



Molecular Genetic Identification of Apple Cultivars Based on Microsatellite DNA Analysis. I. The Database of 600 Validated Profiles

Sanja Baric^{1,2} · Alberto Storti^{1,2} · Melanie Hofer¹ · Walter Guerra¹ · Josef Dalla Via³

Received: 12 March 2020 / Accepted: 24 March 2020 / Published online: 28 April 2020

© The Author(s) 2020

Abstract

Apple (*Malus × domestica* Borkh.) is the most widely grown permanent fruit crop of temperate climates. Although commercial apple growing is based on a small number of globally spread cultivars, its diversity is much larger and there are estimates about the existence of more than 10,000 documented varieties. The varietal diversity can be described and determined based on phenotypic characters of the external and internal traits of fruit, which, however, can be modulated by environmental factors. Consequently, molecular methods have become an important alternative means for the characterisation of apple cultivar diversity. In order to use multilocus microsatellite data for determination of unidentified or misidentified apple varieties, a database with molecular genetic fingerprints of well-determined reference cultivars needs to be available. The objective of the present work was to establish such a database that could be applied for the molecular genetic determination of a large number of historic and modern, diploid and triploid apple cultivars. Based on the analysis of more than 1600 accessions of apple trees sampled in 37 public and private cultivar collections in different European countries at 14 variable microsatellite loci, a database with 600 molecular genetic profiles was finally obtained. The key criterion for considering a molecular genetic profile as confirmed and for including it into the reference database was that at least two accessions of the same cultivar of different provenances generated an identical result, which was achieved for 98% of the apple cultivars present in the database. For the remaining genotypes, the cultivar assignment was supported by a parentage analysis or by comparison to molecular genetic profiles available in published works. The database is composed of 574 scion cultivars, 24 rootstock genotypes and two species of crab apples. Of the 574 scion cultivars, 61% were derived from historic or old cultivars, many of which were grown in Central Europe in the past. The remaining scion cultivars are currently grown or available in testing programmes and may gain importance in the future. In order to validate the genotyping data, parentage analysis was performed involving cultivars and rootstocks that arose after 1900, for which information about at least one parent cultivar was available from pomological and scientific literature and the molecular genetic profiles of the assumed parent(s) were also present in our database. This analysis revealed the presence of null alleles at locus COL, however, when excluding this locus, a mean genotyping error rate of only 0.28% per locus was revealed, which points to a high reliability of the dataset. The datasets with 14 and 13 loci (excluding locus COL) showed a high degree of discrimination power, with a combined non-exclusion probability of identity of 2.6×10^{-20} and 3.4×10^{-19} . Five of the microsatellite loci analysed in the present study overlapped with another published dataset and after the application of conversion values, it was possible to align the allele lengths and compare the molecular genetic profiles of 20 randomly derived cultivars, which were analysed in both studies. This comparison evidenced an exact correspondence of the microsatellite profiles contained in the two datasets, further pointing to the accuracy of our database. Apart from its application to characterise genetic resources or to manage germplasm collections, the here presented database could serve as an important tool for quality control or as a useful instrument in breeding programmes.

Keywords *Malus × domestica* · Cultivar identification · DNA markers · Simple sequence repeats (SSRs)

The authors S. Baric and A. Storti contributed equally to the manuscript.

✉ Sanja Baric
sanja.baric@unibz.it

Extended author information available on the last page of the article

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10341-020-00483-0) contains supplementary material, which is available to authorized users.

Molekulargenetische Bestimmung von Apfelsorten mithilfe der Mikrosatelliten-DNA-Analyse. I. Die Datenbank mit 600 validierten Profilen

Schlüsselwörter *Malus × domestica* · Sortenbestimmung · DNA-Marker · Simple sequence repeats (SSRs)

Introduction

Apple (*Malus × domestica* Borkh.) is the most widely grown permanent fruit crop of temperate climates. In Europe, apple was cultivated on an area of 473,500 ha in 2017 and it represented the most common fruit tree species (Eurostat 2019). The domestic apple is an interspecific hybrid originating from Central Asia that had been cultivated since antiquity (Janick 2005; Cornille et al. 2014). In the course of centuries, a multitude of apple varieties had arisen by spontaneous crossing and the trees with the most desirable properties have been selected by humans and further clonally propagated by grafting. Some of the cultivars were grown locally, while others were distributed over larger geographic areas in Europe (Hartmann 2015). Furthermore, trees, scionwood or apple seeds from European countries were disseminated to other continents during the colonisation of the New World, where the selection of new cultivars had been continued (Janick 2005; Volk and Henk 2016).

There are estimates that more than 10,000 apple cultivars had been documented (Janick et al. 1996; Rieger 2006). Europe saw the highest cultivar diversity of apple in the late 19th century, when many different local cultivars were grown in numerous little orchards (Luby 2003). The number of known cultivars in England most probably exceeded 2500, while more than 6000 cultivars were assumed on the territory of the former Soviet Union (Juniper et al. 1998). In the United States, representing a secondary centre of apple cultivar diversification (Janick 2005), more than 7000 apple cultivars were listed between 1804 and 1904 (cited by Volk and Henk 2016). This number, however, may also include synonymous names.

Even though scientific breeding programmes initiated at the beginning of the 20th century, some of the globally most widely grown apple cultivars, such as 'Golden Delicious', 'Red Delicious' or 'Granny Smith' arose as chance seedlings (Brown and Maloney 2003). Only in the recent decades, cultivars obtained by systematic breeding have been gaining more importance on the market. However, many of the breeding programmes relied on a small number of progenitors, posing a risk of reduced genetic diversity of new apple cultivars (Noiton and Alspach 1996; Bannier 2011). Therefore, conservation of the remaining cultivar diversity in germplasm repositories is of utmost importance in order to prevent a future narrowing of the genetic base of apple (Way et al. 1990).

A prerequisite for efficient germplasm management is an exact determination of the cultivars maintained in a collection. Apple cultivars can be described and determined based on phenotypic characters, which mainly focus on the external and internal traits of fruit (Morgan and Richards 2002). Although in the past, there were strong attempts to implement a systematics and a key for determination of apple cultivars, this initiative had failed because cultivars of the domestic apple do represent the same botanical species. Furthermore, phenotypic traits can be modulated by environmental factors and thus render pomological determination more difficult. In addition, a sufficient number of typical fruit has to be available. Finally, the pomological determination requires experienced specialists, which are becoming scarce, as pomology has been widely excluded from the curricula of horticultural science education (Hartmann 2015).

In the last two decades, molecular tools have been implemented as an alternative or additional means to the characterisation of apple cultivar diversity (Guilford et al. 1997; Hokanson et al. 1998). Such methods rely on the direct analysis of DNA, which can be isolated from plant tissue independent of the phenological stage of the tree and which is not affected by environmental influences. The most commonly applied technique is the analysis of simple sequence repeats (SSRs) or microsatellite markers, which, due to their robustness, reproducibility and high-throughput potential, have been employed to describe the genetic resources of apple in many countries (e.g. Guarino et al. 2006; Pereira-Lorenzo et al. 2007; Routson et al. 2009; van Treuren et al. 2010; Garkava-Gustavsson et al. 2013; Ferreira et al. 2016; Gasi et al. 2016; Urrestarazu et al. 2016; Larsen et al. 2017; Testolin et al. 2019).

The main objective of the present study was to establish a database with molecular genetic fingerprints of reference cultivars that could be used for determination of a large number of unidentified or misidentified apple cultivars. A thorough validation of the dataset comprising historic, old and recent apple cultivars was considered crucial in order to assure a high degree of reliability of the database, making it a suitable tool for characterisation of genetic resources but also for other applications.

Materials and Methods

Samples

The present study comprises genotyping data of 1621 accessions of apple trees that were sampled in 37 public and private cultivar collections in different European countries and that can be attributed to 600 different genotypes (see summary in Tables 1 and 2, and extensive information in Supplementary Table S1). The key criterion for including a molecular genetic profile into the reference database was that at least two accessions of the same cultivar of different provenances generated an identical result. Accessions belonging to 570 cultivars were indeed derived from two or more distinct cultivar collections, whereas 19 cultivars were obtained from a single collection, but comprised at least two accessions of different origin. Eleven cultivars were sampled from a single accession, however, in ten instances their cultivar assignment was supported by a parentage analysis or by molecular genetic data derived from other studies (Table 2). The crab apple species *M. floribunda* 821, which is the progenitor of scab resistance (Rvi6) and was therefore included in the database, was only available from one cultivar collection.

German and English language pomological literature was searched for information about the country and year of origin of each cultivar as well as their parent cultivars (if known). The principal sources of information on old apple cultivars were the books of Morgan and Richards (2002), Silbereisen et al. (2015), Mühl (2001), Votteler (2014), Hartmann (2003, 2015), Bartha-Pichler et al. (2005), Smith (1971), Rolff (2001), Bernkopp et al. (2003) and Bernkopp (2011), cited in the order of consultation significance. For the more recent cultivars, the publications of Sansavini et al. (2012), Brown and Maloney (2003) and Evans et al. (2011) were consulted as were the Community Plant Variety Office (CPVO) Database (<https://cpvo.europa.eu/en/applications-and-examinations/cpvo-varieties-database>), the United States Patent and Trademark Office (USPTO) online database (<http://appft.uspto.gov/netacgi/PTO/index.html>) and the UPOV PLUTO: Plant Variety Database (<http://www.upov.int/pluto/en/>). The information about the origin of the rootstocks investigated in the present study was taken from Webster and Wertheim (2003), NIAB-EMR (2016) and Petzold (1984). In case that the references/databases mentioned above did not provide information about a given cultivar, literature searches specifically targeting that particular cultivar were conducted and cited in Table 2. Based on information about the year of origin, cultivars were classified as (i) *historic*, if they arose before 1900, as (ii) *old*, if they originated between 1900 and 1950 and as (iii) *recent*, if they were bred after 1950.

Nucleic Acid Isolation and Microsatellite DNA Analysis

Nucleic acid was isolated from leaf discs (approximately 100 mg) by direct homogenisation of fresh plant tissue in lysis buffer PL1 of the NucleoSpin Plant II Kit (Macherey-Nagel, Düren, Germany), using a 3-mm tungsten carbide bead (Qiagen, Hilden, Germany) and a Mixer Mill MM300 (Retsch GmbH, Haan, Germany). The remaining steps of the DNA isolation process were performed exactly according to the kit's manual. Quality and quantity of DNA isolates were controlled by electrophoresis on 1% agarose gels stained with ethidium bromide. DNA isolates were maintained at -20 °C until analysis. Aliquots of DNA isolates were obtained of rootstock samples from East Malling Research (UK) and part of the samples from Haidegg Research Station (Austria).

Each DNA sample was analysed at 14 microsatellite DNA loci described by Liebhard et al. (2002) in four multiplex reactions (Table 3). For each reaction pool, a 10 µl reaction mix was prepared, which contained 200 µM dNTPs, the appropriate concentration of each primer (see Table 3), 1 × GeneAmp PCR Buffer II (Life Technologies, Carlsbad, CA, USA), 1.5 mM MgCl₂ (Life Technologies) and 0.5 Units of AmpliTaq Gold Polymerase (Life Technologies). To each 10 µl aliquot of the master mix, 2 µl DNA isolate were added (approximately 10 ng) and amplified on a GeneAmp PCR System 2700 (Life Technologies) under the following conditions: 10 min initial denaturation at 94 °C, 35 cycles with 20 s at 94 °C, 20 s at 57.5 °C and 45 s at 72 °C, followed by 10 min of final extension at 72 °C.

Amplified microsatellite DNA products were separated and visualised on a CEQ 8000 Genetic Analysis System (Beckman Coulter, Fullerton, CA, USA) for 35 min at 7.5 kV. Sizing of fragments relative to the internal CEQ DNA Size Standard 400 (Beckman Coulter) and assignment to specific allele classes were performed by applying the Fragment Analysis Software version 9.0 of the same manufacturer. Each electropherogram was carefully visually inspected for binning accuracy before data were exported. A cross-tabulation matrix in Microsoft Access was employed in order to compare all the molecular genetic profiles at 14 microsatellite loci to each other and to identify exact matches (Baric et al. 2009). All synonymous profiles were represented by a unique genotype (each assigned a distinctive profile number) and included into the final dataset (Supplementary Table S2).

Data Analysis

As the complete dataset comprised diploid and triploid genotypes, the number of alleles per locus and their size ranges were determined by applying the software SPAGeDi

Table 1 List of germplasm collections and organisations, from which accessions of apple cultivars were collected or obtained for the present study

No.	Abbreviation	Name of apple cultivar collection or organisation	Country	No. accessions	No. cultivars
1	ACW	Agroscope Research Station	Switzerland	45	43
2	AGES	Austrian Agency for Health and Food Safety, AGES Linz	Austria	50	46
3	AHH	Private Collection Adam, Hünfelden-Heringen	Germany	1	1
4	AN	Arche Noah – the Austrian Seed Savers Association, Schiltern	Austria	28	16
5	BB	Private Collection Bannier, Bielefeld	Germany	7	5
6	BOKU	Institute of Horticulture and Viticulture, University of Natural Resources and Applied Life Sciences, Vienna	Austria	57	42
7	BSA	Bundessortenamt Prüfstelle Wurzen	Germany	90	85
8	BVC	Bassi Vivai Cuneo	Italy	25	25
9	CIV	Consorzio Italiano Vivaisti, S. Giuseppe di Comacchio	Italy	10	10
10	CReSO	Agrion, Cuneo	Italy	5	5
11	CUB	Corvinus University of Budapest	Hungary	1	1
12	EMR	East Malling Research	UK	23	23
13	FEM	Fondazione Edmund Mach di San Michele all'Adige	Italy	35	34
14	HG	Versuchsstation Obst- und Weinbau Haidegg	Austria	64	63
15	JL	Jardin du Luxembourg, Paris	France	54	52
16	KN	Höhere Bundeslehranstalt und Bundesamt für Wein- und Obstbau Klosterneuburg	Austria	168	92
17	KOB	Kompetenzzentrum Obstbau Bavendorf	Germany	102	102
18	LAG	Lubera AG, Buchs	Switzerland	5	5
19	LB	Laimburg Research Centre	Italy	237	192
20	MSPP	Monastero SS. Pietro e Paolo, Germagno	Italy	16	15
21	NES	Nagano Fruit Tree Experiment Station	Japan	1	1
22	NFC	National Fruit Collection in Brogdale	UK	215	214
23	OIKOS	OIKOS – Institut für angewandte Ökologie & Grundlagenforschung, Gleisdorf	Austria	6	3
24	OJE	Obstbauzentrum Jork Esteburg	Germany	1	1
25	OKR	Obst- und Kulturweg Ratzinger Höhe, Rosenheim	Germany	28	28
26	OWL	Obst- und Weinbauzentrum der Landwirtschaftskammer Kärnten, St. Andrä	Austria	11	11
27	PEM	Pépinières Escande "Millet", Saint Vite	France	8	8
28	PVW	Pomologen-Verein e. V. Baden-Württemberg	Germany	3	2
29	RW	Verein Obstsortensammlung Roggwil	Switzerland	35	34
30	SEGE	Conservation Orchard Alsace, Alteckendorf	France	1	1
31	SGB	Sortengarten Burgenland, Neuhaus am Klausenbach	Austria	4	3
32	SKS	Sortenerneuerungskonsortium Südtirol, Terlan	Italy	9	5
33	SLU	Swedish University of Agricultural Sciences, Uppsala	Sweden	30	29
34	TR	Landwirtschaftliche Lehranstalten Triesdorf	Germany	66	63
35	UB	Department of Agricultural Sciences, University of Bologna	Italy	119	95
36	VA	Veneto Agricoltura – Agenzia Veneta per il Settore Primario, Legnaro	Italy	46	43
37	ZASS	Zisterzienserabtei Stift Stams	Austria	15	15

version 1.4 (Hardy and Vekemans 2002). In addition, the software CERVUS 3.0.7 (Kalinowski et al. 2007) was employed on a dataset including only diploid genotypes of apple. More precisely, allele frequency and identity analyses were performed on (i) a dataset including all diploid genotypes and the 14 microsatellite loci analysed in this study, (ii) a dataset excluding locus COL, and thus containing

data at 13 microsatellite loci, (iii) a dataset containing data at six microsatellite loci (CH01f02, CH02b10, CH02c09, CH02c11, CH02d08, CH01h01) and (iv) a dataset containing data at five microsatellite loci (CH01f02, CH02c09, CH02c11, CH02d08, CH01h01). The latter two reduced sets of microsatellites overlapped with part of the loci employed in the studies of Bus et al. (2012) and Urrestarazu

Table 2 Summary information on the 600 apple cultivars included in the reference database

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
1	Aargauer Jubiläumsapfel	3n	Switzerland	1800s	Historic	–	529	ACW, KOB, TR	6
2	Abbondanza Rossa	2n	Italy	1896	Historic	–	429	NFC, UB, VA	49
3	Adams' Pärmäne	2n	UK	Around 1826	Historic	–	442	AGES, KN	25
4	Adersleber Kalvill	2n	Germany	Around 1870	Historic	Weißer Wintertalwill × Gravensteiner	265	KN, LB	25
5	African Red [Carnine African Red [®]]	2n	South Africa	1996	Recent	Golden Delicious × Red Delicious (CC)	512	HG, LB	41; 54
6	Akane	2n	Japan	1953	Recent	Jonathan × Worcester Parmäne (CC)	678	ACW, BSA, UB	49; 53
7	Alesya	2n	Belarus	1989	Recent	–	424	2LB	54
8	Alkmene	2n	Germany	1930s	Old	Geheimrat Dr. Oldenburg × Cox Orange (CC)	235	BOKU, KN	43
9	Allington Pepping	2n	UK	Before 1884	Historic	Goldparmäne × Cox Orange	530	NFC, SLU	25
10	Almagold	2n	Italy	2008	Recent	–	468	FEM, LB	54
11	Altländer Fettapfel	2n	Germany	Before 1950	Old	–	599	KOB, NFC	38; 44
12	Altländer Pfannkuchenapfel	2n	Germany	Before 1840	Historic	–	542	BSA, NFC	49
13	Altländer Rosenapfel	2n	Germany	Around 1850	Historic	–	607	KOB, NFC, TR	25
14	Ambrosia	2n	Canada	1997	Recent	Golden Delicious × Red Delicious (CC)	421	LB, VA	41; 56
15	Ananas Renette	2n	Netherlands	1820	Historic	–	58	ACW, BOKU, HG, LB, MSPP, RW	43
16	Angold	2n	Czech Republic	1988	Recent	Antonowka (HL A 28/39) × Golden Delicious ^(C)	395	KN, VA	12; 13; 54
17	Anj2007 [Annabelle [®]]	2n	Netherlands	2009	Recent	(Neiprincess × Glosster) × Elstar ^(C)	497	HG, LB	41; 54
18	Annurca	2n	Italy	Before 1876 (antique origin?)	Historic	–	690	FEM, NFC, UB	2; 28
19	Antonowka kamenichka	2n	Ukraine	1889	Historic	–	1008	TR; Bus et al. 2012	25
20	Antonowka polutorafuntowa	2n	Russia	1888	Historic	–	9	BOKU, KOB, NFC; Bus et al. 2012	25
21	Antonowka, gewöhnlicher	2n	Russia	1826	Historic	–	563	NFC, OKR, TR; Bus et al. 2012	25
22	Apex Zagara	2n	France	1800s (?)	Historic	–	918	JL, NFC	25

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
23	Apfel von Åkerö	2n	Sweden (?) or Netherlands (?)	1759	Historic	–	135	NFC, SLU, TR	25
24	Apfel von Grignon (= Contessa)	3n	France	Before 1858	Historic	–	553	BVC, KOB, NFC, UB	44
25	Api Noir	2n	France	1608	Historic	–	873	JL, NFC	25
26	Apollo	2n	Germany	1930s	Old	Geheimrat Dr. Oldenburg × Cox Orange (CC)	782	BSA, TR	34 (p. 13); 49
27	Ariane [Les Naturianes®]	2n	France	2000	Recent	–	402	LB, UB	54
28	Ariwa	2n	Switzerland	1997	Recent	Golden Delicious ^(C) × A 849-5	399	LB, VA	6; 23
29	Arkansas (Syn. Mammoth Black Twig)	3n	USA	1842	Historic	Winesap × unknown	990	NFC, UB	18
30	Arkansas Black	2n	USA	1870	Historic	Winesap × unknown	441	TR, 2UB	18
31	Arlet	2n	Switzerland	1958	Recent	Golden Delicious × Idared (CC)	388	ACW, KN	26
32	Aroma	2n	Sweden	1945	Old	Ingrid Marie × Filippa (CC)	495	BSA, LB, NFC	25
33	Astrachan Large Fruited	2n	Sweden	1850s	Historic	White Astrachan × unknown (?)	931	JL, NFC	25
34	Astramél	2n	Germany	1993	Recent	Roter Astrachan ^(C) × (James Grieve × Melba)	811	BSA, NFC, SLU	25
35	Aurora Golden Gala	2n	Canada	2001	Recent	Splendour × Gala (CC)	503	LB, VA	41; 54
36	AW 106 [Saporá®]	3n	Germany	2010	Recent	Rafzubin × Fuji	487	HG, LB	41; 54
37	Bancroft	2n	Canada	1935	Old	Forest × Mcintosh ^(C)	1038	NFC, TR	49
38	Bänziger	2n	USA	Around 1890	Historic	–	545	ACW, NFC, RW	25
39	Batullenapfel	2n	Romania	Early 1800s	Historic	–	443	AGES, KN, OWL	25
40	Baujade	2n	France	1988	Recent	X-6799 × Granny Smith ^(C)	471	LB, UB	12; 13; 54
41	Baumanns Renette	2n	Belgium	Around 1800	Historic	–	163	AN, BOKU, HG, RW	43
42	BAY 3484 [Bayar Marisa®]	2n	Germany	2009	Recent	–	642	FEM, LB	54
43	Bec d'Oie	2n	France	1670 (?)	Historic	–	967	JL, NFC	25
44	Beffertapfel	2n	Switzerland, Thurgau	n.a.	Historic (local)	–	531	ACW, HG, RW	6
45	Bellefleur Kitajka	2n	Russia	Around 1900	Historic	–	843	NFC, SLU	49
46	Bellida	2n	Netherlands	1990	Recent	Idared × Elstar (CC)	489	CIV, LB, NFC	12; 54
47	Benoni	2n	USA	Around 1830	Historic	–	763	BSA, BVC, NFC	25
48	Berlepsch	2n	Germany	Around 1880	Historic	Ananas Renette × Ribston Pepping	61	AGES, BOKU, LB, RW	43

Table 2 (Continued)

No.	Cultivar name [Trademark name ^a]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
49	Berner Rosen	2n	Switzerland	1888	Historic	Roter Winterkalwill × Sauergrauech Skrzihapel × Komsin Bessemanka	293	ACW, BOKU, HG, RW, KOB, NFC	20; 43
50	Bessemyanka Michurina	2n	Russia	1912	Old	Danziger Kantapfel × unknown	968	KOB, NFC	25
51	Biesterfelder Renette	3n	Germany	1905	Old	Danziger Kantapfel × unknown	60	KOB, NFC	32; 49
52	Birnförmiger Apfel	2n	Germany	1801	Historic	–	142	AGES, AN, KOB	44
53	Bismarckapfel	2n	New Zealand	1870	Historic	–	6	NFC, RW	49
54	Bittenfelder Sämling	2n	Germany	First half 1900	Old	Kasseler Renette ^(C) × unknown	533	KOB, OWL	20; 43
55	Black Ben Davis	2n	USA	Early 1800s (?)	Historic	–	902	BVC, NFC, UB	25
56	Blauacher Wädenswil	3n	Switzerland	1820	Historic	–	86	BSA, KOB	6
57	Blue Pearmain	2n	USA (?)	Early 1800s	Historic	–	1035	NFC, TR, UB	25
58	Blumberger Langstiel	2n	Germany	n.a.	Historic (local)	–	767	BSA, KOB	49
59	Blushing Golden	2n	USA	1968	Recent	Golden Delicious ^(C) × Jonathan ^(NC)	374	KN, NFC	49; 55
60	Böhmischer Brünnlerling	3n	Austria	1600s	Historic	–	74	ACW, AGES, AN, LB, RW, ZASS	7
61	Boikenapfel	2n	Germany	1828	Historic	–	103	HG, RW	43
62	Bondon	2n	France	1948	Old	–	965	ACW, JL, NFC	25
63	Börtlinger Weinapfel	2n	Germany	Around 1827	Historic	–	741	BSA, KOB	43
64	Bozner Apfel	3n	Italy, South Tyrol	1500s	Historic	–	152	HG, LB	30
65	Braeburn	2n	New Zealand	1989	Recent	Lady Hamilton × unknown (?)	232	KN, LB	15
66	Branleys Seedling	3n	UK	1809	Historic	–	190	KN, NFC, ZASS	25
67	Brauner Matapfel	2n	Germany (?)	1798	Historic	–	549	KOB, OKR, TR	17
68	Brettacher	3n	Germany	Around 1900	Historic	Champagner Renette × unknown (?)	52	KN, KOB	43
69	Brina	2n	Italy	1999	Recent	–	470	LB, VA	54
70	Brixner Plattling (Syn. Haslinger)	3n	Hungary	1871	Historic	–	1	AGES, BOKU, HG, LB	8
71	Buras	3n	Italy, Piemonte	n.a.	Historic (local)	–	354	BVC, MSPP	11
72	Burchardts Renette	2n	Russia	1863	Historic	–	961	NFC, TR	44
73	Burgundy	2n	USA	1953	Recent	Monroe ^(C) × (Macoun × Antonowka)	686	NFC, UB	25

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
74	Calvilla San Salvatore (Syn. Calville de Saint-Sauveur)	2n	France	1836	Historic	–	684	NFC, 2UB	25
75	Calville d'Oullins	2n	France	Around 1850	Historic	–	840	JL, NFC, SLU	25
76	Calville Rouge du Mont d'Or	2n	France	1948	Old	Roter Winterkalvill × Kaiser Alexander (CC)	859	JL, NFC	20; 25
77	Campanino	2n	Italy	Late 1800s	Historic	–	575	NFC, UB, VA	25
78	Cardinal	2n	USA	1948	Old	–	899	JL, NFC	25
79	Catarina	2n	Brazil	2002	Recent	Fuji ^(C) × Sel. PWP 377I33	400	LB, VA	23
80	Caudle [Cameo [®]]	2n	USA	1996	Recent	Golden Delicious × Red Delicious (CC)	69	FEM, KN, LB, UB	39; 54
81	Cellini	2n	UK	Around 1828	Historic	Peasgood Sonderleinchen × unknown (?)	14	AGES, KN	25
82	CH101 (ACW 10442) [Galwa [®]]	2n	Switzerland	2011	Recent	K1R20/A44 × Gala(C)	578	HG, LB	56
83	Champagner Renette	2n	France	Before 1770	Historic	–	254	ACW, AGES, BOKU, HG, LB, RW	43
84	Chantecler [Belchard [®]]	2n	France	1958	Recent	Golden Delicious × Reinette Clochard (CC)	696	JL, UB	25
85	Charlamowsky	2n	Russia	Early 1700s	Historic	–	128	AGES, BOKU	25
86	Charlotte	2n	UK	1988	Recent	McIntosh × Greensleeves (CC)	828	BSA, NFC	25
87	Chataignier	2n	France	1873	Historic	–	944	JL, NFC	25
88	Chinook	2n	Canada	1994	Recent	Splendour × Gala (CC)	516	LB, VA	12; 54
89	Chüsentrainer	2n	Switzerland	1861	Historic	–	615	HG, KOB, NFC	6
90	CIV323 [Isaaq [®]]	2n	Italy	2012	Recent	Galaxy × A3-7	831	CIV, LB	41; 56
91	CIVG198 [Modif [®]]	2n	Italy	2006	Recent	Galax × Liberty (CC)	200	KN, LB	39; 56
92	Civni [Rubens [®]]	2n	Italy	2000	Recent	Galax × Elstar (CC)	65	KN, LB	13; 39; 54
93	Civren [Renè [®]]	2n	Italy	2011	Recent	–	834	CIV, LB	41; 54
94	Cludius Herbstapfel	2n	Germany	1850	Historic	–	890	NFC, TR	25
95	Collina	2n	Netherlands	2001	Recent	Priscilla-NL × Elstar(NC)	469	LB, UB	13; 54
96	Comercio	2n	USA	Around 1865	Historic	–	669	BVC, 2UB	44
97	Co-op 29 [Sundance [®]]	2n	USA	2001	Recent	Golden Delicious ^(C) × PRI 1050-201	808	BVC, FEM	41; 56
98	Co-op 33 [Pixie Crunch [®]]	2n	USA	2001	Recent	Sel. 669.205 × PCF W2134	729	LB, PEM	41; 56

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
99	Co-op 38 [GoldRush [®]]	2n	USA	1995	Recent	Co-op 17 × Golden Delicious (CC)	291	KN, LB	38; 54
100	Co-op 39 [Crimson Crisp [®]]	2n	USA	2004	Recent	Sel. 669.205 × PCF W2134	401	LB, UB	41; 56
101	Co-op 43 [Juliet [®]]	2n	USA	1999	Recent	Viking × PRI 1018-101	403	LB, VA	41; 54
102	Coquette	2n	France	1948	Old	—	942	JL, NFC	25
103	Cornish Gilliflower (Syn. Calville d'Angleterre)	2n	UK	1813	Historic	—	795	NFC, SLU	25
104	Cortland	2n	USA	1898	Historic	Ben Davis × McIntosh	387	KN, NFC	25
105	Coulombs Renette	3n	Belgium	1856	Historic	Kasseler Renette × unknown	23	AGES, KOB, NFC	32; 43
106	Cox Orange	2n	UK	Around 1825	Historic	Ribston Pepping × Goldenette von Blenheim (?)	445	KOB, NFC	43
107	Cox Pomona	2n	UK	Around 1825	Historic	Ribston Pepping × unknown (?)	446	NFC, OKR	25
108	CPRO066	2n	Netherlands	2000s (in trials)	Recent	—	579	HG, LB	57
109	Cripps Pink [Pink Lady [®]]	2n	Australia	1973	Recent	Golden Delicious × Lady Williams (CC)	169	3LB	12; 26; 54
110	Cripps Red [Joya [®]]	2n	Australia	1991	Recent	Golden Delicious × Lady Williams (CC)	171	2LB	12; 54
111	Daiane	2n	Brazil	2000	Recent	Gala ^(C) × Princessa	411	LB, UB	41; 54
112	Daliclass	2n	France	2008	Recent	Eistar × Pilot (CC)	580	HG, LB	41; 54
113	Dalilight	2n	France	2007	Recent	Eistar × Cripps Pink (CC)	581	HG, LB	41; 54
114	Dalmibel [Antares [®]]	2n	France	1998	Recent	Eistar ^(C) × unknown	384	KN, LB	54
115	Dalimco	2n	France	2003	Recent	—	475	LB, VA	54
116	Dalinette [Choupette [®]]	2n	France	2002	Recent	X-4598 × X-3174	476	LB, VA	39; 54
117	Dalinsweet	2n	France	2004	Recent	—	988	FEM, UB	54
118	Dalitron [Altess [®]]	2n	France	2005	Recent	Golden Delicious × Pilot (CC)	418	LB, VA	41; 56
119	Damasonrenette	3n	France	1628 (?)	Historic	—	38	ACW, AGES, HG, RW	25
120	Danziger Kantapfel	2n	Poland	1760	Historic	—	62	BOKU, LB	25
121	Dayton (Co-op 21)	2n	USA	1988	Recent	—	692	2UB	43
122	De Bonde	2n	France	Early 1900	Old	—	941	JL, NFC	25
123	De l'Estre	2n	France	Late 1700s	Historic	—	761	BVC, 2LB	25
124	Decio (GM4)	2n	Italy	1500s (?)	Historic	—	574	NFC, UB, VA	25

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
125	Delblush [Tentation [®]]	2n	France	1989	Recent	Golden Delicious × Blushing Golden (CC)	290	LB, VA	12; 54
126	Delcorf [Delbardestivale [®]]	2n	France	1977	Recent	Stark Longrimes × Golden Delicious ^(C)	381	KN, LB, NFC	12; 34
127	Delcoros [Autento [®]]	2n	France	2001	Recent	Delgollune × Cox Orange (CC)	410	LB, VA	41; 54
128	Dearly	2n	France	1988	Recent	Golden Delicious × Stark Earliest (CC)	—	FEM, UB	12; 54
129	Delfloki [Divine [®]]	2n	France	1999	Recent	Golden Delicious × Stark Earliest (CC)	995	LB, VA	54
130	Delflopion	2n	France	2004	Recent	—	412	LB, VA	54
131	Delgollune (Syn. Jubile [®])	2n	France	1981	Recent	Golden Delicious ^(C) × Lundbytrop Golden (CC)	812	BSA, NFC	12; 54
132	Delgrared	2n	France	1986	Recent	Golden Delicious × Akane (CC)	585	CRéSO, LB	41; 54
133	Deljuga	2n	France	2000	Recent	Gala × Delgollune (CC)	582	HG, LB	41; 54
134	Delorgue	2n	France	1990	Recent	—	841	BSA, NFC	54
135	Delorina [Harmonie [®]]	2n	France	1985	Recent	Blushing Golden × Florina (CC)	404	LB, VA	25
136	Delrouval [Cybele [®]]	2n	France	1989	Recent	Delcorf × Akane (CC)	641	LB, UB	12; 54
137	Deltana	2n	France	2004	Recent	Florina × Granny Smith (CC)	583	HG, LB	20; 54
138	Democrat	2n	Australia	Around 1900	Historic	—	962	NFC, 2UB	25
139	Devonshire Quadrorden	2n	UK (?)	1676	Historic	—	693	NFC, UB	25
140	Directeur Lesage	2n	Belgium (?)	Before 1949	Old	Oberländer Himbeer-apfel × Weißer Klarapfel (CC)	939	JL, NFC	20; 44
141	Discovery	2n	UK	Around 1949	Old	Worcester Parmäne × Schöner aus Bath (CC)	390	KN, NFC	25
142	Dolgo	2n	Norway	1988	Recent	—	985	2UB	55
143	Doppelter Prinzenapfel	3n	Germany	Before 1889	Historic	Prinzenapfel × unknown	314	ACW, KOB, TR	4; 48
144	Doriane	2n	France	2000	Recent	X-6823 × X-4638	473	LB, VA	13; 34
145	Drap d'Or	2n	France	1863	Historic	—	673	JL, NFC	25
146	Dülmener Rosenapfel	2n	Germany	1870	Historic	Kasseler Renette × Petite Madeleine	166	AGES, NFC	20; 49
147	Durello	2n	Italy	1949	Old	—	576	NFC, UB, VA	25
148	Ecolette	2n	Netherlands	1990	Recent	Elstar × Prima (CC)	465	LB, VA	12; 54
149	Edelböhmer	2n	Italy, South Tyrol (?)	Before 1850	Historic	—	245	FEM, HG, LB	30

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
150	Edelborsdorfer (Syn. Maschanzker)	2n	Germany	1500s	Historic	–	67	MSPP, PVW, SEGE	44; 47
151	Edelroter	2n	Italy, South Tyrol	1850	Historic	–	85	LB, TR	30
152	Egremont Russet	2n	UK	1872	Historic	–	896	BSA, NFC, UB	25
153	Eir	2n	Norway	1999	Recent	Katja ^(C) × Buckley Giant	839	BSA, SLU	12; 54
154	Elektra	2n	Germany	1930s	Old	Cox Orange × Geheimrat Dr. Oldenburg (CC)	776	BSA, NFC	34 (p. 13); 49
155	Elise [Roblos [®]]	2n	Netherlands	1974	Recent	Septet × Cox Orange (CC)	506	LB, UB	26
156	Ellisons Orange	2n	UK	1904	Old	Cox Orange × Cellini (CC)	7	NFC, SLU, UB	25; 32
157	Elstar	2n	Netherlands	1955	Recent	Golden Delicious × Ingrid Marie (CC)	102	KN, LB, NFC	43
158	Empire	2n	USA	1945	Old	McIntosh × Red Delicious (CC)	994	ACW, NFC, UB	25
159	Engelsberger	2n	Germany	1854	Historic	–	742	BB, BSA, KOB, TR	44
160	Engelstar	2n	Germany	1997	Recent	–	779	2BSA	54
161	Enterprise (Co-op 30)	2n	USA	1993	Recent	PRI 1661-2 × PRI 1661-1	688	2UB	23; 43
162	Erbachhofer	2n	Germany	1925	Old	–	288	KN, KOB, LB	17
163	Ernst Bosch	2n	Germany	Around 1900	Historic	Manks Apfel × Ananas Renette	613	ACW, KOB, NFC	49
164	Erwin Bauer (Syn. Roba)	2n	Germany	1930s	Old	Geheimrat Dr. Oldenburg ^(C) × unknown	768	2BSA, KOB, NFC	49
165	Esopus Spitzenburgh	2n	USA	Before 1790	Historic	–	963	NFC, TR	25
166	Eva (U1215)	2n	Hungary	After 1950	Recent	Jonathan ^(C) × unknown	618	KOB, TR	43 (p. 87, 179)
167	Falchs Gulderling ^g	2n	Austria	Around 1880	Historic	–	270	AGES, HG, KN, OKR	8
168	Fameuse (Syn. Schneeapfel)	2n	Canada (?)	Around 1730	Historic	–	460	BVC, TR	25
169	Fantazia	2n	Poland	1944	Old	McIntosh ^(C) × Linda	826	NFC, SLU	25
170	Faros	2n	France	1800s	Historic	–	898	JL, NFC, TR	25
171	Fearns Pippin	2n	UK	Before 1780	Historic	–	893	BVC, NFC	25
172	Fenouillet Rouge	2n	France (?)	1873	Historic	–	937	JL, NFC	25
173	Fießers Erstling	2n	Germany	1898	Historic	Bismarckapfel × unknown	536	KOB, TR	17
174	Fiesta	2n	UK	1972	Recent	Cox Orange × Idared (CC)	389	KN, NFC	25
175	Filipa	2n	Denmark	1877	Historic	–	800	NFC, SLU	49

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
176	Finkenwerder Prinzenapfel	2n	Germany	Around 1860	Historic	—	592	KOB, NFC, OKR	43
177	Florianer Rossmarin	2n	Austria	Around 1860	Historic	—	269	AGES, KN, LB	7
178	Florina [Querina [®]]	2n	France	1977	Recent	PRI 612-1 × Jonathan ^(C)	262	KN, LB	12; 13; 54
179	FN 3505-130	2n	n.a.	n.a.	Recent	—	730	LB, PEM	57
180	FN 3505-324	2n	n.a.	n.a.	Recent	—	731	LB, PEM	57
181	Forlady	2n	Italy	2006	Recent	Forum × Lady Williams ^(C)	480	LB, VA	41; 54
182	Frauotacher (Syn. Franc Roseau, Chataigne de Leman)	2n	Switzerland or France	Before 1850	Historic	—	75	ACW, NFC, RW	25
183	Freedom (NY58553-1)	2n	USA	1983	Recent	—	679	2UB	43
184	Fresco (CPRQ47) [Wellant [®]]	2n	Netherlands	2002	Recent	Selezione × Elise ^(C)	490	HG, LB	41; 54
185	Freyberg	2n	New Zealand	1934	Old	Golden Delicious × Cox Orange (CC)	806	JL, NFC	25
186	Friedrich von Baden	2n	Germany	1894	Historic	Bismarckapfel × unknown	56	KOB, SLU	49
187	Fronnms Goldrenette (Syn. Seebaer Borsdorfer)	3n	Germany	1869	Historic	Edelborsdorfer × unknown	714	BB, OKR, TR	26; 47
188	Frueru [Red Boy [®]]	2n	Switzerland	2002	Recent	Redwinter × Rafzubin ^(C)	500	LB, UB	41; 54
189	Fujii	2n	Japan	1962	Recent	Ralls Janet × Red Delicious ^(C)	154	CIV, FEM, KN, LB	49
190	Fujion	2n	Italy	2011	Recent	UTL-7 × H-2	810	CIV, LB	41; 56
191	G120	2n	Italy	2000s (in trials)	Recent	Gala × Liberty (CC)	514	HG, LB	57
192	Gaia	2n	Italy	2012	Recent	Gala ^(C) × A3-7	832	CIV, LB	41; 56
193	Gala	2n	New Zealand	1934	Old	Kidds Orange × Golden Delicious (CC)	205	KN, LB	43
194	Galloway Pepping	3n	UK	1871	Historic	—	147	KOB, NFC, OWL	25
195	Galmac [Camelot [®]]	2n	Switzerland	1986	Recent	Gala × Jerseymac (CC)	406	CRESO, LB	6
196	Gamhong	2n	South Korea	1998	Recent	—	409	LB, UB	54
197	Gartenmeister Simon	2n	Germany	1939	Old	—	752	BSA, KOB, OKR	49
198	Gascoynes Scharlachsämling	2n	UK	1871	Historic	—	4	AGES, KOB, NFC	25
199	Geflampter Kardinal	3n	Germany	1801	Historic	—	165	AGES, HG, KOB	17
200	Geheimrat Breuhahn	2n	Germany	1895	Historic	Halberstädter Jungfern-apfel × unknown	600	BSA, KOB, NFC	49
201	Geheimrat Dr. Oldenburg	2n	Germany	1897	Historic	Minister von Hammerstein × Baumanns Renette	264	ACW, BOKU	43

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
202	Gehrers Rambur	3n	Germany	Around 1885	Historic	Roter Trierscher Weinapfel × unknown (?)	535	HG, KOB	43
203	Gelber Bellefleur	2n	USA	Around 1790	Historic	—	317	AGES, AN, BOKU, LB, RW	26
204	Gelber Edelapfel (Syn. Golden Noble)	2n	UK	1820	Historic	—	201	AGES, LB	25
205	Gelber Münsterländer Borsdorfer	2n	Germany	Before 1951	Old	—	863	BB, TR	44; 47
206	Gelber Richard	2n	Germany	1874	Historic	—	233	LB, OKR	26
207	Gemini	2n	Italy	2011	Recent	Gala ^(C) × A3-7	809	CIV, LB	41; 56
208	Geneva Crab	2n	Canada	1930	Old	—	472	BVC, LB	31
209	George Cave	2n	UK	1923	Old	—	593	KOB, NFC	25
210	Gerlinde	2n	Germany	1994	Recent	Eistar ^(C) × TSR15T3	978	OKR, UB	12; 22; 54
211	Gestreifter Titowka	2n	Russia	1876	Historic	—	567	KOB, TR	44
212	Gewürzluiken	2n	Germany	Around 1885	Historic	—	164	AGES, KOB, LB	17
213	Ginger Gold	2n	USA	1995	Recent	Golden Delicious ^(C) × unknown	738	FEM, UB	39; 54
214	Glockenapfel	2n	Germany (?)	Before 1900 (?)	Historic	—	447	AGES, BOKU, KN, RW	43
215	Gloria Mundi	2n	USA (?)	1804	Historic	—	448	NFC, TR	25
216	Glorie von Holland	2n	Netherlands	Around 1890	Historic	—	601	KOB, NFC, TR	25
217	Gloster	2n	Germany	1951	Recent	Glockenapfel × Red Delicious (CC)	383	KN, NFC	43
218	Gold Pink [Gold Chief [®]]	2n	Italy	1998	Recent	Red Delicious × Golden Delicious (CC)	414	LB, VA	41; 54
219	Golden Delicious	2n	USA	Around 1890	Historic	Grimes Golden ^(C) × unknown	112	KN, KOB, LB	25; 39
220	Golden Orange	2n	Italy	1979	Recent	Golden Delicious ^(C) × PRI 1956-6	398	LB, VA	23
221	Golden Russet of Western New York	2n	USA	1905	Old	—	1039	NFC, UB	25
222	Goldor	2n	France	2001	Recent	—	590	LB, UB	54
223	Goldparmäne (Syn. King of the Pippins)	2n	France (?)	Before 1700	Historic	—	97	ACW, AN, BOKU, HG, JL, LB, RW, UB	43
224	Goldrenette von Blenheim	3n	UK	Around 1740	Historic	Golden Reinette × unknown	25	ACW, NFC	25; 32
225	Goro	2n	Switzerland	1972	Recent	Golden Delicious × Schweizer Orangen (CC)	130	JL, OKR	6

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
226	Grahams Jubiläumsapfel	2n	UK	1888	Historic	–	281	HG, KOB, LB	25
227	Granny Smith	2n	Australia	1868	Historic	–	34	KN, LB	25
228	Graue Herbstrenette (Syn. Reinette Gris d'Angleterre)	3n	UK (?)	1670	Historic	–	45	AN, HG, NFC	25
229	Graue Portugiesische Renette	2n	Germany	1798	Historic	–	355	ACW, RW, TR	44
230	Gravensteiner	3n	Denmark (?)	1669	Historic	–	186	ACW, AGES, AN, BOKU, HG, LB, RW	43
231	Greensleeves	2n	UK	1966	Recent	James Grieve × Golden Delicious (CC)	1034	NFC, TR	25
232	Grenadier	2n	UK	1862	Historic	–	894	BVC, NFC, UB	25
233	Grimes Golden	2n	USA	1832	Historic	–	705	JL, NFC	25
234	Gris Canavoit	2n	Italy, Piemonte	n.a.	Historic	(local)	357	BVC, MSPP, UB	11
235	Großer Apfel	2n	France (?)	1873 (?)	Historic	–	897	JL, NFC	25
236	Grüner Stettiner	3n	n.a.	Around 1700	Historic	–	151	AGES, KN	26
237	Halberstädtner Jungfern-apfel	2n	Germany	1885	Historic	–	564	KOB, NFC	25
238	Hansaprinz	3n	Germany	n.a.	Historic	(local)	1071	KOB, TR	38
239	Hansens baccata #2	2n	Former Soviet Union	n.a.	<i>M. baccata</i>	–	211	FEM, LB	33
240	Hartert Renette	3n	Germany	1828	Historic	Golden Reinette × unknown	79	HG, LB, NFC	25; 32
241	Harmensz. (Vrdso401) [Rembrandt [®]]	2n	Netherlands	2006	Recent	–	499	HG, LB	54
242	Hausmütterchen	3n	Ukraine	1805	Historic	–	701	KOB, TR	8
243	Haukäpfel	2n	Germany	1920s	Old	Roter Trierscher Weinapfel ^(C) × unknown	780	BSA, KOB	43
244	Heimenhofer	2n	Switzerland	1800s	Historic	–	755	ACW, FEM, HG	6
245	Helios	2n	Germany	1930s	Old	Geheimrat Dr. Oldenburg ^(C) × unknown	822	BSA, NFC	49
246	Herma	2n	Germany	1930s	Old	Jonathan ^(C) × unknown	825	BSA, NFC	49
247	Herzogin Olga	2n	Germany	1860	Historic	–	787	KOB, TR	17
248	Heslacher Gereutapfel	2n	Germany	Around 1820	Historic	Luikenapfel × unknown (?)	786	BSA, TR	17
249	Hibernal	3n	Russia or USA	1880	Historic	–	616	KOB, NFC, OKR	25
250	Himbeerapfel aus Holzovous	2n	Czech Republic	Around 1850	Historic	–	202	KN, OWL	16

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
251	Holsteiner Cox	3n	Germany	Around 1920	Old	Cox Orange × unknown (?)	769	BSA, NFC, OKR	32; 43
252	Horneburger Pflämkuchenapfel	3n	Germany	Around 1850	Historic	Boikenapfel × unknown	89	KOB, NFC, OKR	25; 32
253	Idared	2n	USA	1935	Old	Jonathan × Wagener Apfel (CC)	263	KN, LB	43
254	Iduna	2n	Switzerland	1971	Recent	Golden Delicious × Glockenapfel (CC)	820	BSA, NFC	6
255	Idunn	2n	Norway	1999	Recent	Katja ^(C) × Buckley Giant	836	BSA, SLU	12; 54
256	Ilzer Rosenapfel	2n	Austria	n.a.	Historic	—	243	HG, KN, ZASS	8
257	Ingol	2n	Germany	1954	Recent	Ingrid Marie × Golden Delicious (CC)	672	2UB	43
258	Ingrid Marie	2n	Denmark	1910	Old	Cox Orange × Cox Pomona (CC)	449	AGES, KN	19; 40; 43
259	Initial	3n	France	1998	Recent	Gala × Redfree	481	LB, VA	12; 54
260	Ivette	2n	Netherlands	1958	Recent	Golden Delicious × Cox Orange (CC)	611	KOB, NFC, UB	25; 49
261	Jakob Fischer	3n	Germany	1903	Old	—	309	BSA, KOB, OKR	43
262	Jakob Lebel	3n	France	1825	Historic	—	298	ACW, AN, HG, RW	43
263	Jamba 69	2n	Germany	1954	Recent	Melba × James Grieve (CC)	116	KN, NFC	43
264	James Grieve	2n	UK	1893	Historic	Cox Orange ^(C) × Potts Sämling	203	ACW, AGES, BOKU	13; 25
265	Jeanne Hardy	2n	France	1878	Historic	Kaiser Alexander × unknown	704	JL; parentage analysis	49
266	Jerseymac	2n	USA	1956	Recent	—	382	KN, VA	25
267	Jonafree (Co-op 22)	2n	USA	1979	Recent	PRI 855-102 × NI31	760	BSA, UB	39; 43
268	Jonagold	3n	USA	1943	Old	Golden Delicious × Jonathan	81	KN, LB, MSPP	15; 32
269	Jonathan	2n	USA	1826	Historic	Esopus Spitzenburgh × unknown (?)	330	BOKU, KN, LB	25
270	Joseph Musch	3n	Belgium	1872	Historic	Baumanns Renette × unknown	614	JL, KOB, NFC	43
271	Julia	2n	Czech Republic	1986	Recent	Quintet × Discovery ^(C)	773	BSA, OWL	12; 13; 54
272	July Red	2n	USA	1949	Old	(Peterel × Early McIntosh) × (Lady Williams × Starr)	517	LB, NFC	25
273	Jupiter	3n	UK	1966	Recent	Cox Orange × Red Delicious	845	NFC, TR	25; 32
274	Kaiser Alexander	2n	Ukraine (?)	1700s	Historic	—	19	BOKU, KN	25
275	Kaiser Wilhelm	3n	Germany	1864	Historic	Golden Reinette × unknown	24	AGES, KN	32; 43

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
276	Kalterer Böhmer	2n	Italy, South Tyrol	Around 1850	Historic	—	248	BOKU, HG, LB, MSPP	30
277	Kanada Renette	3n	France (?)	1771	Historic	—	83	ACW, AN, BOKU, HG, LB, MSPP	43
278	Kandil Sinap	2n	Russia	Early 1800s	Historic	—	282	BVC, NFC, OWL	25
279	Kansas Queen (Syn. Nouvelle Europe)	2n	USA	Before 1870	Historic	—	938	JL, NFC, TR	25
280	Kardinal Bea	2n	Germany	Around 1930	Old	—	450	KN, KOB	26
281	Kardinal Graf Galen	2n	Germany (?)	After 1946 (?)	Old?	—	538	BOKU, TR	1
282	Karmeliter Renette	2n	France	1667	Historic	—	219	LB, TR	49
283	Karmijn de Sonnaville	3n	Netherlands	1948	Old	Cox Orange × Jonathan	451	KN, KOB, NFC	32; 43
284	Karneval	2n	Czech Republic	2007	Recent	Vanda × Cripps Pink ^(C)	640	ACW, LB	41; 54
285	Kasseler Renette	2n	Germany (?)	1853	Historic	—	167	ACW, RW	26
286	Katja	2n	Sweden	1947	Old	James Grieve × Worcester Parlane (CC)	617	KOB, NFC	25
287	Katrina	2n	Norway	1997	Recent	—	814	BSA, SLU	54
288	Kidds Orange	2n	New Zealand	1924	Old	Red Delicious × Cox Orange (CC)	544	BSA, NFC, RW	25
289	King of Tompkins County	3n	USA	1804	Historic	Esopus Spitzenburg × unknown	943	BVC, NFC, TR	25; 32
290	Klöcher Maschanzer	3n	Austria	1800s	Historic	Steirischer Maschanzer × unknown	37	AGES, HG, LB, KN, OIKOS, SGB	45; 47
291	Königinapfel (Syn. Queen)	2n	UK	1858	Historic	—	13	AGES, KOB	25
292	Königlicher Kurzstiel	2n	Europe	Around 1613	Historic	—	115	KOB, NFC, RW	25
293	Konstanzer (Syn. Schnabelsapfel)	2n	Germany	1790	Historic	—	539	AGES, KOB, TR	17
294	Köstlicher von Zallinger	2n	Italy, South Tyrol	1800s	Historic	—	277	LB, MSPP, UB	30
295	Krippele Apfel (Syn. Kleiner Apf)	2n	Italy, South Tyrol	1800s	Historic	—	267	JL, LB, NFC, TR	30; 38
296	Kronprinz Rudolph	2n	Austria	Around 1860	Historic	—	268	BOKU, HG, LB, RW	17
297	Krügers Dickstiel	2n	Germany	Around 1850	Historic	—	624	BSA, NFC, OKR	17
298	La Flamboyante [Mairac [®]]	2n	Switzerland	1986	Recent	Gala × Maigold (CC)	195	LB, UB	6

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
299	Lady Williams	2n	Australia	Around 1935	Old	—	570	NFC, UB	25
300	Landsberger Renette	2n	Poland	Around 1850	Historic	—	5	AGES, HG, ZASS	43
301	Lanes Prinz Albert	2n	UK	Before 1841	Historic	Nonpareil × Wellington (?)	903	NFC, SLU	25
302	Latvianaler Bananenapfel (Syn. American Mother)	2n	USA	1844	Historic	Cox Orange × unknown (?)	64	AGES, BOKU, HG, KN, ZASS	25; 26
303	Laxtons Exquisit	2n	UK	1902	Old	Cellini × Cox Orange (CC)	887	NFC; parentage analysis	25
304	Laxtons Superb	2n	UK	1897	Historic	Cellini × Cox Orange	225	KOB, NFC, OKR	25; 46
305	Leathercoat Russet (= Reinette Parmentier)	3n	UK	Before 1949	Old	—	427	ACW, BVC, JL, NFC	25
306	Leunapfel	2n	Switzerland (?)	1855	Historic	—	540	ACW, RW, TR	6
307	Liberty (NY55140-19)	2n	USA	1978	Recent	Macoun ^(C) × Purdue 54-12	261	KN, ZASS	43
308	Ligol	2n	Poland	1991	Recent	Linda × Golden Delicious ^(C)	413	LB, VA	12; 54
309	Ligolina	2n	Poland	1998	Recent	Linda × Golden Delicious ^(C)	507	BSA, LB	13; 54
310	Limoncella	2n	Italy	Antique origin (?)	Historic	—	680	3UB	25; 28
311	Linsenhofer Sämling	2n	Germany	Before 1950	Old	Goldparmäne ^(C) × unknown (?)	775	BSA, KOB	38; 43
312	Lodi	2n	USA	1911	Old	Montgomery × Weißer Klarapfel ^(C)	595	KOB, NFC, SLU	25
313	Lohrer Rambur (Syn. Schwäbheimer Rambur)	3n	Germany	Around 1900	Historic	—	774	BSA, OKR, TR	27
314	Lombarts Kalvill	2n	Netherlands	1906	Old	Weißer Winterkalvill ^(NC) × unknown (?)	610	KOB, NFC, OKR	25
315	London Pepping	2n	UK	1500s	Historic	—	297	AGES, BOKU, HG	25
316	Lord Derby	2n	UK	1862	Historic	—	901	HG, NFC, TR	25
317	Lord Lambourne	2n	UK	1907	Old	James Grieve × Worcester Parmäne (CC)	452	BOKU, NFC	25
318	LUB A11706	2n	Switzerland	2000s	Recent	Weirouge ^(C) × Series Re	637	LAG, LB	41
319	Luna [Top Gold [®]]	2n	Czech Republic	2002	Recent	Topaz × Golden Delicious (CC)	467	LB, VA	41; 54
320	Lurefresh (LUB A2605) [Era [®] /Redlove [®]]	2n	Switzerland	2009	Recent	Weirouge ^(C) × Series Re	638	LAG, LB, SKS	41; 54
321	Luregust [Calypso [®] /Redlove [®]]	2n	Switzerland	2014	Recent	Weirouge ^(C) × Series Re	636	LAG, LB	41; 56

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
322	Lureprec (LUB A0905) [Circe®/Redlove®]	2n	Switzerland	2009	Recent	Weirouge ^(C) × Series Re	830	LAG, LB	41; 54
323	Luresweet [Odysso®/Redlove®]	2n	Switzerland	2014	Recent	Weirouge ^(C) × Series Re	639	LAG, LB	41; 56
324	Luxemburger Renette (Syn. Coastresse)	2n	Luxembourg	Around 1800	Historic	—	541	BOKU, JL	9; 21 (p. 706)
325	Luxemburger Triumph (Syn. Doppelte Luxemburger Renette)	3n	Luxembourg	Around 1860	Historic	Luxemburger Renette × unknown (?)	565	NFC, OKR, TR	9
326	M.1	2n	UK	Around 1912	Rootstock	—	866	BSA, EMR	29; 34 (p. 16)
327	M.2	2n	UK	Around 1912	Rootstock	—	296	BSA, EMR	29; 34 (p. 16)
328	M.3	2n	UK	Around 1912	Rootstock	—	340	BSA, EMR	29; 34 (p. 16)
329	M.4	2n	UK	Around 1912	Rootstock	—	299	BSA, EMR	29; 34 (p. 16)
330	M.6	2n	UK	Around 1912	Rootstock	—	272	BSA, EMR	29; 34 (p. 16)
331	M.7	2n	UK	Around 1912	Rootstock	—	341	BSA, EMR	29; 34 (p. 16)
332	M.8	2n	UK	Around 1912	Rootstock	—	710	BSA, EMR	29; 34 (p. 16)
333	M.9	2n	UK	Around 1912	Rootstock	—	711	BSA, LB	29; 34 (p. 16)
334	M.11	2n	UK	Around 1912	Rootstock	—	846	BSA, EMR	29; 34 (p. 16)
335	M.13	2n	UK	Around 1912	Rootstock	—	332	BSA, EMR	29; 34 (p. 16)
336	M.14	2n	UK	Around 1912	Rootstock	—	335	BSA, EMR	29; 34 (p. 16)
337	M.16	2n	UK	Around 1912	Rootstock	—	336	BSA, EMR	29; 34 (p. 16)
338	M.20	2n	UK	1924	Rootstock	—	338	BSA, EMR	29
339	M.26	2n	UK	1959	Rootstock	M.16 × M.9 (CC)	847	BSA, EMR	29; 50
340	M.27	2n	UK	1975	Rootstock	M.13 × M.9 (CC)	823	BSA, EMR, NFC	29; 50
341	Macoun	2n	USA	1909	Old	McIntosh ^(C) × Jersey Black	604	KOB, NFC	26
342	Magnolia Gold	2n	USA	1960	Recent	Golden Delicious ^(C) × unknown	992	NFC, UB	25
343	Maigold	2n	Switzerland	1964	Recent	Frauotacher × Golden Delicious (CC)	349	LB, NFC	6
344	Majesty (YX4-CIV PJ 1)	2n	Italy	2013	Recent	Co-op 25 × CIVCP-142	725	CIV, FEM, LB, SKS	56
345	Malling Kent	2n	UK	1949	Old	Cox Orange ^(C) × unknown (not Jonathan.)	817	BSA, NFC	25; 39
346	<i>Malus floribunda</i> 821	2n	Japan	n.a.	<i>M. floribunda</i>	—	3	FEM	33
347	Manet	2n	Canada	1928	Old	Tetofsky × unknown	816	NFC, SLU	43

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
348	Margol	2n	Germany	1968 or 1986	Recent	Ingrid Marie × Golden Delicious (Gloster × Meiprincess) × Elstar ^(C)	842	BSA, NFC	26; 38
349	Marielle (Riky2000) [Lola [®]]	2n	Netherlands	2007	Recent	Maigold × Arlet (CC)	498	HG, LB	41; 54
350	Mariella (ACW 06375)	2n	Switzerland	1982	Recent	Kidds Orange × Idared (CC)	577	HG, LB	52
351	Marina	2n	Switzerland	1970	Recent	Cox Orange × unknown (?)	631	LB, UB	6
352	Martini	2n	Germany	1875	Historic		603	KOB, NFC	17
353	Mauks Hybride	2n	Germany	n.a.	Historic?		758	BSA, HG, KOB	57
354	Maunzenapfel	2n	Germany	Before 1928	Old	—	236	KN, ZASS	17
355	May Queen	2n	UK	1888	Historic	—	895	BVC, NFC	25
356	McIntosh	2n	Canada	1796	Historic	—	386	KN, NFC	43
357	Megumi	2n	Japan	1931	Old	Ralls Janet × Jonathan ^(C)	983	2UB	44
358	Melba	2n	Canada	1898	Historic	McIntosh × unknown	598	JL, KOB, NFC	25
359	Melrose	2n	USA	1932	Old	Jonathan × Red Delicious (CC)	391	JL, KN	43
360	Meran	2n	Italy	1976	Recent	Golden Delicious × Jonathan (CC)	137	KN, LB, NFC	5
361	Merton Worcester	2n	UK	1914	Old	Cox Orange × Worcester Par-mäne (CC)	959	NFC, TR, UB	25
362	Millers Seedling	2n	UK	1848	Historic	—	764	BSA, HG	25
363	Millicent Barnes	2n	UK	Around 1903	Old	Gascoynes Scharlachsämling ^(NC) × Cox Orange ^(C)	596	KOB, NFC, TR	25
364	Milwa [Junami [®] /Diwa [®]]	2n	Switzerland	1982	Recent	(Idared × Maigold) × Elstar ^(C)	220	LB, VA	6; 41
365	Minister von Hammerstein	2n	Germany	1882	Historic	Landsberger	17	AGES, KN	25
366	Minnieska [Sweetango [®]]	2n	USA	2005	Recent	Renette × unknown			
367	Minnewashta [Zestar [®]]	2n	USA	1997	Recent	Honeycrisp × Minnewashta ^(C)	508	HG, LB	41; 56
368	Mio	2n	Sweden	1932	Old	State Fair × MN 1691	522	LB; parent to Minneiska	56
						Worcester	837	NFC, SLU	25
369	MM.101	2n	UK	1950s		Parmäne ^(C) × Oranie			
370	MM.102	2n	UK	1950s		Rootstock	343	BSA, EMR	29
371	MM.104	2n	UK	1950s		Northern Spy ^(C) × unknown	344	BSA, EMR	29
372	MM.105	2n	UK	1950s		Rootstock	346	BSA, EMR	29; 50
373	MM.106	2n	UK	1950s		Northern Spy ^(C) × unknown	347	BSA, EMR	29
						Rootstock	284	BSA, EMR	29; 50

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
374	MM.109	2n	UK	1950s	Rootstock	Northern Spy × M.2 (CC)	434	EMR; parentage analysis	29; 50
375	MM.110	2n	UK	1950s	Rootstock	Northern Spy ^(C) × unknown	551	BSA, EMR	29
376	MM.111	2n	UK	1950s	Rootstock	Northern Spy ^(C) × Merton 793	708	BSA, EMR	29; 50
377	MM.115	2n	UK	1950s	Rootstock	Northern Spy × Ben Davis (CC)	366	BSA, EMR	24; 29
378	Monroe	2n	USA	1910	Old	Jonathan × Morgenduft (CC)	1018	NFC; parentage analysis	25
379	Morgenduft (Syn. Rome Beauty)	2n	USA	1817	Historic	–	181	KN, LB, NFC	25
380	Muskatrenette	2n	France (?)	1608	Historic	–	213	KOB, LB	17
381	Mutsu (Syn. Crispin)	3n	Japan	1930	Old	Golden Delicious × Indo	682	NFC, 2UB	43
382	My Gold	2n	n.a.	n.a.	Recent	–	727	LB, PEM	57
383	Nathusius Taubenapfel	2n	Germany	1824	Historic	–	63	OKR, TR	17
384	Nebuta	2n	Japan	1981	Recent	Kitakami × Tsugaru	980	NFC, UB	25
385	Nevison [Sonya [®]]	2n	New Zealand	1996	Recent	Gala ^(C) × Red Delicious ^(NC)	68	LB, UB	39; 56
386	Nicogreen [Greenstar [®]]	2n	Belgium	2001	Recent	Delcorf × Granny Smith (CC)	32	LB, VA	41; 56
387	Nicola	2n	Canada	2005	Recent	Gala × Splendour (CC)	420	LB, VA	41; 54
388	Nicoter [Kanzi [®]]	2n	Belgium	2001	Recent	Gala × Braeburn (CC)	198	LB, VA	41; 56
389	Nonpareil	2n	France (?)	1500s	Historic	–	934	2JL, NFC	25
390	Northern Spy	2n	USA	Around 1800	Historic	–	283	NFC, UB	25
391	Obelisk (Syn. Flamenco)	2n	UK	1991	Recent	(Cox Orange × Königlicher Kurzstiel) × McIntosh ^(C) , Wijcik	844	BSA, NFC	25
392	Oberdiecks Renette	2n	Germany	Around 1850	Historic	–	122	BOKU, KOB	17
393	Oberländer Himbeerapfel	2n	Germany	1854	Historic	–	756	JL, KOB, SLU	17
394	Oberlausitzer Muskat-renette	2n	Germany	Before 1938	Old	–	594	KOB, NFC, TR	38
395	Odenwälder	2n	Germany (?)	n.a.	Historic?	–	28	AGES, KN, KOB	17
396	Öhringer Blutstreifling	2n	Germany	Around 1860	Historic	–	753	BSA, KOB, OKR	26
397	Ontario	2n	USA	1874	Historic	Wagner Apfel × Northern Spy	238	ACW, BOKU, LB, RW	43
398	Orangenburg	2n	Germany	1930	Old	Cox Orange × Geheimrat Dr. Oldenburg (CC)	605	KOB, NFC, TR	49
399	Oriole	2n	USA	1914	Old	–	905	JL, NFC, TR	25
400	Orion	3n	Czech Republic	2006	Recent	Golden Delicious × Otava	765	FEM, LB	41; 56

Table 2 (Continued)

No.	Cultivar name [Trademark name ^a]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
401	Orleans Renette	3n	France (?)	1776	Historic	Golden Reinette × unknown	606	JL, KOB, NFC	25; 32
402	Osnabrücker Renette	3n	Germany	Before 1802	Historic	—	111	ACW, AGES, KN	25
403	Ostpreußischer Adamsapfel	2n	Germany	Before 1936	Old	—	591	KOB, NFC	38
404	Otava	2n	Czech Republic	1988	Recent	Shampion × Jonala	303	LB; parent to Orion	38; 54
405	Pamyat Syubarovoj	2n	Russia	1992	Recent	—	663	LB, UB	54
406	Parfum d'Ète	2n	Belgium	2002	Recent	—	818	BSA, NFC	54
407	Parkers Pepping	2n	UK	Early 1800	Historic	—	301	AN, NFC	25
408	Peasgood Sondergleichen	2n	UK	1853	Historic	—	369	ACW, JL, KN	25
409	Pfaffenhofer Schmelzling	2n	Germany	Around 1900	Historic	—	555	KOB, OKR	10
410	Pfirsichroter Sommerapfel	2n	France (?)	1837	Historic	—	573	BSA, KOB, NFC	17
411	Pia	2n	Germany	1992	Recent	Idared × Helios (CC)	739	FEM, UB	26
412	Pigeon de Jérusalem (Syn. Roiter Winterbaubapfel)	2n	France	Late 1600s (?)	Historic	—	936	JL, NFC	25
413	Pikant	2n	Germany	1962	Recent	Undine ^(C) × Kalco	815	BSA, SLU	26
414	Pikkolo	2n	Germany	1993	Recent	Clivia × Tumanga ^(C)	989	BSA, NFC	25
415	Pilot	2n	Germany	1962	Recent	Clivia × Undine ^(C)	208	KN, LB	26
416	Pimona	2n	Germany	1962	Recent	Clivia × Undine ^(NC)	813	BSA, SLU	26
417	Pingo	2n	Germany	1995	Recent	Idared × Bancroft (CC)	734	FEM, OKR	26
418	Pink Pearl	2n	USA	1944	Old	—	1032	ACW, BVC	51
419	Pinova	2n	Germany	1965	Recent	Clivia × Golden Delicious ^(C)	207	FEM, KN, LB, UB	26
420	Pirella [Piro!®]	2n	Germany	1992	Recent	Golden Delicious × Alkmene (CC)	996	FEM, UB	41; 54
421	Piros	2n	Germany	1963	Recent	Helios × Apollo (CC)	724	FEM, OWL	26
422	Plumac (Kotabau) [Koru [®]]	2n	New Zealand	2010	Recent	Fuji ^(NC) × Braeburn ^(C)	722	2LB	56
423	Pohorka	2n	Slowenia	1960	Recent	Cox Orange × Ontario (CC)	602	KOB, NFC	49
424	Pomme Violette	2n	France	1628	Historic	—	919	JL, NFC	25
425	Pomo Rusenetic	2n	Italy, Veneto	n.a.	Historic (local)	—	1070	2VA	35
426	Prem A17 [Smitten [®]]	2n	New Zealand	2010	Recent	A045RL3T007 × A020R02T167	586	CReSO, LB	56
427	Prem A280 [Sweetie [®]]	2n	New Zealand	2005	Recent	Braeburn × Royal Gala (CC)	511	FEM, LB	41; 56
428	Priam (370-16)	2n	USA and France	1956	Recent	PRI 14-126 × Jonathan ^(C)	697	JL, UB	26; 43
429	Prima (Co-op 2)	2n	USA	1960	Recent	—	393	KN, NFC	26; 43

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
430	Prime Gold	2n	USA	1965	Recent	Golden Delicious ^(NC) × unknown	991	NFC, UB	25
431	Prime Red	2n	Italy	1999	Recent	Prima × Summerred (CC)	415	BVC, LB	12; 54
432	Primiera (Co-op 42)	2n	USA and Italy	1998	Recent	Golden Delicious × Co-op 17 (CC)	681	2UB	23
433	Prinz Albrecht von Preußien	2n	Poland	1865	Historic	Kaiser Alexander × unknown	10	KN, NFC	17
434	Prinzenapfel	2n	Germany	1700s	Historic	–	315	AGES, NFC	16
435	Priscilla (Co-op 4)	2n	USA	1972	Recent	Red Delicious ^(C) × PRI 610-2	851	LB, NFC	39; 43
436	Pristine (Co-op 32)	2n	USA	1994	Recent	–	687	2UB	43
437	Purpurroter Cousinot	2n	Netherlands or Germany	1766	Historic	–	572	BSA, KOB, NFC	25
438	Rafzubin [Rubinette [®]]	2n	Switzerland	1966	Recent	Golden Delicious × Cox Orange (CC)	57	KN, LB	13; 43
439	Rajka	2n	Czech Republic	1994	Recent	Shampion × Katka	100	KN, LB	22
440	Rambour Papelau	3n	Russia	Around 1853	Historic	Goldparmäne × unknown	95	JL, NFC	25; 32
441	Reale d'Entraygues	2n	France	1920s	Old	–	966	JL, NFC	25
442	Realka	2n	Germany	1984	Recent	–	977	BSA, UB	43
443	Reanda	2n	Germany	1988	Recent	Clivia × F3: <i>Malus floribunda</i>	807	FEM, SLU	12; 43; 54
444	Rebella	2n	Germany	1993	Recent	Golden Delicious × Remo (CC)	838	FEM, SLU	12; 54
445	Red Delicious	2n	USA	Around 1870	Historic	–	274	KN, LB	25
446	Red Foxwhelp	2n	UK	1600s	Historic	–	964	BVC, NFC	25
447	Redfree (Co-op 13)	2n	USA	1977	Recent	Raritan × PRI 1018-101	667	OWL, UB	23; 43
448	Regine	2n	Germany	1988	Recent	–	833	CIV, SLU	43
449	Reglindis	2n	Germany	1967	Recent	James Grieve ^(NC) × F2: Antonowka	723	FEM, UB	26
450	ReINETTE Clochard	2n	France	Mid 1800s	Historic	–	695	JL, NFC, UB	25
451	ReINETTE d'Amorique	2n	France	1948	Old	–	932	JL, NFC	25
452	ReINETTE de France	3n	Belgium (?)	1853	Historic	Königlicher Kurzstiel × unknown	933	JL, NFC, TR	25; 32
453	ReINETTE Descardre	3n	Belgium	Around 1820	Historic	Golden Reinette × unknown	935	JL, NFC	25; 32
454	ReINETTE Simirenko (= Renetta Walder)	2n	Ukraine	1895	Historic	–	362	BVC, MSPP, NFC, TR, UB	25
455	Reka	2n	Germany	1984	Recent	James Grieve ^(C) × F2: <i>Malus pumila</i>	759	BSA, UB	26; 43

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
456	Releta	2n	Germany	1984	Recent	—	771	BSA, UB	43
457	Remo	2n	Germany	1984	Recent	James Grieve ^(C) × F3: <i>Malus floribunda</i>	397	KN, VA	12; 26; 54
458	Renura	2n	Germany	1988	Recent	—	770	BSA, UB	43
459	Renetta Grigia di Torriana	2n	Italy	Around 1905	Old	—	361	MSPP, NFC, UB	25
460	Renette von Bihořel	2n	France	1859	Historic	—	1042	ACW, TR	6
461	Resi	2n	Germany	1992	Recent	Clivia × seab resistant	735	FEM, OKR	22; 43
462	Resista	2n	Czech Republic	1979	Recent	Prima × NJ 56	628	LB, UB	23
463	Retina	2n	Germany	1988	Recent	Apollo ^(C) × F3: <i>Malus floribunda</i>	737	FEM, UB	26; 43
464	Rewena	2n	Germany	1988	Recent	(Cox Orange × Geheimrat Dr. Oldenburg) × F3: <i>Malus floribunda</i>	396	KN, NFC	26; 43
465	Rheinischer Bohnapfel	3n	Germany	After 1750	Historic	—	132	AN, BOKU, HG, LB	43
466	Rheinischer Krummstiel	2n	Germany	1821	Historic	—	93	AGES, KN, ZASS	43
467	Rheinischer Winterrambur	3n	Belgium or Netherlands	Before 1800	Historic	—	108	AGES, BVC, RW, ZASS	43
468	Rhode Island Greening	3n	USA	Early 1700s	Historic	—	144	BVC, NFC, UB	25
469	Ribston Pepping	3n	UK	Around 1707 (?)	Historic	Muskatrenette × unknown	39	AN, KN, LB	25; 32
470	Riesenboiken	3n	Germany (?)	Before 1900	Historic	—	22	KOB, ZASS	16; 26
471	Rival	2n	UK	1900	Historic	Peasgood Sondergliechen × Cox Orange	597	JL, KOB, NFC	25
472	RM-1 [Red Moon [®]]	2n	France	2015	Recent	—	733	LB, PEM	56
473	Rosa Gentile	2n	Italy	Before 1890	Historic	—	1069	2VA	42
474	Rose de Bénauge (Syn. Dieu)	2n	France	1800s (?)	Historic	—	904	JL, NFC	25
475	Rote Schafnase (Syn. Steirische Schafnase)	2n	Austria	Around 1800	Historic	—	279	HG, KN, ZASS	8
476	Rote Sternrenette	2n	Germany (?)	1800s	Historic	—	180	AGES, RW	49
477	Roter Astrachan	2n	Russia	1780	Historic	—	204	ACW, AGES, KN	25
478	Roter Ausbacher	2n	Germany	Late 1800s	Historic	—	751	KOB, OKR	49
479	Roter Eisernapf	3n	Germany	Early 1700s	Historic	—	231	KN, NFC	25
480	Roter Herbstkalvill	2n	France (?)	1617	Historic	—	316	HG, KN, LB	17

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
481	Roter Jungfernäpfel	2n	Austria (?)	Before 1800	Historic	—	27	AGES, KN, KOB	8
482	Roter Rosmarinäpfel	2n	Austria	1839	Historic	—	363	LB, MSPP	45
483	Roter Stettiner	3n	Germany	1776	Historic	—	251	LB, OWL	25
484	Roter Trierscher Weinäpfel	2n	Germany	1872	Historic	—	70	BOKU, KOB, ZASS	17
485	Roter von Simonoff	2n	Hungary	1876	Historic	—	260	AN, CUB, KN	25
486	Roter Winterkalvill	2n	France or UK (?)	Around 1600	Historic	—	352	KOB, MSPP, NFC	44
487	RS1 [Red Moon [®]]	2n	France	2015	Recent	—	736	LB, PEM	56
488	Rubin	2n	Czech Republic	1988	Recent	Golden Delicious × Lord Lambourne (CC)	819	BSA, NFC	13; 54
489	Rubinola	2n	Czech Republic	1990	Recent	Prima × Rubin (CC)	394	KN, LB	26; 39
490	Rubinstep [Pirouette [®]]	2n	Czech Republic	1995	Recent	Clivia × Rubin ^(C)	392	HG, KN	13; 54
491	Ruhm aus Kirchwerder	2n	Germany	Early 1900	Old	—	948	KOB, TR	38; 43
492	Runseé	2n	Italy	After 1850	Historic	—	365	BVC, MSPP, NFC, UB	11; 25
493	Saint Edmund's Pippin	2n	UK	1875	Historic	—	871	NFC, TR	25
494	Sansa	2n	Japan	1986	Recent	Gala × Akane (CC)	515	LB, VA	12; 13; 54
495	Santana	2n	Netherlands	1993	Recent	Elstar ^(C) × Priscilla-NL	483	LB, NFC	13; 54
496	Saturn	2n	UK	1997	Recent	PRI 1235 × Golden Delicious ^(C)	587	CRso, FEM	25; 39
497	Sauergräuech	2n	Switzerland	1800s	Historic	—	456	BOKU, KN, RW	49
498	Schmalprinz	2n	Germany	Before 1941	Old	—	1072	KOB, TR	38
499	Schmidberger Renette (Syn. Plankenäpfel)	2n	Austria	Around 1832	Historic	—	94	AGES, KN, LB, ZASS	25
500	Schneideräpfel	3n	Switzerland	1764	Historic	—	20	FEM, KOB, OWL	6
501	Schöner aus Bath	2n	UK	Around 1864	Historic	—	212	KOB, NFC, UB	25
502	Schöner aus Hernenhut	2n	Germany	1880	Historic	—	612	KOB, NFC	49
503	Schöner aus Pontaise	2n	France	1869	Historic	Kaiser Alexander × unknown	694	JL, NFC	17; 25
504	Schöner von Boskoop	3n	Netherlands	1856	Historic	Kasseler Renette × unknown	160	BOKU, HG, KN, LB	37; 43
505	Schöner von Fontanette (Syn. Belle de Fontanette)	2n	Switzerland	1924	Old	—	1036	ACW, RW	6
506	Schöner von Nordhausen	2n	Germany	1820	Historic	—	92	KOB, NFC	26
507	Schöner von Wilshire	2n	UK	Before 1883	Historic	—	319	AGES, KN, LB	17
508	Schweizer Orangen	2n	Switzerland	1935	Old	Ontario × Cox Orange (CC)	237	ACW, BOKU	6; 34

Table 2 (Continued)

No.	Cultivar name [Trademark name ^a]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
509	Sciearly [Pacific Beauty [®]]	2n	New Zealand	1993	Recent	Galax × Splendour (CC)	509	LB, UB	12; 34
510	Scifresh [Jazz [®]]	2n	New Zealand	1997	Recent	Galax × Braeburn (CC)	417	HG, LB	41; 34
511	Sciired [Pacific Queen [®]]	2n	New Zealand	1993	Recent	Galax × Splendour (CC)	510	LB, UB	12; 34
512	Sciros [Pacific Rose [®]]	2n	New Zealand	1989	Recent	Galax × Splendour (CC)	524	LB, UB	12; 34
513	SEL. P.R.I. Co-op 16	2n	USA	1978	Recent	PRI 764-200 × PRI 672-100	987	2UB	56
514	SEL. P.R.I. Co-op 17 (1689/110)	2n	USA	Before 1972	Recent	—	986	2UB	56 (mentioned as parent cultivar)
515	Senshu	2n	Japan	1978	Recent	—	981	3UB	54
516	Sepfer	2n	Netherlands	After 1952	Recent	Jonathan × Golden Delicious (CC)	621	NFC, parentage analysis	25
517	Shalimar [Tolinda [®]]	2n	Czech Republic	2001	Recent	Topaz × Golden Delicious (CC)	466	HG, LB	54
518	Shamrock	2n	Canada	1992	Recent	McIntosh × Golden Delicious (CC)	984	2UB	12; 34
519	Shinagold	2n	n.a.	n.a.	Recent	—	732	LB, PEM	57
520	Shinano Gold [yellow [®]]	2n	Japan	1996	Recent	Golden Delicious × Senshu (CC)	419	LB, NES, OJE, SKS	41; 34
521	Siebenkant	2n	Austria	n.a.	Historic?	Seedling Minister von Hammerstein (?)	295	BOKU, KN, ZASS	14
522	Signe Tillisch	2n	Denmark	1866	Historic	Weißer Winterkärrill × unknown (?)	307	BOKU, HG	43
523	Silken	2n	Canada	1997	Recent	Honeygold × Sunrise	523	HG, LB	12; 56
524	Sinfonia (YX2)	2n	Italy	2013	Recent	Co-op 25 × CIVCP-142	588	CReSO, LB, SKS	56
525	Sinta	2n	Canada	1955	Recent	Golden Delicious ^(C) × Grimes Golden ^(NC)	982	NFC, UB	25
526	Sir Prize (Co-op 5)	3n	USA	1975	Recent	Doud Golden Delicious (4n) × PRI 14-152	689	OWL, 2UB	32; 43
527	Smeralda	2n	Italy	2011	Recent	DA-85 × B9-5	835	CIV, LB	41; 56
528	Sommerköniger	2n	Italy, South Tyrol	Before 1900	Historic	—	105	FEM, LB, OKR	38
529	Sommerregent	2n	Germany	1950	Old	Anton Fischer × James Grieve ^(C)	805	BOKU, BSA	38
530	Sonnenwirtsapfel	3n	Germany	1932	Old	Geflammter Kardinal × unknown (?)	777	BSA, KOB, TR	17
531	Spartan	2n	Canada	1926	Old	McIntosh × Red Delicious (CC)	385	KN, NFC	25; 39
532	Spätablühender Täffet	2n	Germany	1872	Historic	—	240	AGES, KN, NFC	43

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
533	Spijon	2n	USA	1944	Old	Northern Spy, Red × Monroe (CC)	979	NFC, UB	25
534	Splendour	2n	New Zealand	1948	Old	—	824	BVC, NFC	25
535	SQ133 (CPRO1.33) [Allure [®]]	2n	Netherlands	2014	Recent	Golden Delicious ^(C) × 1980-015-047	484	HG, LB	3
536	SQ159 (CPRO1.59) [Natyra [®]]	2n	Netherlands	2016	Recent	—	488	HG, LB	54
537	Stahls Winterprinz	2n	Germany	Before 1936	Old	—	766	BSA, KOB, TR	38
538	Stark Earliest	2n	USA	1938	Old	—	87	BOKU, NFC	25
539	Stayman Winesap	3n	USA	1866	Historic	Winesap × unknown	189	KN, LB	25
540	Steirischer Maschanzker	2n	Austria (?)	Before 1800	Historic	—	78	AN, BOKU, HG, KN, OIKOS, SGB	8; 47
541	Steirischer Passamaner	2n	Austria (?)	1891	Historic	—	861	20IKOS	8 (p. 230); 47
542	Sternapfel	2n	Europe	Early 1600s	Historic	—	117	BVC, JL, RW	44
543	Stina Lohmann (= Korbiniensapfel)	2n	Germany	1841	Historic	—	804	AN, BSA, NFC, OKR, TR	25
544	Strauwaldts Goldparmäne (Syn. Neue Goldparmäne)	2n	Germany	1905	Old	Goldparmäne ^(C) × Parkers Peppin ^(NC)	312	KOB, NFC, RW	25; 49
545	Summerfree	2n	Italy	1998	Recent	Golden Delicious ^(C) × PRI 1956-6	474	LB, VA	23
546	Summerred	2n	Canada	1961	Recent	Summerland × unknown	380	KN, NFC	26
547	Sunset	2n	UK	1933	Old	Cox Orange × James Grieve (CC)	850	NFC, TR	32; 40
548	Suntan	3n	UK	1956	Recent	Cox Orange × Königlicher Kurzstiel	762	BSA, JL, NFC	25; 32
549	Süßer Pfaffenapfel	2n	Switzerland	1850	Historic	—	754	KOB, RW	6
550	Talimi	2n	Italy, Veneto	n.a.	Historic (local)	—	1074	2VA	36
551	Telamon (Syn. Waltz)	2n	UK	1976	Recent	McIntosh, Wijcik × Golden Delicious (CC)	997	NFC, UB	25
552	Thurgauer Weinapfel	2n	Switzerland	1860	Historic	Frauotacher × unknown (?)	622	ACW, KOB, TR	49
553	Tiroler Maschanzker	2n	Austria	n.a.	Historic (local)	—	860	HG, SGB	47
554	Tiroler Spitzlederer	2n	Italy, South Tyrol	1855	Historic	—	174	KN, LB, MSPP, NFC	25
555	Tobiasler	2n	Switzerland	1805	Historic	—	1040	ACW, NFC	25
556	Topaz	2n	Czech Republic	1991	Recent	Rubin ^(C) × Vanda	140	KN, LB	41; 54
557	Trajan (Syn. Polka)	2n	UK	1976	Recent	McIntosh, Wijcik × Golden Delicious (CC)	829	NFC, SLU	25

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
558	Transparent aus Cronceis	2n	France	1869	Historic	Antonowka × unknown (?)	138	ACW, AGES, RW	43
559	Tumanga (Syn. Auralia)	2n	Germany	1930s	Old	Cox Orange × Schöner aus Nordhausen (CC)	683	KOB, UB	26; 43
560	Tunda	2n	Belgium	2005	Recent	Delcorf ^(C) × Liberty ^(NC)	491	LB, VA	41; 54
561	Tuscan (Syn. Bolero)	2n	UK	1976	Recent	McIntosh, Wijcik × Greensleaves (CC)	827	NFC, SLU	25
562	UEB 26002 [Mars [®]]	2n	Czech Republic	2005	Recent	—	501	FEM, LB	54
563	UEB 32642 [Opal [®]]	2n	Czech Republic	2001	Recent	Topaz × Golden Delicious (CC)	405	LB, VA	41; 54
564	Uhlhorns Augustkalvill	2n	Germany	Around 1880	Historic	—	757	HG, KOB	34
565	Undine	2n	Germany	Around 1930	Old	Jonathan ^(C) × unknown	608	KOB, NFC	43
566	Usterapfel	2n	Switzerland	1760	Historic	—	543	ACW, RW, TR	6
567	Van Mons Renette	2n	Belgium	1821	Historic	—	950	JL, TR	44
568	Vernade (Syn. Versane)	2n	France	1948	Old	—	940	JL, NFC	25
569	Vesna	2n	Czech Republic	1996	Recent	—	778	BSA, FEM	54
570	Vista Bella	2n	USA	1956	Recent	—	900	ACW, BSA, NFC	25
571	Wagnerer Apfel	2n	USA	1791	Historic	—	257	KOB, LB, NFC	25
572	Wealthy	2n	USA	Around 1861	Historic	—	802	JL, NFC, SLU	25; 49
573	Weidhers Goldrenette	2n	Germany	1844	Historic	Seedling Orleans Renette	561	NFC; parentage analysis	25
574	Weilburger	2n	Germany	Early 1800s	Historic	—	1030	AHH, BB	44
575	Weirouge	2n	Germany	1999	Recent	—	457	BSA, LB	54
576	Weißer Griesapfel	2n	Austria	1800s	Historic	—	378	HG, KN	38
577	Weißer Klarpfälz	2n	Russia	Early 1800s	Historic	—	98	AN, HG, KN, ZASS	25
578	Weiüber Rosmarin	2n	Italy, South Tyrol	Early 1800s	Historic	—	294	AGES, BOKU, LB	25
579	Weiüber Winterkalvill	2n	France	1596	Historic	—	249	BOKU, KN, MSPP	43
580	Weiüber Winterkäferapfel	2n	Germany	1800	Historic	—	218	ACW, RW	25
581	Wellington (Syn. Dumelow's Seedling)	2n	UK	Late 1700s	Historic	—	691	KOB, TR, UB	25
582	“Wellington rot”	2n	n.a.	n.a.	Historic	—	858	ACW, SLU	57
583	Welchbrunner	3n	Austria	1825	Historic	—	55	KN, KOB	49
584	Wettinger Taubenapfel	2n	Germany	Late 1800s	Historic	—	558	KOB, OKR	17
585	Williams Pride (Co-op 23)	2n	USA	1988	Recent	—	772	BSA, UB	43

Table 2 (Continued)

No.	Cultivar name [Trademark name [®]]	Ploidy	Country of origin	Year ^a	Classification ^b	Assumed parentage (if available) ^c	Profile No. ^d	Sample provenance from collection ^e	Reference(s) ^f
586	Wilsteder	2n	Germany	Before 1936	Old	—	609	KOB, NFC, TR	38
587	Winter Lemon	2n	Ukraine	1968	Recent	—	569	NFC, UB	25
588	Winterbananenapfel	2n	USA	1876	Historic	—	125	BOKU, KN, LB	25
589	Winterprinzenapfel	3n	n.a.	1933	Old	—	1076	BB, PVW	17
590	Worcester Parmäne	2n	UK	1873	Historic	Devonshire Quarrenden × unknown (?)	571	NFC, SLU	25
591	Wyken Pippin	2n	UK	Early 1700s	Historic	—	955	NFC; Ordidge et al. 2018	25
592	Xelevén [Swing [®]]	2n	France	2018	Recent	—	728	LB, PEM	55
593	YX1	2n	Italy	2000s (in trials)	Recent	Cripps Pink ^(C) × unknown	634	FEM, LB	57
594	YX6	2n	Italy	2000s (in trials)	Recent	Cripps Pink ^(C) × unknown	726	FEM, LB, SKS	57
595	YX7	2n	Italy	2000s (in trials)	Recent	—	635	FEM, LB	57
596	Zabergäu Renette	3n	Germany	1885	Historic	Goldparmäne × unknown	459	BOKU, KOB, NFC	32; 43
597	Zari	2n	Belgium	2005	Recent	Eistar × Delcorf (CC)	518	LB, VA	41; 56
598	Zarya Alatau	2n	Belarus	1999	Recent	—	645	LB, SLU	54
599	Zonga	3n	Belgium	2005	Recent	Alkmene × Delcorf	492	LB, VA	41; 54
600	Zuccalmaglio Renette	2n	Germany	1878	Historic	Ananas Renette × Purpurroter Agatapfel	90	AGES, NFC	43

^an.a. not available; ^b2n diploid; ^c3n triploid^aThe year provides the earliest dating of a cultivar that was retrieved from references or databases. It can be the year when a cultivar was raised or found, when it was brought to notice, recorded or described, when application for varietal protection was submitted, varietal protection was granted or a cultivar was introduced to the market. The dating was used to classify scion cultivars as historic, old and recent^bScion cultivars were classified as *historic*, if they were derived before 1900; as *old*, if they originated between 1900 and 1950; and as *recent*, if they were bred after 1950. Rootstocks and crab apples were considered as distinct categories^cInformation on parentages was taken from pomological literature, if available. Superscript letters provided in parentheses on the right of a cultivar name indicate that a single parentage was confirmed (C) or refuted (NC), while regular type letters (CC) in parentheses on the right of a parent pair indicate that both assumed parents were confirmed by molecular genetic data obtained in the present study^dEach molecular genetic profile at the complete set of 14 microsatellite loci, representing a specific cultivar that was included in the reference database, was assigned a unique profile number, which can be used for identification along with the cultivar denomination^eThe abbreviations of the collection names, from which accessions of apple cultivars were sampled and analysed, are explained in Table 1. Detailed information on the accessions analysed of each cultivar can be found in Supplementary Table S1. A number in front of the abbreviation code indicates that two or more accessions of a cultivar, but of different origin, were obtained from that particular collection^fEach reference, from which information about the country and year of origin of each cultivar as well as their parent cultivars (if known) were taken, was abbreviated with a number: 1, Aigner and Schalansky (2013); 2, Aliotta and Grassi (2008); 3, Baab (2011); 4, Baric et al. (2009); 5, Baric et al. (2012); 6, Barthä-Pichler et al. (2005); 7, Bernkopp (2011); 8, Bernkopp et al. (2003); 9, Bosch (2006); 10, Bosch (2017); 11, Bounous (2006); 12, Brown and Maloney (2003); 13, Evans et al. (2011); 14, Gaber (2020); 15, Hampson and Kemp (2003); 16, Hartmann (2015); 18, Jacobsen (2014); 19, Larsen et al. (2017); 20, Lassois et al. (2016); 21, Leroy (1873); 22, Link (2002); 23, Maurizi (2001); 24, Melville and Cripps (1970); 25, Morgan and Richards (2002); 26, Mühl (2001); 27, Müller et al. (1905–1930); 28, Neti (2004); 29, NIAB-EMR (2016); 30, Oberhofer (2007); 31, Orange Pipkin (2019); 32, Ordidge et al. (2018); 33, Perazzoli et al. (2014); 34, Petzold (1984); 35, Provincia di Vicenza (2005a); 36, Provincia di Vicenza (2005b); 37, Ramos-Cabrera et al. (2007); 38, Rolff (2001); 39, Salvini et al. (2014); 40, Sanders (2012); 41, Sansavini et al. (2012); 42, Schiavon (2010); 43, Silbereisen et al. (2015); 44, Smith (1971); 45, Stoll (1888); 46, Storti et al. (2012); 47, Storti et al. (2013); 48, Szalatnay and Frei (2009); 49, Votteler (2014); 50, Webster and Wertheim (2003); 51, Whealy and Thuneit (2017); 53, Yoshida (1977); 54, CPVO Database; 55, PLUTO Database; 56, USPTO Database; 57, n.a.

Table 3 List of microsatellite loci (Liebhard et al. 2002) analysed in the present study in four multiplex reactions

PCR	Locus	Fluorophore	Primer concentration [μM]	Size range (bp)	N _A ALL (N _A 2n)	PIC	Linkage group
Multiplex 1	CH01c06	WellRED D4	0.8	146–190	19 (17)	0.774	8
	CH02b10 ^b	WellRED D2	1.0	107–155	18 (18)	0.897	2
	CH03a04	WellRED D4	0.4	86–134	20 (20)	0.845	5
Multiplex 2	CH01d08	WellRED D4	0.7	238–294	20 (19)	0.750	15
	CH01f02 ^a	WellRED D4	0.3	160–228	27 (27)	0.856	12
	CH02d12	WellRED D2	0.6	169–223	23 (22)	0.764	11
Multiplex 3	CH02h11a	WellRED D3	0.8	98–130	12 (12)	0.791	4
	CH02c02a	WellRED D3	0.9	125–209	32 (31)	0.897	2
	CH02c09 ^a	WellRED D3	0.6	233–259	12 (12)	0.821	15
	CH02c11 ^a	WellRED D4	0.52	210–268	20 (19)	0.879	10
Multiplex 4	CH01h01 ^a	Cy5	0.25	102–146	17 (17)	0.831	17
	CH01f07a	WellRED D3	0.3	173–205	16 (16)	0.840	10
	CH02d08 ^a	WellRED D2	0.9	208–262	19 (19)	0.825	11
	COL	WellRED D4	0.5	203–243	17 (17)	0.751	10

N_A number of alleles; PIC polymorphic information content

^a Locus analysed in study of Bus et al. (2012) and Urrestarazu et al. (2016)

^b Locus analysed in study of Bus et al. (2012)

et al. (2016) (see Table 3). The aim of the latter analyses was to calculate the average exclusion probabilities of identical genotypes by using different numbers of loci and to test whether the reduced number of microsatellites would provide sufficient resolution to distinguish genotypes of different apple cultivars, when used as a tool for determination of unknown apple genotypes.

In order to get an impression about the accuracy of genotyping data, parentage analyses were carried out. In a first step, the analysis involved the dataset at 14 microsatellite loci and focused on 85 diploid genotypes of old and recent cultivars, and rootstocks that arose after 1900, for which information about at least one parent cultivar was available and the molecular genetic profile of the assumed parent was also present in the database. This dataset also included the cultivars ‘Golden Delicious’ and ‘James Grieve’ that arose before 1900, but their parentage was confirmed by genotypic data in the studies of Evans et al. (2011) and Salvi et al. (2014). This analysis, however, excluded other historic cultivars, for which information about parentages provided in the literature may be less reliable as they were not derived from systematic breeding activities. The analysis was performed with the software ML-Relate (Kalinowski et al. 2006), which can calculate the maximum likelihood estimates for each of the four relationships: unrelated, half siblings, full siblings and parent/offspring. In the course of these analyses, it was noticed that seven assumed parent-offspring combinations showed mismatches at locus COL, likely due to the presence of null alleles. Consequently, this locus was excluded from the dataset and the analyses were

repeated with the remaining 13 loci. Furthermore, locus COL was omitted from all further parentage analyses.

In a second step, the analysis targeted 116 diploid genotypes, again comprising old and recent cultivars, and rootstocks, for which information about both parents was available from the literature and which genotypes were also present in the dataset. The software CERVUS 3.0.7 was employed in order to identify the statistically most likely candidate parent pairs. A simulation of parentage analysis was performed in order to determine the critical LOD values for parent pairs without known sexes at a strict confidence of 95% and a relaxed confidence of 80%. The simulation was based on the following parameters: N offspring: 20,000; N candidate parents: 1000; proportion of candidate parents sampled: 0.30; proportion of loci typed: 0.99; proportion of loci mistyped: 0.01; and error rate in likelihood calculations: 0.01. The confidence was determined using the log-likelihood ratio or LOD score. The parent pair analysis without known sexes was run based on the output of the parentage simulation and by allowing for typing errors.

In order to use the here described microsatellite dataset as a reference database for determination of unknown apple cultivars and to handle the presence of diploid and triploid genotypes, a new “Apple Fingerprint Identifier” script was generated in Microsoft Access (Baric and Radmüller, unpublished). This programme allows comparing the genotype of an unknown variety to all the 600 entries present in the reference database including the full set of 14 microsatellite loci. The programme permits manually inserting the genotypic data of the target cultivar or to import a list of cultivars from an Excel file comprising three columns

Table 4 Conversion values used to align the allele lengths of the dataset of Urrestarazu et al. (2016) with the dataset obtained in the present study at five common loci. Depending on the length of alleles in the Urrestarazu et al. (2016) dataset (that are given in parentheses), two conversion values may be required for the same locus. The conversion values need to be subtracted from the allele lengths derived from the dataset of Urrestarazu et al. (2016) in order to achieve an alignment with the here presented dataset (compare Supplementary Table S6)

Locus	Conversion value
CH01f02	-3 (163–199); -2 (>202)
CH02c09	0
CH02c11	-1
CH01h01	-2 (104–128); -3 (>131)
CH02d08	-1 (209–233); 0 (>244)

per locus. For each target genotype, the alleles at each locus are compared to each entry of the database. Finally, a ranked list of the genotypes from the database with the highest similarity to the target is generated, which is based on the number of matches. In order to visually facilitate identification, all matching alleles between the target genotype and the genotypes from the database are highlighted in green, whereas mismatching alleles are highlighted in red. In this way, the genotype of an unknown apple variety can be assigned to the reference cultivar, if it shares all alleles with the reference genotype or displays a tolerated number of mismatches. The Access programme can also be used with a lower number of microsatellite loci, if the set of microsatellite loci analysed in different projects or laboratories is only partially overlapping.

Finally, a preliminary trial was performed to assess the potential of combining genotyping data obtained in the present study with published microsatellite data (Urrestarazu et al. 2016). First, the allele lengths of five common cultivars ('Fuji', 'Gala', 'Golden Delicious', 'Granny Smith' and 'Red Delicious') were compared at a set of five microsatellite loci that were analysed in both studies in order to determine conversion values necessary to align the allele lengths (Table 4). After conversion of the allele lengths in the dataset of Urrestarazu et al. (2016), a set of 20 cultivars that were present in both datasets were randomly selected and their allele lengths were compared.

Results

The dataset includes a total of 600 genotypes at 14 microsatellite loci, of which 533 are diploid and 67 are triploid. The ploidy was determined exclusively based on molecular genetic data and the genotypes identified as triploids displayed three different alleles at three or more microsatellite loci. Of the 600 genotypes included in the database, two belonged to the crab apples *Malus baccata*

and *M. floribunda*, while the remaining were 24 rootstocks and 574 scion cultivars of *M. domestica*. Of the latter, 264 were classified as historic, 87 as old and 223 as recent cultivars. Of the historic cultivars, 51 (19.3%), of the old cultivars, 9 (10.3%) and of the recent cultivars only 7 (3.1%) were triploid (Fig. 1).

The complete dataset of 600 genotypes comprised a mean number of 19.4 alleles per locus, ranging from 12 to 32 (see Table 3). The average number of alleles per locus was slightly smaller in the dataset with 533 diploid genotypes and amounted to 19.0. Six alleles at five different loci were exclusively present in triploid genotypes. The number of missing genotypic information in the dataset was observed at a very low frequency; for cultivar 'Vista Bella' genotypic information was missing at locus Ch02c02a, while for the rootstocks 'M.4' and 'M.6' genotypic information was partially missing at locus Ch02d08 and for the rootstock 'M.11' at locus CH02h11a.

The dataset comprising 533 diploid genotypes was used to determine the combined non-exclusion probability of identity, which amounted to 2.6×10^{-20} , to 3.4×10^{-19} , to 8.8×10^{-10} , and to 5.0×10^{-8} in the dataset with 14, 13, six and five microsatellite loci, respectively, showing that the probability of finding identities by chance increases with the decrease of the number of loci employed. In fact, the identity analysis, which compared 533 individuals in 141,778 pairwise comparisons, did not result in any matching genotype in the datasets containing 14 and 13 loci, whereas in the datasets reduced to six and five microsatellite loci one matching genotype combination was found. The dataset containing six or five microsatellite loci did not allow distinguishing the genotypes of the cultivars 'Jeanne Hardy' and 'Adersleber Kalvill' as they showed an exact match at all these loci. The probability of identity and the probability of sib identity for the exact match of these two genotypes were 5.8×10^{-11} and 9.3×10^{-4} , respectively, when using the dataset with six loci.

The initial analysis aiming to validate the dataset indicated the presence of null alleles at locus COL. In 7 out of 85 presumed parent-offspring combinations tested, a mismatch was found at this locus (see Supplementary Table S3). A closer look at the genotyping data revealed that six of these parent-offspring combinations were homozygous for different alleles at locus COL, which strongly suggests the presence of null alleles. This assumption is further supported by the low observed heterozygosity found at this locus, which amounted to 0.72 (data not shown). In comparison, the average observed heterozygosity for the remaining loci was 0.84 (± 0.03 S.D.). When omitting locus COL from the dataset and repeating the parentage analysis with software ML-Relate, no further indication for a genotyping error was noticed. Of the 85 diploid cultivars tested, for which one documented parent was included in the dataset,

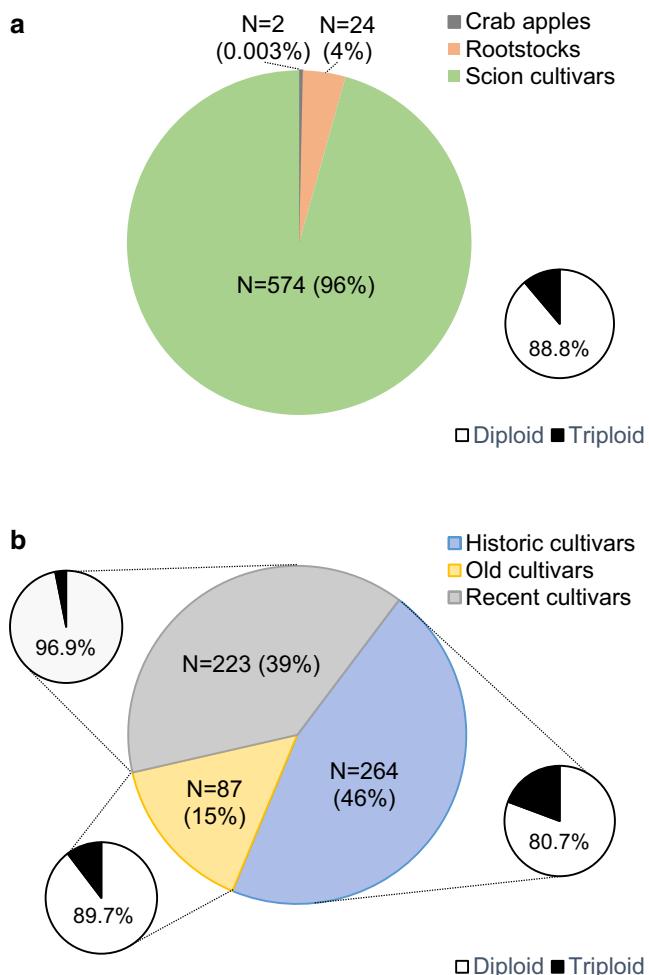


Fig. 1 Composition of the database as regards the proportion of molecular genetic profiles belonging to scion cultivars, rootstocks and crab apples (a). The proportion of historic (derived before 1900), old (originated between 1900 and 1950) and recent (bred after 1950) apple cultivars is shown exclusively for scion cultivars (b). The small black-and-white pie charts indicate the proportion of diploid and triploid genotypes within the entire dataset (a) or within each category of scion cultivars (b). The percentages provided as numbers in the small pie charts specify the share of diploid cultivars

the highest likelihood for a parent-offspring relationship was found in 77 instances. In three cases, the highest likelihood supported a full sibling relationship, however, the log likelihoods for the parent-offspring relationship were only 0, 0.56, 0.85 lower, respectively (Supplementary Table S3). For the cultivars ‘Collina’, ‘Pimona’, ‘Prime Gold’ and ‘Reglindis’, the parent cultivar suggested from the literature could be excluded (see Table 2), while another cultivar with the highest likelihood for a parent-offspring relationship was identified (Supplementary Table S3). Moreover, while for ‘Prime Gold’ the parentage of ‘Golden Delicious’ was excluded, a parent-offspring relationship was identified for ‘Morgenduft’ and ‘Red Delicious’. In the case of ‘Lom-

barts Kalvill’, ‘Weißer Winterkalvill’ present in our dataset could be excluded as a parent.

The next analysis focused on a dataset with 116 diploid genotypes, for which information about both parents was available from the literature or other sources, and the molecular genetic profiles of the suggested parent cultivars were also present in the dataset. This analysis confirmed the parentage for 108 genotypes. While 104 offspring genotypes showed an exact match with both parent genotypes at all 13 loci, a single mismatch was observed for the offspring genotype and one of its parents in four cases (Supplementary Table S4). In each mismatch, a different locus was involved, which results in a mean genotyping error rate of 0.28% per locus. For five apple cultivars, ‘Millicent Barnes’, ‘Nevson’, ‘Plumac’, ‘Strauwaldts Goldparmäne’ and ‘Tunda’, one of the assumed parents could be excluded, while another parent was found as the most probable parent (see Supplementary Tables S4 and S5). All confirmed or identified parent-offspring combinations showed positive LOD scores that ranged from 17.01 to 45.31, with an average value of 27.97 (± 4.79 S.D.). All LOD scores but one exceeded the critical LOD value of 17.56 (Supplementary Table S4). For all but three cultivars, the parentage assignment was made at the strict confidence level of 95%. For the cultivar ‘Melrose’, which is an offspring of ‘Jonathan’ × ‘Red Delicious’ (Silbereisen et al. 2015), a higher likelihood was found for the combination ‘Akane’ × ‘Red Delicious’, ‘Akane’ being an offspring of ‘Jonathan’. Similarly, for the cultivar ‘Rubinola’, an offspring of ‘Prima’ × ‘Rubin’ (Salvi et al. 2014), a higher likelihood was found for the combination ‘Prima’ × ‘Topaz’, ‘Topaz’ being an offspring of ‘Rubin’. In case of the cultivar ‘Dalilight’, one mismatch was found for the parent combination ‘Elstar’ × ‘Cripps Pink’ and the LOD score was below the critical threshold of 17.56. For this cultivar a higher LOD score, also below the threshold, was found for the combination ‘Elstar’ × ‘Golden Delicious’, ‘Golden Delicious’ being a parent of ‘Cripps Pink’.

For two cultivars, ‘Blushing Golden’ and ‘Sinta’, the presumed parent pairs (see Table 2) could not be confirmed by the analysis. While in both cases ‘Golden Delicious’ was confirmed as one of the parents, the second parent suggested by the literature was rejected. For these cultivars, it was not possible to identify a genotype in our dataset that may represent the second most likely parent (Supplementary Table S5). In addition, the two possible parents of ‘Prime Gold’, identified in the ML-Relate analysis, ‘Morgenduft’ and ‘Red Delicious’ (Supplementary Table S3), were further confirmed as the probable parent pair with a LOD score of 28.89.

The comparison of molecular genetic profiles obtained in the present study with a set of data of common cultivars that were randomly derived from the dataset of Ur-

restarazu et al. (2016) showed a very good comparability at the five microsatellite loci that were in common. For four microsatellite loci, it was necessary to apply a conversion value in order to align the allele lengths (Baric et al. 2008). For three of these loci, it was even necessary to apply a second conversion value for longer alleles as a shift from odd to even allele lengths (or from even to odd numbers) occurred in the longer allele range of the dataset of Urrestarazu et al. (2016). Nevertheless, after applying the conversion values shown in Table 4 and comparing the molecular genetic profiles of the five cultivars used to determine the conversion values and the 20 randomly derived cultivars, an exact match between the data of the two studies could be found (see Supplementary Table S6).

Discussion

In the last years, there has been an increasing interest in the characterisation and maintenance of heirloom cultivars of apple at the regional and national level of many countries. Multilocus microsatellite analysis has become a standard tool for the assessment of genetic variability and the identification of duplicate accessions in order to contribute to a more efficient management of germplasm collections (e.g. Guarino et al. 2006; Pereira-Lorenzo et al. 2007; Routson et al. 2009; van Treuren et al. 2010; Garkava-Gustavsson et al. 2013; Ferreira et al. 2016; Gasi et al. 2016; Urrestarazu et al. 2016; Larsen et al. 2017; Testolin et al. 2019). Furthermore, molecular data can provide a complementary or alternative means for the determination of apple cultivars based on phenotypic traits. However, while the comparison of molecular genetic profiles of accessions present in a collection or geographic area can help to disclose identical genotypes, such an approach does not automatically lead to a correct cultivar determination. Frequently, trees are maintained in germplasm collections under their local names and without the possibility to compare their molecular genetic profiles to standard cultivars, they could be regarded as local even if they in fact represented widely grown international cultivars (Urrestarazu et al. 2016; Testolin et al. 2019). In addition, several studies have pointed to the problem of misclassified accessions preserved in germplasm collections, which can occur due to phenotypic determination errors, due to mix-up of grafting and/or planting material or due to documentation mistakes (Hokanson et al. 1998; Baric et al. 2009; van Treuren et al. 2010; Urrestarazu et al. 2016).

With regard to using multilocus microsatellite data for determination of unidentified or misidentified apple varieties, a database with molecular genetic fingerprints of well-determined reference cultivars needs to be available (Thomas et al. 1994). Based on the results of a genotyping study of Dutch genetic resources of apple, van Treuren

et al. (2010) presented a database with 121 confirmed or verified multilocus microsatellite profiles to identify apple cultivars. The aim of the present study was to set up a more comprehensive reference database comprising 600 unique multilocus microsatellite profiles that could be applied for the identification of historic, old and recent apple cultivars, with focus on the Central European cultivation area. In order to generate a representative dataset, a targeted sampling procedure involving 37 European cultivar collections and more than 1600 accessions of apple trees was implemented. One of the intended applications of the database was to characterise and determine the local genetic resources of apple from the regions of Tyrol in Austria and South Tyrol in Italy that were collected in a common research project (Baric et al., in preparation). Therefore, the apple cultivars to be sampled and genotyped for the establishment of the database were selected based on the study of pomological references. A large part of the database covers apple cultivars that were grown in the Central European area in the past. The database includes 72 out of 74 common German apple cultivars described by Silbereisen et al. (2015), 24 out of 27 cultivars considered as widespread in South Tyrol (Northern Italy) in the first half of the 20th century (Amonn and Meier 1934), and approximately 50% of the cultivars listed in the Austrian-Hungarian Pomology published in 1888 (Stoll 1888), to name but a few. Another utilisation potential of our database was seen as a tool for the support of breeding programmes or the production of propagation material, as the database also comprises a considerable proportion of recent cultivars, many of which are still in the process of technical examination and variety testing.

In order to diminish the inclusion of molecular genetic profiles belonging to erroneously assigned cultivars into the reference database, an important goal of the present study was to sample at least two independent accessions of distinct provenances of each cultivar (Baric et al. 2009; Evans et al. 2011). If two or more (up to eight) accessions carrying the same cultivar name displayed identical molecular genetic fingerprints, they were considered as confirmed and the multilocus microsatellite genotypes were included in the reference database. This objective was reached for 98% of the apple cultivars present in the database. Three or even more independent accessions were analysed of one third of the cultivars present in the database. Among the historic cultivars raised before 1900, the percentage of molecular genetic profiles that were verified by three or more accessions was considerably higher and amounted to 56%. Nevertheless, as discussed by Urrestarazu et al. (2016), an identical molecular genetic profile of two accessions with different origins does not always prove the trueness-to-type, as graft cuttings have been exchanged for centuries on a large geographical scale and erroneously determined accessions could have been maintained and transmitted from

one germplasm collection to another. This may indeed be the case for some historic cultivars, as was shown for ‘Edelborsdorfer’, one of the oldest German apple cultivars documented in the 16th century. In a study employing the same set of microsatellite markers as used in the present work, several distinct genotypes denominated ‘Edelborsdorfer’ were found in different cultivar collections (Storti et al. 2013). Among these were accessions with an identical triploid genotype that by the integration of genotyping data and pomological characterisation could successively be identified as the cultivar ‘Seebaer Borsdorfer’, which is a synonym of ‘Fromms Renette’, and also an offspring of the true-to-type ‘Edelborsdorfer’ (Storti et al. 2013). Therefore, the presence of a small number of misidentified cultivars in the here described reference database cannot be completely ruled out and may be rectified in the course of future pomological evaluations of the germplasm collections sampled. For this reason, whenever using the database to determine an unknown apple variety, it is recommended to provide the cultivar name followed by an indication about the germplasm collection where accessions with a matching multilocus genotype can be found. In this way, a subsequent comparative pomological assessment based on reference material from defined cultivar collections could be performed.

In order to acquire high quality multilocus microsatellite fingerprints of each apple cultivar, every sample obtained from a different accession was analysed independently by using an anonymous sampling code. Before data was exported, each electropherogram was visually assessed for binning accuracy. The comparison of the multilocus microsatellite genotypes in a cross-tabulation matrix finally allowed identifying identical or highly similar molecular genetic profiles. In case of incongruences between samples supposed to represent the same apple cultivar, the data were reviewed and, if necessary, the DNA analyses were repeated. Each cultivar was finally represented by a unique genotype that was included into the reference database.

Due to the rigorous quality control performed during laboratory and data analyses, we feel confident that the here presented dataset is reliable and robust. Nevertheless, a parentage analysis performed on a set of multilocus microsatellite genotypes of apple cultivars with previously known parent-offspring relationships permitted to get an impression about the rate of genotyping errors present in our dataset. Genotyping errors affect all kinds of datasets, but the rate of their occurrence is generally addressed by few studies (Hoffman and Amos 2005; Pompanon et al. 2005).

Hoffman and Amos (2005) found that one of the most common errors affecting microsatellite data is the misinterpretation of allele banding patterns due to confusion between homozygote and heterozygote genotypes with adjacent alleles. In particular, dinucleotide microsatellite repeats that

are prone to “stutter” peaks are affected by this type of genotyping error (Litt et al. 1993). However, a study comparing microsatellite profiles of apple cultivars at a set of five microsatellite loci obtained independently by two laboratories showed that the most common type of discordance among laboratories was ‘dropout of longer alleles’ due to preferential amplification of shorter alleles during PCR, followed by mis-scoring of “stutter” patterns as homozygous or heterozygous, and complete allele mismatch (Baric et al. 2008). Another issue, that can in particularly affect the success of parentage analyses, is the occurrence of ‘null alleles’ that are caused by a non-amplification of alleles due to a mutation at the primer binding site (Hoffman and Amos 2005). In the present study, one of the loci analysed (COL) was found to be considerably affected by null alleles and consequently, this locus had to be excluded from parentage analysis. Other genotyping incongruences between parent-offspring trios with known parentages were observed at very low rates, resulting in a mean genotyping error rate of 0.28% per locus, which points to a high reliability of the dataset. Nevertheless, as the presence of genotyping errors cannot be completely excluded, it is recommended to allow for at least one mismatch when using the database for cultivar identification or for parentage analysis. The parentage analysis used to verify the dataset included apple cultivars that were derived after 1900 and for which information about parent-offspring relationships were provided by different references. Multilocus microsatellite genotypes of more than 100 scion cultivars and rootstocks could be compared to the genotypes of both documented parents, while more than 80 could be compared to one of their parents. This means that approximately one third of the cultivars included in the reference database are supported by the matching of their multilocus microsatellite profiles with one or even two parental genotypes suggested by the pomological literature. Among these is a small number of cultivars for which only one accession could be analysed, but that were still included in the reference database because their multilocus microsatellite profiles matched with the documented parents. The remaining cultivars, which multilocus microsatellite profiles are based on the analysis of a single accession, were not supported as offspring but as a parent, such as ‘Otava’ and ‘Minnewashta’ in the group of recent cultivars. ‘Wyken Pippin’, a British cultivar from the early 1700s could only be obtained from the National Fruit Collection in Brogdale (UK), but was inserted in the database as it is listed as a parent of some historic and old apple cultivars (Smith 1971).

Parentage analyses revealed a smaller percentage of cultivars, which documented pedigrees were not supported by multilocus microsatellite data, as was observed in previous studies (e.g. Evans et al. 2011; Moriya et al. 2011; Salvi et al. 2014). The cultivar ‘Nevson’ was patented as

a controlled cross between ‘Gala’ and ‘Red Delicious’ (United States Patent PP12,415; USPTO Database of the United States Patent and Trademark Office), while for ‘Plumac’ the cultivars ‘Fuji’ and ‘Braeburn’ were assumed as the “... probable parents based on their characteristics and their proximity to the new cultivar in the area of discovery.” (United States Patent PP23,418; USPTO Database of the United States Patent and Trademark Office). For each of the two cultivars, multilocus microsatellite data refuted one of the proposed parents and indicated that both are likely to be the offspring of the same cultivar pair, ‘Gala’ × ‘Braeburn’, and can thus be considered sister cultivars. Similar, one of the parents proposed for the cultivar ‘Tunda’, which was described as an offspring of ‘Delcorf’ × ‘Liberty’ (Sansavini et al. 2012) could not be supported by molecular data and instead the parentage of ‘Delcorf’ × ‘Alkmene’ was proposed. The American cultivar ‘Prime Gold’, introduced in 1965, was assumed to be a seedling of ‘Golden Delicious’, also because of their resemblance (Morgan and Richards 2002). However, the most likely parent pair found in our database and supported by matching of multilocus microsatellite data was ‘Red Delicious’ × ‘Morgenduft’, while ‘Golden Delicious’ was excluded as a possible parent. Based on parent-offspring analysis involving only one of the potential parents, new inferences were possible for the cultivars ‘Pimona’ and ‘Reglindis’. Both cultivars were derived from the Dresden-Pillnitz breeding programme (Germany) in the 1960s. ‘Pimona’ was documented as a cross of ‘Clivia’ × ‘Undine’ (Mühl 2001) and microsatellite analysis performed by Reim et al. (2009) confirmed the maternal parent, while ‘Undine’ was excluded as the possible pollen donor. The parent-offspring analyses based on our database identified ‘Tumanga’ as an alternative cultivar that could represent the second parent of ‘Pimona’. The reported parentage of ‘Reglindis’ as ‘James Grieve’ × ‘Antonowka’ F2 was put in doubt in previous studies (Reim et al. 2009; Bus et al. 2012). It was suggested that two different genotypes of ‘Reglindis’ existed and that the commercially grown cultivar did not represent the original selection. The commercialised genotype in fact carried a rare allele at the CH-Vf1 locus, which is analysed as a marker for scab resistance. As the rare allele was known to occur in ‘Geheimrat Dr. Oldenburg’ and its progeny, it was speculated that ‘Apollo’, ‘Helios’ or ‘Alkmene’ may be a parent of the commercialised ‘Reglindis’ (Bus et al. 2012). Indeed, the parent-offspring analysis using our database identified ‘Apollo’ as a parent of ‘Reglindis’, while the parentage of the latter two cultivars was not supported. The parent-offspring relationships of ‘Pimona’ and ‘Reglindis’ proposed by our analyses appear sound as both ‘Apollo’ and ‘Tumanga’ (Syn. ‘Auralia’) were used as ancestors and are

confirmed parents of a number of cultivars derived from the Dresden-Pillnitz breeding programme (Reim et al. 2009).

It is likely that our database may have revealed a higher number of parent-offspring relationships among recent apple cultivars, for which no documented information was found. However, this group of cultivars was excluded from parentage analysis because many modern apple cultivars were derived from a limited number of founding clones and their pedigrees may be interconnected (Noiton and Alspach 1996). Consequently, genetically and genealogically closely related cultivars could be mistakenly assigned a parent-offspring relationship, especially if the number of analysed microsatellite loci is restricted (Salvi et al. 2014). This was also evident from the parentage analysis performed in the present study involving cultivars with known pedigrees. For the cultivars ‘Melrose’, ‘Rubinola’ or ‘Dalilight’ higher likelihoods of parentage were found for siblings or grandparents than for the established parents. Whether this is the case for the parent-offspring relationship of the cultivar ‘Collina’, could not be fully clarified in the present study. ‘Collina’ was described as a cross of ‘Priscilla-NL’ × ‘Elstar’, but its multilocus microsatellite profile in our database was not supported as a direct progeny of ‘Elstar’, but of ‘Santana’. The latter is an offspring of the same parent pair (‘Elstar’ × ‘Priscilla-NL’), but the maternal and paternal parent being inverted. These cultivars originated from the Dutch breeding programme and their pedigree was previously analysed by a set of 80 microsatellite markers (Evans et al. 2011). While the postulated pedigree of ‘Santana’ was fully supported by molecular genetic data, that of ‘Collina’ showed two mismatches, leading to the conclusion that “... this pedigree is not yet fully correct, but nevertheless close.” (Evans et al. 2011). Indeed, our dataset comprising a much smaller set of loci also revealed two mismatches between ‘Collina’ and ‘Elstar’ at loci CH02b10 and CH02h11a, while ‘Collina’ and ‘Santana’ showed an exact match at one of the two alleles of all analysed loci. Therefore, it could be speculated that ‘Collina’ (a cultivar from the 2000s) and ‘Santana’ (a cultivar from the 1990s) are not in a full-sibling but in a parent-offspring relationship. However, this speculation would need to be tested by analysing a larger set of microsatellite loci and including the second parent, ‘Priscilla-NL’, in the analysis, which was not available in the present study.

Hundreds of microsatellite markers have been described so far (Guilford et al. 1997; Liebhard et al. 2002; Silfverberg-Dilworth et al. 2006), leading to a high diversity of laboratory protocols and marker sets that have been employed by different laboratories (Sehic et al. 2011). Nevertheless, in the last years there has been a tendency towards harmonisation of microsatellite marker sets employed by different studies in order to allow exchange of data (Larsen et al. 2017; Lassois et al. 2016; Urrestarazu et al. 2016;

Testolin et al. 2019). Five of the microsatellite loci analysed in the present study overlapped with the marker set analysed by Urrestarazu et al. (2016), who investigated a large number of accessions from different European germplasm collections. The comparison of microsatellite data obtained in different laboratories is, however, not straightforward, as allele lengths do not represent absolute measures, but can be affected by different capillary electrophoresis systems and chemistries (Haberl and Tautz 1999; Delmotte et al. 2001). Therefore, locus- and laboratory-specific conversion values need to be applied to make datasets directly comparable (Baric et al. 2008). Another issue to be considered in this regard is the occurrence of ‘allelic drift’, which can affect the accuracy of allele binning in automated electrophoresis systems (Idury and Cardon 1997). This is the reason, why we had to apply two conversion values for some of the loci in order to align our dataset with the one of Urrestarazu et al. (2016). In the latter, a shift deviating from the expected pattern for dinucleotide microsatellite repeats with even and odd fragment lengths was observed for three of the five loci compared. Nevertheless, the application of the conversion values and the comparison of 25 cultivars analysed in both studies finally resulted in an exact correspondence of the microsatellite profiles and demonstrated that our data are comparable with those obtained in a different study. This comparison also confirmed that the triploid accessions of ‘Winesap’ that were sampled from two cultivar collections in fact represented the cultivar ‘Stayman Winesap’. The triploid genotype, which is an offspring of ‘Winesap’, seems to be maintained under the name of its parent in several European germplasm collections (Ordidge et al. 2018). In addition, the molecular genetic profiles of the cultivar ‘Wyken Pippin’ at five loci that were in common to the present study and the microsatellite dataset of Ordidge et al. (2018) showed a perfect match. Similarly, by comparing genotyping data at six microsatellite loci that overlapped among our dataset and that of Bus et al. (2012), it was possible to confirm the identity of three ‘Antonowka’ cultivars (Storti et al. 2012). However, it needs to be considered that the probability of finding identities by chance increases with the decreasing number of microsatellite loci included in the analysis. While for the dataset with 14 microsatellite loci, the combined non-exclusion probability of identity and sib identity amounted to 2.6×10^{-20} and 2.7×10^{-7} , respectively, these values were considerably higher, 5.0×10^{-8} and 3.9×10^{-3} , for the dataset with five microsatellite loci. Indeed, all the 600 genotypes included in the database could be distinguished from each other with the set of 14 and 13 microsatellite loci. When reducing the number of microsatellites to five and six loci, it was still possible to distinguish 599 genotypes, but not the cultivars ‘Jeanne Hardy’ and ‘Adersleber Kalvill’ that showed identical profiles at these loci. Consequently, a re-

duced number of microsatellite loci needs to be employed with great attention, especially if the dataset comprises data of closely related genotypes. In such a situation, the resulting identities should be used as a first indication for follow-up confirmation studies of the correctness of the molecular genetic determination.

The full set of microsatellite markers analysed in the present study showed a high degree of variability and a good resolution allowing to distinguish all 600 apple genotypes present in the database. As demonstrated in previous studies, the application of microsatellite loci was not suitable to distinguish clones or spurs of the same cultivar (e.g. Patzak et al. 2012; Gasi et al. 2016; Larsen et al. 2017). Accordingly, the microsatellite data did not permit to differentiate the common and the red clones of the cultivars ‘Gravensteiner’ and ‘Jonathan’. In addition, the same genotype was identified for the accessions denominated ‘Tiroler Spitzlederer’ and ‘Plattlederer’ indicating that this local cultivar may display a considerable degree of phenotypic plasticity. It also appears probable that the accession ‘Plattlederer’ had a falsely assigned name and that the true genotype was in fact not analysed in the present study. It is intriguing that the book “Bozner und Meraner Obstsorten” (Amonn and Meier 1934), which describes the 27 most important apple cultivars grown in the area of South Tyrol in the first half of the 20th century, only lists ‘Spitzlederer-Apfel’ (Syn. ‘Tiroler Spitzlederer’), but does not mention the cultivar ‘Plattlederer’. If ‘Tiroler Spitzlederer’ and ‘Plattlederer’ indeed represented two distinct cultivars, the former was obviously more common in the last century and could thus be preserved, while the latter, less widespread cultivar, may have become lost over time. Our database furthermore allowed identifying several synonym names, such as the synonymy of ‘Köstlicher von Zallinger’, ‘Napoleone’ and ‘Carla’ or the synonymy of ‘Stina Lohmann’ and ‘Korbiniansapfel’. Finally, the here presented database proved useful at several occasions to identify unknown or misidentified apple cultivars (Baric 2012). Therefore, apart from its application to characterise genetic resources or to manage germplasm collections, the database could serve as an important tool for quality control. This instrument could prove useful for the selection of parents and the confirmation of crosses in breeding programmes, for the confirmation of true-to-type ness during the production of propagation and planting material in nurseries or to verify the cultivar declaration in the retail process of fresh and/or processed apple fruit.

Acknowledgements The following people and institutions are greatly acknowledged for providing samples of apple cultivar accessions: M. Kellerhals (Agroscope Research Station), S. Bernkopf (Austrian Agency for Health and Food Safety, AGES Linz), M. Adam (Private Collection Adam, Hünfelden-Heringen), B. Kajtna (Arche Noah—the Austrian Seed Savers Association, Schiltern), H.-J. Bannier (Private Collection Bannier, Bielefeld), P. Modl (Institute of Horticulture and

Viticulture, University of Natural Resources and Applied Life Sciences, Vienna), E. Schulte (Bundessortenamt Prüfstelle Wurzen), G. Bassi (Bassi Vivai Cuneo), A. Martinelli (Consorzio Italiano Vivaisti, S. Giuseppe di Comacchio), L. Berra (Agrion, Cuneo), Corvinus University of Budapest, F. Fernandez (East Malling Research), P. Magnago (Fondazione Edmund Mach di San Michele all'Adige), S. Monschein, T. Rühmer (Versuchsstation Obst- und Weinbau Haidegg), G. Bachelier (Jardin du Luxembourg, Paris), K. Vogl, L. Wurm (Höhere Bundeslehranstalt und Bundesamt für Wein- und Obstbau Klosterneuburg), U. Mayr (Kompetenzzentrum Obstbau Bavendorf), M. Kobelt (Lubera AG, Buchs), R. Stainer (Laimburg Research Centre for Agriculture and Forestry), C. Soldavini (Monastero SS. Pietro e Paolo, Germagno), H. Koike (Nagano Fruit Tree Experiment Station), M. Ordidge (National Fruit Collection in Brogdale), A. Wilfling (OIKOS – Institut für angewandte Ökologie & Grundlagenforschung, Gleisdorf), R. Stehr (Obstbauzentrum Jork Esteburg), J. Stein (Obst- und Kulturweg Ratzinger Höhe, Rosenheim), K. Dianat (Obst- und Weinbauzentrum der Landwirtschaftskammer Kärnten, St. Andrä), B. Escande (Pépinières Escande ‘Millet’, Saint Vite), H. W. Schreweis, H.-T. Bosch (Pomologen-Verein e.V. Baden-Württemberg), H. Daepf (Verein Obstsortensammlung Roggwil), M. Matter[†] (Conservation Orchard Alsace, Alteckendorf), C. Holler (Sortengarten Burgenland, Neuhaus am Klausenbach), K. Werth, M. Bradlwarter (Sortenerneuerungskonsortium Südtirol, Terlan), H. Nybom (Swedish University of Agricultural Sciences, Uppsala), S. Schnell, M. Heinz (Landwirtschaftliche Lehranstalten Triesdorf), S. Tartarini, R. Gregori (Department of Agricultural Sciences, University of Bologna), G. Mezzalira, M. Giannini, L. Schiavon, F. Salmaso (Veneto Agricoltura – Agenzia Veneta per il Settore Primario, Legnaro) and Br. Franz (Zisterzienserabtei Stift Stams). The authors thank C. Kerschbamer and I. Wild for exceptional technical assistance, W. Radmüller for programming the “Apple Fingerprint Identifier” Access database for identification of unknown genotypes and H.-J. Bannier for critical comments on the manuscript. The study was conducted in the course of the projects “GENE-SAVE” and “APPLE-FINGERPRINT” funded by the European Union under the INTERREG IIIA programme between Italy and Austria, and by the Governments of South Tyrol (Italy) and Tyrol (Austria), as well as the project “Health and Nutrition – Old and New Apple Varieties at the Service of Health” (“Apfel-Fit”, 1-1a-56) that was funded within the ERDF 2007–2013 Programme of the European Union.

The authors thank the Department of Innovation, Research and University of the Autonomous Province of Bozen-Bolzano for covering the Open Access publication costs.

Conflict of interest S. Baric, A. Storti, M. Hofer, W. Guerra and J. Dalla Via declare that they have no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Aigner K, Schalansky J (2013) Äpfel und Birnen: das Gesamtwerk. Matthes & Seitz, Berlin. ISBN 978-3-88221-051-4
- Aliotta G, Grassi G (2008) La storia naturale del melo in Europa e le radici culturali dell’Annurca. In: Aliotta G, Ciarallo A, Salerno CR (eds) Le piante e l'uomo in Campania. Le radici culturali e scientifiche. Istituto per la Diffusione delle Scienze Naturali, Torre Annunziata, pp 139–163
- Amonn W, Meier L (1934) Bozner und Meraner Obstsorten. J. F. Amonn, Bozen
- Baab G (2011) Die neuen resistenten Apfelsorten aus den Niederlanden. Öko-Obstbau 2011/1:4
- Bannier HJ (2011) Moderne Apfelzüchtung: Genetische Verarmung und Tendenzen zur Inzucht. Erwerbs-Obstbau 52:85–110
- Baric S (2012) Molecular tools applied to the advancement of fruit growing in South Tyrol – a review. Erwerbs-Obstbau 54:125–135
- Baric S, Monschein S, Hofer M, Grill D, Dalla Via J (2008) Comparability of genotyping data obtained by different procedures – an interlaboratory survey. J Hortic Sci Biotechnol 83:183–190
- Baric S, Storti A, Hofer M, Dalla Via J (2009) Molecular genetic characterisation of apple cultivars from different germplasm collections. Acta Hortic 817:347–353
- Baric S, Storti A, Hofer M, Dalla Via J (2012) Resolving the parentage of the apple cultivar ‘Meran’. Erwerbs-Obstbau 54:143–146
- Bartha-Pichler B, Brunner F, Gersbach K, Zuber M (2005) Rosenapfel und Goldparmäne. 365 Apfelsorten – Botanik, Geschichte und Verwendung. AT Verlag, Baden, München. ISBN 3-03800-209-7
- Bernkopf S (2011) Von Rosenäpfeln und Landbirnen. Ein Streifzug durch Oberösterreichs Apfel- und Birnensorten. Trauner, Linz
- Bernkopf S, Keppel H, Novak R (2003) Neue alte Obstsorten. Äpfel, Birnen und Steinobst, 5th edn. Club Niederösterreich, Wien. ISBN 3-7040-1350-1
- Bosch HT (2017) Pfaffenhofer Schmelzling. Sortenportraits Apfel, Erhalternetzwerk Obstsortenvielfalt, Pomologen-Verein Deutschland. <https://obstsortenerhalt.de/obstart/details/21140>. Accessed 21 Jan 2020
- Bosch HT (2006) Rambur, Renette, Rotbirn...: lebendige Vielfalt der Äpfel und Birnen. Eine Bestandsaufnahme der Apfel- und Birnensorten im Saarland und der Westpfalz. Verband der Gartenbauvereine Saarland-Pfalz, Schmelz
- Bounous G (2006) Antiche cultivar di melo in Piemonte. Supplemento al n. 52 dei “Quaderni della Regione Piemonte – Agricoltura”. Regione Piemonte, Assessorato Agricoltura, Torino
- Brown ŠK, Maloney KE (2003) Genetic improvement of apple: breeding, markers, mapping and biotechnology. In: Ferree DC, Warrington IJ (eds) Apples: botany, production and uses. CABI, Oxon, Cambridge, pp 31–59
- Bus VG, van de Weg WE, Peil A, Dunemann F, Zini E, Laurens FN, Blažek J, Hanke V, Forsline PL (2012) The role of Schmidt ‘Antonovka’ in apple scab resistance breeding. Tree Genet Genomes 8:627–642
- Cornille A, Giraud T, Smulders MJM, Roldán-Ruiz I, Gladieux P (2014) The domestication and evolutionary ecology of apples. Trends Genet 30:57–65
- Delmotte F, Leterme N, Simon JC (2001) Microsatellite allele sizing: difference between automated capillary electrophoresis and manual technique. Biotechniques 31:810–814
- Eurostat (2019) Agricultural production – orchards. Source: Statistics Explained. https://ec.europa.eu/eurostat/statistics-explained/index.php/Agricultural_production_-_orchards#Apple_trees. Accessed 21 Jan 2020
- Evans KM, Patocchi A, Rezzonico F, Mathis F, Durel CE, Fernández-Fernández F, Boudichevskaia A, Dunemann F, Stankiewicz-Kosyly M, Gianfranceschi L, Komjanc M, Lateur M, Madduri M, Noordijk Y, van de Weg WE (2011) Genotyping of pedigree apple

- breeding material with a genome-covering set of SSRs: trueness-to-type of cultivars and their parentages. *Mol Breed* 28:535–547
- Ferreira V, Ramos-Cabrer AM, Carnide V, Pinto-Carnide O, Assunção A, Marreiros A, Rodrigues R, Pereira-Lorenzo S, Castro I (2016) Genetic pool structure of local apple cultivars from Portugal assessed by microsatellites. *Tree Genet Genomes* 12:36
- Gaber R (2020) Siebenkant. Obstsortenblätter, Arche Noah. https://www.arche-noah.at/files/siebenkant_beschreibung_und_foto.pdf. Accessed 21 Jan 2020
- Garkava-Gustavsson L, Mujaju C, Sehic J, Zborowska A, Backes GM, Hietaranta T, Antonius K (2013) Genetic diversity in Swedish and Finnish heirloom apple cultivars revealed with SSR markers. *Sci Hortic* 162:43–48
- Gasi F, Kanlić K, Stroil BK, Pojskić N, Asdal Å, Rasmussen M, Kaiser C, Meland M (2016) Redundancies and genetic structure among ex situ apple collections in Norway examined with microsatellite markers. *HortScience* 51:1458–1462
- Guarino C, Santoro S, De Simone S, Lain O, Cipriani G, Testolin R (2006) Genetic diversity in a collection of ancient cultivars of apple (*Malus × domestica* Borkh.) as revealed by SSR-based fingerprinting. *J Hortic Sci Biotechnol* 81:39–44
- Guilford P, Prakash S, Zhu JM, Rikkerink E, Gardiner S, Bassett H, Forster R (1997) Microsatellites in *Malus × domestica* (apple): abundance, polymorphism and cultivar identification. *Theor Appl Genet* 94:249–254
- Haberl M, Tautz D (1999) Comparative allele sizing can produce inaccurate allele size differences for microsatellites. *Mol Ecol* 8:1347–1349
- Hampson CR, Kemp K (2003) Characteristics of important commercial apple cultivars. In: Ferree DC, Warrington IJ (eds) Apples: Botany, Production and Uses. CABI, Oxon, Cambridge, pp 61–89
- Hardy OJ, Vekemans X (2002) SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Mol Ecol Notes* 2:618–620
- Hartmann W (2003) Farbatlas Alte Obstsorten, 2nd edn. Ulmer, Stuttgart. ISBN 3-8001-4394-1
- Hartmann W (2015) Farbatlas Alte Obstsorten, 5th edn. Ulmer Verlag, Stuttgart. ISBN 978-3-8001-0316-4
- Hoffman JL, Amos W (2005) Microsatellite genotyping errors: detection approaches, common sources and consequences for paternal exclusion. *Mol Ecol* 14:599–612
- Hokanson SC, Szewc-McFadden AK, Lamboy WF, McFerson JR (1998) Microsatellite (SSR) markers reveal genetic identities, genetic diversity and relationships in a *Malus × domestica* Borkh. core subset collection. *Theor Appl Genet* 97:671–683
- Idury RM, Cardon LR (1997) A simple method for automated allele binning in microsatellite markers. *Genome Res* 7:1104–1109
- Jacobsen R (2014) Apples of Uncommon Character. Bloomsbury, New York. ISBN 978-1-62040-227-6
- Janick J (2005) The origins of fruits, fruit growing and fruit breeding. *Plant Breed Rev* 25:255–321
- Janick J, Cummins JN, Brown SK, Hemmat M (1996) Apples. In: Janick J, Moore JN (eds) Trees and tropical fruits. Fruit Breeding, vol 1. John Wiley & Sons, New York, pp 1–77
- Juniper BE, Watkins R, Harris SA (1998) The origin of the apple. *Acta Hortic* 484:27–33
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* 16:1099–1106
- Kalinowski ST, Wagner AP, Taper ML (2006) ML-Relate: a computer program for maximumlikelihood estimation of relatedness and relationship. *Mol Ecol Notes* 6:576–579
- Larsen B, Toldam-Andersen TB, Pedersen C, Ørgaard M (2017) Unravelling genetic diversity and cultivar parentage in the Danish apple gene bank collection. *Tree Genet Genomes* 13:14
- Lassois L, Denancé C, Ravon E, Guyader A, Guisnel R, Hibrand-Saint-Oyant L, Poncelet C, Lasserre-Zuber P, Feugey L, Durel CE (2016) Genetic diversity, population structure, parentage analysis, and construction of core collections in the French apple germplasm based on SSR markers. *Plant Mol Biol Rep* 34:827–844
- Leroy A (1873) Dictionnaire de Pomologie: contenant l'histoire, la description, la figure des fruits anciens et des fruits modernes les plus généralement connus et cultivés. Tome IV – Pommes, M–Z, Variétés N° 259 à 527. Dans Les Principales Librairies Agricoles et Horticoles, Angers, Paris
- Liebhard R, Gianfranceschi L, Koller B, Ryder CD, Tarchini R, Van de Weg E, Gessler C (2002) Development and characterisation of 140 new microsatellites in apple (*Malus × domestica* Borkh.). *Mol Breed* 10:217–241
- Link H (2002) Lucas' Anleitung zum Obstbau, 32nd edn. Ulmer, Stuttgart. ISBN 3-8001-5545-1
- Litt M, Hauge X, Sharma V (1993) Shadow bands seen when typing polymorphic dinucleotide repeats: some causes and cures. *Biotechniques* 15:280–284
- Luby JJ (2003) Taxonomic classification and brief history. In: Ferree DC, Warrington IJ (eds) Apples: botany, production and uses. CABI, Oxon, Cambridge, pp 1–14
- Maurizzi S (2001) Il melo. Il Sole 24 Ore Edagricole, Bologna
- Melville F, Cripps JEL (1970) Better rootstocks for apple trees. *J Agric* 11:267–269
- Morgan J, Richards A (2002) The new book of apples. Ebury, London. ISBN 978-0-09-188398-0
- Moriya S, Iwanami H, Okada K, Yamamoto T, Abe K (2011) A practical method for apple cultivar identification and parent-offspring analysis using simple sequence repeat markers. *Euphytica* 177:135–150
- Mühl F (2001) Alte und neue Apfelsorten, 4th edn. Obst- und Gartenbauverlag, München. ISBN 978-3-87596-093-8
- Müller J, Bissmann O, Poenicke W, Rosenthal H, Schindler O (1930) Deutschlands Obstsorten. Eckstein & Stähle, Stuttgart
- Neri D (2004) Low-input apple production in central Italy: tree and soil management. *J Fruit Orn Plant Res* 12:69–76
- NIAB-EMR (2016) Rootstock research at East Malling: a history. <http://www.emr.ac.uk/projects/rootstock-research-east-malling-history/>. Accessed 21 Jan 2020
- Noiton DAM, Alspach PA (1996) Founding clones, inbreeding, coancestry, and status number of modern apple cultivars. *J Am Soc Hortic Sci* 121:773–782
- Oberhofer H (2007) Obst- und Weinbau im Wandel der Zeit. Südtiroler Beratungsring für Obst- und Weinbau, Lana
- Orange Pippin (2019) Geneva crab crab-apple. Fruit varieties descriptions. <https://www.orangepippin.com/varieties/crab-apples/geneva>. Accessed 21 Jan 2020
- Ordidge M, Kirdwichei P, Baksh MF, Venison EP, Gibbings JG, Dunwell JM (2018) Genetic analysis of a major international collection of cultivated apple varieties reveals previously unknown historic heteroploid and inbred relationships. *PLoS ONE* 13:e202405
- Patzak J, Paprštein F, Henychová A, Sedláček J (2012) Comparison of genetic diversity structure analyses of SSR molecular marker data within apple (*Malus × domestica*) genetic resources. *Genome* 55:647–665
- Perazzolli M, Malacarne G, Baldo A, Righetti L, Bailey A, Fontana P, Velasco R, Malnoy M (2014) Characterization of resistance gene analogues (RGAs) in apple (*Malus × domestica* Borkh.) and their evolutionary history of the Rosaceae family. *Plos One* 9(2):e83844. <https://doi.org/10.1371/journal.pone.0083844>
- Pereira-Lorenzo S, Ramos-Cabrer AM, Diaz-Hernandez MB (2007) Evaluation of genetic identity and variation of local apple cultivars (*Malus × domestica* Borkh.) from Spain using microsatellite markers. *Genet Resour Crop Evol* 54:405–420
- Petzold H (1984) Apfelsorten, 3rd edn. Neumann-Verlag, Leipzig, Radebeul. ISBN 3-7888-0363-0
- Pompanon F, Bonin A, Bellemain E, Taberlet P (2005) Genotyping errors: causes, consequences and solutions. *Nat Rev Genet* 6:847–859

- Provincia di Vicenza (2005a) Scheda descrittiva: Ruseñente – *ITAVAGM087. Istituto di Genetica e Sperimentazione Agraria “N. Strampelli”. Banca Dati, Biodiversità del Veneto. http://biodiversita.provincia.vicenza.it/schdett.php?c=*ITAVAGM087. Accessed 21 Jan 2020
- Provincia di Vicenza (2005b) Scheda descrittiva: Talimi – *ITAVAGM073. Istituto di Genetica e Sperimentazione Agraria “N. Strampelli”. Banca Dati, Biodiversità del Veneto. http://biodiversita.provincia.vicenza.it/schdett.php?c=*ITAVAGM073. Accessed 21 Jan 2020
- Ramos-Cabrer A, Diaz-Hernandez M, Pereira-Lorenzo S (2007) Use of microsatellites in the management of genetic resources of Spanish apple cultivars. *J Hortic Sci Biotechnol* 82:257–265
- Reim S, Flachowsky H, Hanke MV, Peil A (2009) Verifying the parents of the Pillnitzer apple cultivars. *Acta Hortic* 814:319–323
- Rieger M (2006) Introduction to fruit crops. Chapter 3: Apple (*Malus domestica*). The Haworth Press, Binghampton, pp 47–64
- Rolff JH (2001) Der Apfel. Sortennamen und Synonyme. Selbstverlag Johann-Heinrich Rolff, Kiefersfelden
- Routson KJ, Reilley AA, Henk AD, Volk GM (2009) Identification of historic apple trees in the Southwestern United States and implications for conservation. *HortScience* 44:589–594
- Salvi S, Micheletti D, Magnago P, Fontanari M, Viola R, Pindo M, Velasco R (2014) One-step reconstruction of multi-generation pedigree networks in apple (*Malus × domestica* Borkh.) and the parentage of Golden Delicious. *Mol Breed* 34:511–524
- Sanders R (2012) Das Apfel-Buch. Delius Klasing, Bielefeld. ISBN 978-3-7688-3467-4
- Sansavini S, Guerra W, Pellegrino S (2012) Gli obiettivi del miglioramento genetico e le nuove varietà per l’Europa. *Riv Fruttic* 2012/11:10–25
- Schiavon M (2010) Antiche varietà di mele e pere del Veneto. Veneto Agricoltura: Azienda Regionale per i Settori Agricolo Forestale e Agroalimentare, Legnaro
- Sehic J, Garkava-Gustavsson L, Nybom H (2011) More harmonization needed for DNA-based identification of apple germplasm. *Acta Hortic* 976:277–283
- Silbereisen R, Götz G, Hartmann W (2015) Obstsorten Atlas. Nikol, Hamburg. ISBN 978-3-86820-219-9
- Silfverberg-Dilworth E, Matasci CL, Van de Weg WE, Van Kaauwen MP, Walser M, Kodde LP, Soglio V, Gianfranceschi L, Durel CE, Costa F, Yamamoto T (2006) Microsatellite markers spanning the apple (*Malus × domestica* Borkh.) genome. *Tree Genet Genomes* 2:202–224
- Smith MWG (1971) National apple register of the United Kingdom. Ministry of Agriculture, Fisheries and Food, London. ISBN 1-897604-28-9
- Stoll R (1888) Österreichisch-Ungarische Pomologie, 2nd edn. Selbstverlag, Klosterneuburg bei Wien
- Storti A, Bannier HJ, Holler C, Kajtna B, Rühmer T, Wilfling A, Soldavini C, Dalla Via J, Baric S (2013) Molekulargenetische Analyse des ‘Maschanzker’/‘Borsdorfer’-Sortenkomplexes. *Erwerbs-Obstbau* 55:99–107
- Storti A, Dalla Via J, Baric S (2012) Comparative molecular genetic analysis of apple genotypes maintained in germplasm collections. *Erwerbs-Obstbau* 54:137–141
- Szalatnay D, Frei A (2009) Wie aus einem deutschen Prinzen ein schöner Engländer wurde. *Schweiz Z Obst Weinbau* 145:11–13
- Testolin R, Foria S, Baccichet I, Messina R, Danuso F, Losa A, Scarbolo E, Stocco M, Cipriani G (2019) Genotyping apple (*Malus × domestica* Borkh.) heirloom germplasm collected and maintained by the Regional Administration of Friuli Venezia Giulia (Italy). *Sci Hortic* 252:229–237
- Thomas MR, Cain P, Scott NS (1994) DNA typing of grapevines: a universal methodology and database for describing cultivars and evaluating genetic relatedness. *Plant Mol Biol* 25:939–949
- van Treuren R, Kemp H, Ernsting G, Jongejans B, Houtman H, Visser L (2010) Microsatellite genotyping of apple (*Malus × domestica* Borkh.) genetic resources in the Netherlands: application in collection management and variety identification. *Genet Resour Crop Evol* 57:853–865
- Urrestarazu J, Denancé C, Ravon E, Guyader A, Guisnel R, Feugey L, Poncet C, Lateur M, Houben P, Ordidge M, Fernandez-Fernandez F, Evans KM, Paprstein F, Sedlak J, Nybom H, Garkava-Gustavsson L, Miranda C, Gassmann J, Kellerhals M, Suprun I, Pikunova AV, Krasova NG, Torutaeva E, Dondini L, Tartarini S, Laurens F, Durel CE (2016) Analysis of the genetic diversity and structure across a wide range of germplasm reveals prominent gene flow in apple at the European level. *BMC Plant Biol* 16:130
- Volk GM, Henk AD (2016) Historic American apple cultivars: identification and availability. *J Am Soc Hortic Sci* 141:292–301
- Votteler W (2014) Verzeichnis der Apfel- und Birnensorten. Bayrischer Landesverband für Gartenbau und Landespflege e. V., München. ISBN 978-3-87596-086-0
- Way RD, Aldwinckle HS, Lamb RC, Rejman A, Sansavini S, Shen T, Watkins R, Westwood MN, Yoshida Y (1990) Apples (*Malus*). *Acta Hortic* 290:1–62
- Webster AD, Wertheim SJ (2003) Apple rootstocks. In: Ferree DC, Warrington IJ (eds) Apples: botany, production and uses. CABI, Oxon, Cambridge, pp 91–124
- Whealy K, Thuente J (2001) Fruit, berry and nut inventory: an inventory of nursery catalogs listing all fruit, berry and nut varieties available by mail order in the United States. Seed Savers Exchange, Decorah, Iowa. ISBN 1-882424-57-3
- Widmer C, Schütz S, Inderbitzin J, Kellerhals M, Stadler P (2017) Die neue Apfelsorte Mariella. *Schweiz Z Obst Weinbau* 153:12–15
- Yoshida Y (1977) Progress of apple breeding in Japan. *Japan Agric Res Q* 11:56–59

Affiliations

Sanja Baric^{1,2} · Alberto Storti^{1,2} · Melanie Hofer¹ · Walter Guerra¹ · Josef Dalla Via³

¹ Laimburg Research Centre, Laimburg 6, Pfatten-Vadena, 39040 Auer-Ora, Italy

² Present address: Faculty of Science and Technology, Free University of Bozen-Bolzano, Universitätsplatz 5, 39100 Bozen-Bolzano, Italy

³ Department of Innovation, Research and University of the Autonomous Province of Bozen-Bolzano, Raiffeisenstraße 5, 39100 Bozen-Bolzano, Italy