 14 different patterns, VVMD28 gave 12 and VVMD14 gave 10. All 20 Muscat genotypes were easily separated by simultaneous comparison of their profiles at just two microsatellite loci (VVMD36 and VVS1).

The similarity tree, constructed by only one representative of each group, led to a further grouping (Fig. 2). Two main groups, which appear in the centre and at the right-hand side of the tree, showed the closest relationship among the accessions grouped at any distance: the most ancient

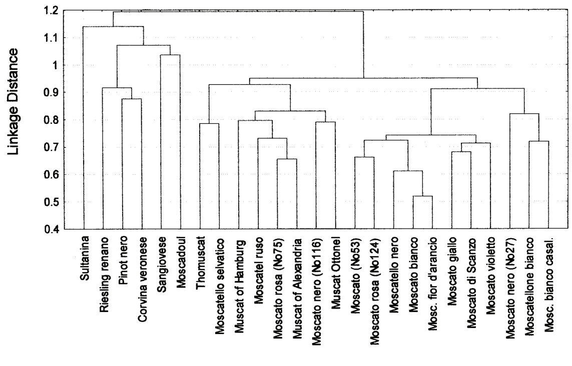

Fig. 2: Dendrogram produced by UPGA using the DICE's coefficient for the 20 Muscat genotypes and further 5 grape cultivars.

cultivar in each group was identified as Muscat of Alexandria in the first group and Moscato bianco in the second.

These groupings agree with the pedigree analysis, carried out by checking the compatibility as parent-offspring for each pair of accessions, independently of the parentage direction, which cannot be deduced by marker data (Fig. 3).

Discussion

The fingerprinting of 64 cultivars of the Muscat family allowed to identify several accessions showing identical banding pattern. These accessions were considered as synonyms and grouped together (Tab. 1). The main groups are discussed below.

Homonyms and synonyms in the Muscat family: The **Moscato bianco** is cited in literature as a very old variety known to have many different names representing small variants of the name Moscato (Muscat, Muskat, Moscatello, Muskateller) or which add the name of the region where the variety had been introduced to the basic name (*e.g.* d'Alsace, de Frontignan, di Montalcino, di Tempio). We checked 27 different accessions (Tab. 1) of which 18 were named differently; the remaining had their names in common with other accessions but originated from a different repository.

The group included also variants for berry colour, *e.g.* the Moscato rosa of the University of Belgrade, the Muscat d'Alsace rouge and the Moscato rosso. All ampelographers

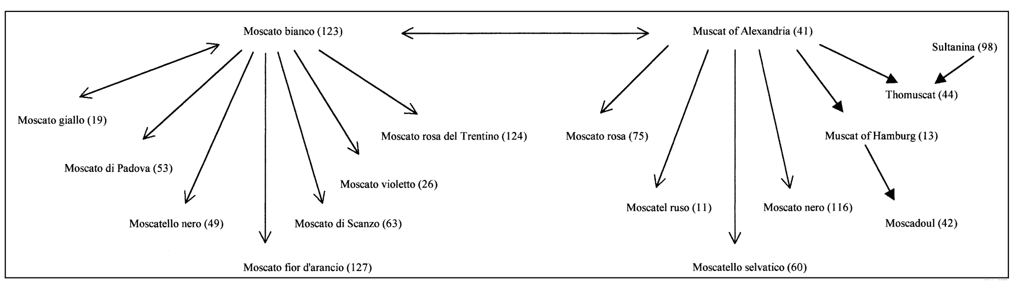

Fig. 3: Putative genetic relationships parent-offspring among 16 of the 20 identified Muscats. In brackets the accession numbers referred to Tab. 1. Double arrows: the descent direction is highly uncertain; single arrows: probable direction of crosses; thick arrows: safe direction.

agree that Moscato rosso resembles perfectly Moscato bianco; the intensity of colour may change due to the cultivation site, which explains names such as Muscat rose and Muscat gris (Molon 1906). This is not surprising, since mutation of skin colour is a rather common event in grape and in other fruit. A mutation of skin colour often occurs as a sport mutation and this makes it difficult to find differences in the marker profile between the new genotype and the original one, if a small amount of the genome is screened; moreover, a random intense genome screening, for example with AFLP markers, may bring about disappointing results (Sefc *et al.* 1998).

Muscat of Alexandria is also a very ancient cultivar with many different names. Molon (*l.c.*) reports about the history of some of them: *e.g.* the name Muscat of Alexandria seems to be relatively recent, since it was found for the first time in a Catalogue of Certosini frères in Paris, printed in 1713; the oldest wide-spread name of the variety is Zibibbo bianco, which reminds on the name of a cape at the African coast. It is likely that the name Muscat of Alexandria is derived from Alexandria in Egypt, where it was extensively grown.

Muscat of Alexandria has also mutants for berry colour, *e.g.* Muscat de Alexandria rouge, with red berries (not analysed here, see Galet 1964).

As far as the **Moscato giallo** group is concerned, Cosmo and Calò (1964) noted some analogies with Moscato sirio; our data confirm that the two varieties are synonyms. The group includes also Moscato armeno, Moscato saraceno and Moscato fior d'arancio grown in the province of Padova. The latter is genetically quite different from the true Moscato fior d'arancio grown in the area of Trento.

Two new varieties have entered the list of varieties related to **Muscat of Hamburg**: the Muscat noir de H. Marsel and the Muscat Madresfield Court. Thanks to this fortuitous comparison, it was possible to discover the origin of Muscat of Hamburg, since Muscat Madresfield Court is a known cross between Muscat of Alexandria and Black Morocco.

Moscato fior d'arancio was shown to be different from Moscato giallo, with which it has been confused sometimes; it includes two further accessions, Muscat Jesus and Moscato bianco grosso, confirming the observations of Di Rovasenda (1877). Also Viala and Vermorel (1901), report that Moscato fior d'arancio is a synonym of Muscat Jesus.

Finally a few cases of homonymy have to be described. The two accessions called Moscato nero showed a different marker profile: the Moscato nero from the Di Rovasenda's collection and the Moscato nero found in the province of Vicenza are different, each one showing a unique profile. The three accessions of Moscatello nero analysed here resulted, in another comparison, to be identical to three accessions of Aleatico nero at 12 microsatellite loci and for both GPI and PGM isozymes (data not shown). Effectively, the names Moscatello nero and Moscato nero are used in some Italian areas to indicate the Aleatico nero (Di Rovasenda *l.c.*).

The two Moscato fior d'arancio analysed in the present work are two different varieties: the one grown in the area of Padova (No 20) belongs to the Moscato giallo group of synonyms, whereas the second one, grown in the area of Trento, has been grouped together with Moscato Jesus and Moscato bianco grosso and is the true Moscato fior d'arancio cited by ampelographers.

We analysed three accessions of Moscato rosa: one (No 38) is a mutant of the Moscato bianco for the berry colour; another (No 124), cultivated in Trentino, is well known for its rose smelling and has black berries (Scienza *et al. l.c.*); the third (No 75) was found in the province of Vicenza. All three were found to be different varieties.

G e n e t i c s i m i l a r i t y a n d p e d i g r e e a n a l y s i s : The data of the VVMD8 locus were not used in these comparisons, since the fact of null alleles has already been reported (Crespan *et al.* 1999).

Molecular data were elaborated in two ways: by drawing a dendrogram with Dice coefficients (Fig. 2) and by simply comparing the data locus by locus for pairs of varieties (Fig. 3).

For 16 of the unique Muscat genotypes it was possible to establish a direct parent-offspring link, since they shared at least one allele per locus, isoenzymatic alleles included (Fig. 3). This link is indicated by arrows in Fig. 3 (thick arrows: known or easily understandable cross directions; thin arrows: the direction may only be guessed; double points: no hypotheses). So far, two families were identified: one referred to Moscato bianco and the other to the Muscat of Alexandria. Moscato bianco is directly linked (parenthood relationship) to Moscato from Padova (No 53), Moscatello nero, Moscato fior d'arancio, Moscato di Scanzo, Moscato violetto, Moscato rosa of Trentino (No 124) and Moscato giallo; the latter was joined with a double pointed arrow, since it originates from the Middle East, the supposed origin of *Vitis vinifera* L. Muscat of Alexandria is linked to the Moscato rosa of Vicenza (No 75), Moscatel ruso, Moscatello selvatico, Moscato nero (No 116), Muscat of Hamburg and Thomuscat.

Moscato nero (No 27), Moscato bianco casalese (No 24), Moscatellone bianco (No 54) and Muscat Ottonel (No 10) showed no close parentage. Nevertheless, from Fig. 2 we may gather some information on a probable indirect parentage: in fact, these 4 varieties are part of a huge family of Muscats and are well separated from the outgroup varieties, which forms a lateral branch at the left side. Moreover, Moscato nero (No 27), Moscato bianco casalese (No 24) and Moscatellone bianco (No 54) resemble much more to Moscato bianco while Muscat Ottonel (No 10) belongs to the family of Muscat of Alexandria. An indirect descent from Moscato bianco and Muscat of Alexandria, respectively, through subsequent crosses may be assumed.

The Muscat lineage figured out in this paper, with Moscato bianco and Muscat of Alexandria as the main progenitors of the great Muscat family, is supported by historical evidence since both Moscato bianco and Moscato of Alexandria are described in ampelographic manuals as very ancient grapevine cultivars.

Interestingly, Moscato bianco and Muscat of Alexandria share at least one allele per locus, so that a direct parent-offspring relationship can be postulated for these two varieties. From our molecular data it is not possible to infer the direction of the cross and therefore we can not establish which is older.

In addition, we can confirm reports in literature that the Californian Thomuscat, obtained in 1949 by Henderson (EYNARD *et al.* 1981) is a crossing of Muscat of Alexandria and Sultanina bianca.

The Moscadoul is the only Muscat grouped in the dendrogram of Fig. 2 with the outgroup varieties. This classification may be due to the fact that it is a hybrid of the Galimbert-Coulondre collection, obtained by crossing of 12375 and Muscat of Hamburg (GALET 1956). According to our molecular data Muscat of Hamburg has confirmed to be a parent.

None of the 20 primary Muscat varieties identified in this work derived from self-pollination of any other variety of the study.

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Erratum

In the paper

The Muscats: A molecular analysis of synonyms, homonyms and genetic relationships within a large family of grapevine cultivars

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Vitis **40** (1), 23-30 (2001)

some numbers of alleles were misprinted in Tab. 2.
Part of Tab. 2 is given below with corrected numbers in bold.

DNA-No/Muscat varieties		Col.	GPI*	PGM*	VVMD17	VVMD21	VVMD25	VVMD26	VVMD28	VVMD31	VVMD36	VRZAG21
42	Moscadoul	B	ab	aa	222 220	256 235	259 245	251 251	239 237	214 212	295 240	206 200
54	Moscatellone bianco	W	ab	aa	222 221	266 249	245 243	251 249	261 251	212 212	270 254	206 206
79	Moscatello nero	B	bb	aa	221 220	266 **243**	**259** 253	251 **249**	**249 239**	216 **212**	**254 244**	**206 206**
60	Moscatello selvatico	W	ab	aa	221 220	266 249	267 253	251 251	251 247	216 213	266 254	206 190
11	Moscatel ruso	W	ab	aa	220 220	266 249	253 249	249 249	247 237	216 214	288 254	206 200
53	Moscato	B	ab	aa	222 212	256 249	259 245	263 251	261 249	216 212	266 244	206 206
123	Moscato bianco	W	ab	aa	222 220	266 249	253 245	251 251	271 249	216 212	264 244	206 206
24	Moscato bianco casalese	W	aa	aa	222 220	249 249	253 245	251 249	261 247	212 212	264 254	214 206
63	Moscato di Scanzo	B	aa	aa	222 221	266 249	259 245	255 251	249 237	216 216	295 244	206 190
19	Moscato giallo	W	aa	aa	222 212	266 256	259 245	251 249	249 239	212 210	295 264	206 190
127	Moscato fior d'arancio	W	aa	aa	222 212	266 249	253 245	251 249	271 249	216 212	264 244	206 200
116	Moscato nero	B	ab	aa	221 220	266 256	253 245	251 249	271 271	224 196	264 264	190 190
27	Moscato nero	B	aa	aa	222 220	266 249	259 259	251 249	261 231	224 212	254 252	206 190
75	Moscato rosa	Rs	ab	aa	222 220	266 266	253 245	249 249	271 247	224 216	264 254	206 200
124	Moscato rosa	B	ab	aa	222 222	266 243	259 245	251 251	271 251	216 212	264 254	206 200
26	Moscato violetto	B	aa	aa	222 222	266 256	253 245	251 249	261 249	216 216	270 244	206 190
41	Muscat of Alexandria	W	aa	ad	220 220	266 256	253 253	251 249	271 247	224 216	264 254	206 190
13	Muscat of Hamburg	B	aa	ad	222 220	256 249	259 253	251 249	247 239	216 212	295 254	206 190
10	Muscat Ottonel	W	aa	aa	222 212	266 266	259 253	251 249	271 261	216 212	276 264	206 206
44	Thomuscat	W	ab	ad	222 220	266 256	253 243	249 249	247 **221**	224 212	254 250	202 190
Outgroup varieties												
129	Corvina veronese	B	ad	ac	224 212	249 249	267 245	251 251	261 261	216 212	276 254	206 190
68	Pinot nero	B	bc	ab	220 212	249 249	253 243	255 249	239 221	216 216	254 254	206 200
18	Riesling renano	W	cc	ab	221 220	249 249	259 253	251 251	237 231	214 204	264 254	206 202
80	Sangiovese	B	ab	aa	221 **212**	249 243	245 245	249 249	247 237	212 212	264 264	204 202
98	Sultanina	W	ab	ad	222 222	256 249	253 243	251 249	247 221	212 212	268 250	202 190