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

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Abstract

Apple (\textit{Malus} \times \textit{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 \times 10^{-20} and 3.4 \times 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 \textit{Malus} \times \textit{domestica} · Cultivar identification · DNA markers · 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), Bernkopf et al. (2003) and Bernkopf (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/netahtml/PTO/index.html) and the UPOV PLUTO: Plant Variety Database (http://www.upov.int/pluto/en/).

The information about the origin of the rootstockst 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, Schiltbern                          | 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 Worzen                                                    | Germany         | 90             | 85           |
| 8   | BVC          | Bassi Viva 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           | Lainburg 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, Alteckendor                                               | France          | 1              | 1            |
| 31  | SGB          | Sortengarten Burgenland, Neuhaus am Klausenbach                                       | Austria         | 4              | 3            |
| 32  | SKS          | Sortenverwertungskonsortium 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 | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenance from collectione | 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 Parmâne                    | 2n     | UK                | Around 1826 | Historic           | –                                 | 442         | AGES, KN                         | 25             |
| 4   | Adersleber Kalvill               | 2n     | Germany           | Around 1870 | Historic           | Weißer Winterkalvill × Gravensteiner | 265       | KN, LB                             | 25             |
| 5   | African Red [Carmine 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 Parmâne (CC) | 678        | ACW, BSA, UB                      | 49; 53         |
| 7   | Alesya                           | 2n     | Belorus           | 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        | Goldparmâne × 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 (CC) | 395        | KN, VA                            | 12; 13; 54     |
| 17  | Anj2007 [Annabelle®]             | 2n     | Netherlands       | 2009  | Recent          | (Neiprincess × Gloster) × Elstar (CC) | 497        | HG, LB                            | 41; 54         |
| 18  | Anmurca                          | 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 polutoraufun-towa-j     | 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  | Apez Zagarra                     | 2n     | France            | 1800s (?) | Historic        | –                                 | 918        | JL, NFC                           | 25             |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenance from collectione | 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 × 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  | Astramel                        | 2n     | Germany           | 1993  | Recent         | Roter Astrachan × (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 [Sapora®]                | 3n     | Germany           | 2010  | Recent         | Raffzubin × Fuji                 | 487         | HG, LB                          | 41; 54         |
| 37  | Bancroft                        | 2n     | Canada            | 1935  | Old            | Forest × McIntosh (CC)           | 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, RBW | 25 |
| 40  | Baujade                         | 2n     | France            | 1988  | Recent         | X-6799 × Granny Smith (CC)      | 471         | LB, UB                          | 12; 13; 54     |
| 41  | Baumanns Renette                | 2n     | Belgium           | Around 1800 | Historic | – | 163 | AN, BOKU, HG, RW | 43 |
| 42  | BAY 3484 [Baya Marisa®]         | 2n     | Germany           | 2009  | Recent         | –                                | 642         | FEM, LB                         | 54             |
| 43  | Bec d’Oé                        | 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 |

*Note: All values are approximate and may vary depending on additional research.
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year* | Classificationb | Assumed parentage (if available)c | Profile No.4 | Sample provenance from collectione | Reference(s)f |
|-----|---------------------------------|--------|-------------------|-------|-----------------|---------------------------------|--------------|----------------------------------|---------------|
| 49  | Berner Rosen                    | 2n     | Switzerland       | 1888  | Historic        | Roter Winterkalvill×Sauergraeche | 293          | ACW, BOKU, HG, RW                  | 20; 43        |
| 50  | Bessemyanka Michurina           | 2n     | Russia            | 1912  | Old             | Skrzijaple×Komsin Bessemyanka   | 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 Renette2C1×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 Delicious2C1×Jonathan5NC  | 374          | KN, NFC                           | 49; 55        |
| 60  | Böhmischer Brünnerling          | 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  | Börlinger 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  | Bramleys 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  | Bria                            | 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  | Burchards Renette               | 2n     | Russia            | 1863  | Historic        | –                               | 961          | NFC, TR                           | 44            |
| 73  | Burgundy                        | 2n     | USA               | 1953  | Recent          | Monroe2C1× (Macoun×Antonowka)   | 686          | NFC, UB                           | 25            |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year* | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenance from collectione | Reference(s)f |
|-----|---------------------------------|--------|-------------------|-------|-----------------|----------------------------------|-------------|----------------------------------|---------------|
| 74  | Calvila San Salvatore (Syn. Calville de Saint-Saunier) | 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 d'Or             | 2n     | France            | 1948  | Old             | Roter Winterkalville × 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 37T133 (CC) | 400         | LB, VA                          | 23            |
| 80  | Caudle [Camero®]               | 2n     | USA               | 1996  | Recent          | Golden Delicious × Red Delicious (CC) | 69          | FEM, KN, LB, UB                | 39; 54        |
| 81  | Cellini                        | 2n     | UK                | Around 1828 | Historic | Peasgood Sondergletschen × unknown (?) | 14          | AGES, KN                       | 25            |
| 82  | CH101 (ACW 10442) [Galiwa®]     | 2n     | Switzerland       | 2011  | Recent          | KIR20A44 × Gala(C)               | 578         | HG, LB                          | 56            |
| 83  | Champagner Renette             | 2n     | France            | Before 1770 | Historic | –                    | 254         | ACW, AGES, BOKU, HG, LB, RW    |               |
| 84  | Chantecler [Belard®]           | 2n     | France            | 1958  | Recent          | Golden Delicious × Reinette Clochard (CC) | 696         | JL, UB                          | 25            |
| 85  | Charlamovsky                   | 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  | Chüsenrainer                   | 2n     | Switzerland       | 1861  | Historic | –                    | 615         | HG, KOB, NFC                    | 6             |
| 90  | CIV323 [Isaa®]                 | 2n     | Italy             | 2012  | Recent          | Galaxy × A3-7                   | 831         | CIV, LB                         | 41; 56        |
| 91  | CIVG198 [Modi®]                | 2n     | Italy             | 2006  | Recent          | Gala × Liberty (CC)              | 200         | KN, LB                          | 39; 56        |
| 92  | Civni [Rubens®]                | 2n     | Italy             | 2000  | Recent          | Gala × Elstar (CC)              | 65          | KN, LB                          | 13; 39; 54    |
| 93  | Civren [Renè®]                 | 2n     | Italy             | 2011  | Recent          | –                                | 834         | CIV, LB                         | 41; 54        |
| 94  | Claudius Herbstapel             | 2n     | Germany           | 1850  | Historic        | –                                | 890         | NFC, TR                         | 25            |
| 95  | Collina                        | 2n     | Netherlands       | 2001  | Recent          | Priscilla-NL × Elstar (NC)       | 469         | LB, UB                          | 13; 54        |
| 96  | Commercio                      | 2n     | USA               | Around 1865 | Historic | –                    | 669         | BVC, 2UB                        | 44            |
| 97  | Co-op 29 [Sundance®]           | 2n     | USA               | 2001  | Recent          | Golden Delicious (CC) × 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 | Classification | Assumed parentage (if available) | Profile No. | Sample provenance from collection | Reference(s) |
|-----|---------------------------------|--------|-------------------|------|----------------|----------------------------------|------------|-----------------------------------|--------------|
| 99  | Co-op 38 [GoldRush®]           | 2n     | USA               | 1995 | Recent         | Co-op 17 x Golden Delicious (CC) | 291        | KN, LB                            | 38; 54       |
| 100 | Co-op 39 [Crimson Crisp®]      | 2n     | USA               | 2004 | Recent         | Sel. 669.205 x PCF W2134         | 401        | LB, UB                            | 41; 56       |
| 101 | Co-op 43 [Juliet®]             | 2n     | USA               | 1999 | Recent         | Viking x 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 x McIntosh             | 387        | KN, NFC                           | 25          |
| 105 | Coulons Renette                | 3n     | Belgium           | 1856 | Historic       | Kasseler Renette x unknown       | 23         | AGES, KOB, NFC                    | 32; 43       |
| 106 | Cox Orange                     | 2n     | UK                | Around 1825 | Historic | Ribston Pepp x Goldrenette von Blenheim (?) | 445     | KOB, NFC | 43 |
| 107 | Cox Pomona                     | 2n     | UK                | Around 1825 | Historic | Ribston Pepp x Goldrenette von Blenheim (?) | 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 x Lady Williams (CC) | 169 | 3L, B | 12; 26; 54 |
| 110 | Cripps Red [Joya®]             | 2n     | Australia         | 1991 | Recent         | Golden Delicious x Lady Williams (CC) | 171 | 2L, B | 12; 54 |
| 111 | Daiane                         | 2n     | Brazil            | 2000 | Recent         | Gala(C) x Princes sa             | 411        | LB, UB                            | 41; 54       |
| 112 | Daliclass                      | 2n     | France            | 2008 | Recent         | Elstar x Pilot (CC)              | 580        | HG, LB                            | 41; 54       |
| 113 | Dalilight                      | 2n     | France            | 2007 | Recent         | Elstar x Cripps Pink (CC)        | 581        | HG, LB                            | 41; 54       |
| 114 | Dalinbel [Antares®]            | 2n     | France            | 1998 | Recent         | Elstar(C) x unknown              | 384        | KN, LB                            | 54          |
| 115 | Dalinco                        | 2n     | France            | 2003 | Recent         | –                                | 475        | LB, VA                            | 54          |
| 116 | Dalinette [Chouvette®]         | 2n     | France            | 2002 | Recent         | X-4598 x X-3174                  | 476        | LB, VA                            | 39; 54       |
| 117 | Dalinseet                      | 2n     | France            | 2004 | Recent         | –                                | 988        | FEM, UB                           | 54          |
| 118 | Dalitron [Altess®]             | 2n     | France            | 2005 | Recent         | Golden Delicious x Pilot (CC)    | 418        | LB, VA                            | 41; 56       |
| 119 | Damasonrenette                 | 3n     | France            | 1628 (?) | Historic | – | 38 | ACW, AGES, HG, RW | 25 |
| 120 | Dunziger 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, 2L | 25 |
| 124 | Decio (GM4)                    | 2n     | Italy             | 1500s (?) | Historic | – | 574 | NFC, UB, VA | 25 |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenance from collectione | Reference(s)f |
|-----|--------------------------------|--------|-------------------|-------|-----------------|----------------------------------|-------------|----------------------------------|--------------|
| 125 | Delblush [Tentation®]         | 2n     | France            | 1989  | Recent          | Golden Delicious× Blushing Golden (CC) | 290         | LB, VA                           | 12; 54       |
| 126 | Delcof [Delbardestivale®]     | 2n     | France            | 1977  | Recent          | Stark Jongrimes× Golden Delicious(CC) | 381         | KN, LB, NFC                      | 12; 54       |
| 127 | Delcoros [Autento®]           | 2n     | France            | 2001  | Recent          | Delgollune× Cox Orange (CC)         | 410         | LB, VA                           | 41; 54       |
| 128 | Delearly                      | 2n     | France            | 1988  | Recent          | Golden Delicious× Stark Earliest (CC) | 995         | FEM, UB                          | 12; 54       |
| 129 | Delfloki [Divine®]            | 2n     | France            | 1999  | Recent          | –                                 | 412         | LB, VA                           | 54           |
| 130 | Delflopion                    | 2n     | France            | 2004  | Recent          | –                                 | 482         | LB, VA                           | 54           |
| 131 | Delgollune (Syn. Jubilé)      | 2n     | France            | 1981  | Recent          | Golden Delicious× Lundbytrop (CC)   | 812         | BSA, NFC                         | 12; 54       |
| 132 | Delgrared                     | 2n     | France            | 1986  | Recent          | Golden Delicious× Akane (CC)        | 585         | CReSO, 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 Quarrenden         | 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 Parmâne× 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; 54       |
| 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           |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenience from collectione | Reference(s)f |
|-----|---------------------------------|--------|-------------------|------|----------------|---------------------------------|-------------|-----------------------------------|---------------|
| 150 | Edelborsdorfer (Syn. Maschanzker) | 2n     | Germany           | 1500s| Historic       | –                               | 67          | MPP, 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 | Ein                              | 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         | Septer × 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 | Erbacherhofer                    | 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                | 2n     | Austria           | Around 1880 | Historic | –                               | 270         | AGES, HG, KN, OKR                    | 8            |
| 168 | Fameuse (Syn. Schneepfel)        | 2n     | Canada (?)        | Around 1730 | Historic | –                               | 460         | BVC, TR                            | 25           |
| 169 | Fantazja                         | 2n     | Poland            | 1944 | Old            | McIntosh(C) × Linda             | 826         | NFC, SLU                           | 25           |
| 170 | Faros                            | 2n     | France            | 1800s| Historic       | –                               | 898         | JL, NFC, TR                        | 25           |
| 171 | Fearn's Pippin                   | 2n     | UK                | Before 1780 | Historic | –                               | 893         | BVC, NFC                           | 25           |
| 172 | Fenouillet Rouge                 | 2n     | France (?)        | 1873 | Historic       | –                               | 937         | JL, NFC                            | 25           |
| 173 | Fiebers 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 | Filippa                          | 2n     | Denmark           | 1877 | Historic       | –                               | 800         | NFC, SLU                           | 49           |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year<sup>a</sup> | Classification<sup>b</sup> | Assumed parentage (if available)<sup>c</sup> | Profile No.<sup>d</sup> | Sample provenance from collection<sup>e</sup> | Reference(s)<sup>f</sup> |
|-----|---------------------------------|--------|-------------------|-----------------|-----------------|---------------------------------|-----------------|---------------------------------|------------------|
| 176 | Finkenwerder Prinzenapfel       | 2n     | Germany           | Around 1860     | Historic        | –                               | 592             | KOB, NFC, OKR                     | 43               |
| 177 | Florianer Rosmarin             | 2n     | Austria           | Around 1860     | Historic        | –                               | 269             | AGES, KN, LB                      | 7                |
| 178 | Florina [Querina®]             | 2n     | France            | 1977            | Recent          | PRI 612-1 × Jonathan<sup>(C)</sup> | 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<sup>(C)</sup> | 480             | LB, VA                           | 41; 54           |
| 182 | Fraurotacher (Syn. Franc        | 2n     | Switzerland       | Before 1850     | Historic        | –                               | 75              | ACW, NFC, RW                      | 25               |
|     | Roseau, Chataigne de Leman)     |        |                   |                 |                 |                                  |                 |                                  |                  |
| 183 | Freedom (NY58553-1)            | 2n     | USA               | 1983            | Recent          | –                               | 679             | 2UB                              | 43               |
| 184 | Fresco (CPRO47) [Wellant®]     | 2n     | Netherlands       | 2002            | Recent          | Selezione × Elise<sup>(C)</sup>  | 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        | Bismarkapfel × unknown           | 56              | KOB, SLU                         | 49               |
| 187 | Fromms Goldrenette (Syn.        | 3n     | Germany           | 1869            | Historic        | Edelborsdorfer × unknown         | 714             | BB, OKR, TR                       | 26; 47           |
|     | Seebaer Borsdorfer)            |        |                   |                 |                 |                                  |                 |                                  |                  |
| 188 | Frureru [Red Boy®]             | 2n     | Switzerland       | 2002            | Recent          | Redwinter × Raffuzbin<sup>(C)</sup> | 500             | LB, UB                           | 41; 54           |
| 189 | Fuji                           | 2n     | Japan             | 1962            | Recent          | Ralls Janet × Red Delicious<sup>(C)</sup> | 154             | CIV, FEM, KN, LB                 | 49               |
| 190 | Fujion                         | 2n     | Italy             | 2011            | Recent          | U7L-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<sup>(C)</sup> × A3-7         | 832             | CV, 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 | Gambong                        | 2n     | South Korea       | 1998            | Recent          | –                               | 409             | LB, UB                           | 54               |
| 197 | Gartenmeister Simon            | 2n     | Germany           | 1939            | Old             | –                               | 752             | BSA, KOB, OKR                     | 49               |
| 198 | Gascoynes Scharfachsammlung    | 2n     | UK                | 1871            | Historic        | –                               | 4               | AGES, KOB, NFC                    | 25               |
| 199 | Geflammtter Kardinal           | 3n     | Germany           | 1801            | Historic        | –                               | 165             | AGES, HG, KOB                     | 17               |
| 200 | Geheimrat Breuhahn             | 2n     | Germany           | 1895            | Historic        | Halberstäder Jungfernsapfel × unknown | 600             | BSA, KOB, NFC                     | 49               |
| 201 | Geheimrat Dr. Oldenburg        | 2n     | Germany           | 1897            | Historic        | Minister von Hammerstein × Baumanns Renette | 264             | ACW, BOKU                        | 43               |
| 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 | Gehlers 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             | Elstar($^c$) × TSR15T3               | 978            | OKR, UB                         | 12; 22; 54     |
| 211 | Gestreifter Titowa             | 2n     | Russia            | 1876       | Historic           | –                                    | 567            | KOB, TR                         | 44             |
| 212 | Gewürztrauben                  | 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 | Glorie von Holland             | 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              |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year | Classification | Assumed parentage (if available) | Profile No. | Sample provenance from collection | Reference(s) |
|-----|--------------------------------|--------|-------------------|------|---------------|------------------------------|------------|--------------------------------|--------------|
| 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 Api | 2n | France (?) | 1873 (?) | Historic | – | 897 | JL, NFC | 25 |
| 236 | Grüner Stettiner | 3n | n.a. | Around 1700 | Historic | – | 151 | AGES, KN | 26 |
| 237 | Halberstädter Jungfernaphel | 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. | M. baccata | – | 211 | FEM, LB | 33 |
| 240 | Harberts Renette | 3n | Germany | 1828 | Historic | Golden Reinette × unknown | 79 | HG, LB, NFC | 25, 32 |
| 241 | Harmenz (Vrds0401) [Rembrandt®] | 2n | Netherlands | 2006 | Recent | – | 499 | HG, LB | 54 |
| 242 | Hausmütterehen | 3n | Ukraine | 1805 | Historic | – | 701 | KOB, TR | 8 |
| 243 | Hausapfel | 2n | Germany | 1920s | Old | Roter Trierscher Weinapfel® × 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® × unknown | 822 | BSA, NFC | 49 |
| 246 | Herma | 2n | Germany | 1930s | Old | Jonathan® × 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 Holovous | 2n | Czech Republic | Around 1850 | Historic | – | 202 | KN, OWL | 16 |
Table 2 (Continued)

| No. | Cultivar name | Trademark name® | Ploidy | Country of origin | Year of origin | Assumed parentage (if available) | Classification | Sample provenance from collection | Profile No. | Reference(s) |
|-----|---------------|-----------------|--------|-------------------|----------------|----------------------------------|----------------|-----------------------------------|-------------|--------------|
| 260 | Ingrid Marie  | 2n              | France | 1910              |                | Recent                           | Historic       | AGES, BOKU                        | 203         | 13; 25       |
| 261 | Jakob Fischer | 3n              | Germany | 1903              |                | Old                              | Historic       | AGES, KN                          | 309         | 43           |
| 262 | Jakob Lebel   | 3n              | Germany | 1825              |                | Old                              | Historic       | AGES, KN                          | 298         | 43           |
| 263 | Jamba 69      | 2n              | Austria | n.a.              |                | Historic                         |                | AGES, KN                          | 116         | 43           |
| 264 | James Grieve  | 2n              | UK     | 1853              |                | Old                              | Historic       | ACW, KN                           | 611         | 12; 43       |
| 265 | Jeanne Hardy  | 2n              | France | 1878              |                | Old                              | Historic       | BOKU, KN                          | 1844        | 43           |
| 266 | Jerseymum     | 2n              | USA    | 1956              |                | Recent                           | Historic       | BOKU, KN                          | 382         | 43           |
| 267 | Jonaace (Co-122) | 2n          | USA    | 1979              |                | Recent                           | Historic       | BOKU, KN                          | 760         | 43; 39       |
| 268 | Jonagold      | 2n              | USA    | 1943              |                | Old                              | Historic       | BOKU, KN                          | 81          | 15; 32       |
| 269 | Jonatan       | 2n              | Ukraine | 1864              |                | Old                              | Historic       | BOKU, KN                          | 350         | 13; 24       |
| 270 | Joseph Massch | 2n              | Belgium | 1872              |                | Recent                           | Historic       | BOKU, KN                          | 614         | 12; 13; 54  |
| 271 | Julia         | 2n              | Czech Republic | 1986          |                | Recent                           | Historic       | BOKU, KN                          | 773         | 25           |
| 272 | July Red      | 2n              | USA    | 1949              |                | Old                              | Historic       | BOKU, KN                          | 517         | 25           |
| 273 | Jupiler       | 2n              | UK     | 1966              |                | Recent                           | Historic       | BOKU, KN                          | 845         | 19           |
| 274 | Kaiser Alexander | 3n           | Germany | 1864              |                | Old                              | Historic       | BOKU, KN                          | 17008       | 32; 43       |
| 275 | Kaiser Wilhelm | 3n              | Germany | 1864              |                | Old                              | Historic       | BOKU, KN                          | 1864        | 32; 43       |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year | Classification | Assumed parentage (if available) | Profile No. | Sample provenance from collection | Reference(s) |
|-----|---------------------------------|--------|-------------------|------|----------------|--------------------------------|------------|----------------------------------|--------------|
| 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 | Kammeliner Renette              | 2n     | France            | 1667 | Historic        | –                              | 219        | LB, TR                           | 49           |
| 283 | Kammijn de Sonnville            | 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 Pomäne (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 Spitzenburgh × 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 | Krippel 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 | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenance from collectione | 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 | Lavanttaler 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 | Ligolna                         | 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 Klanaufel[C] | 595          | KOB, NFC, SLU                    | 25            |
| 313 | Lohrer Rambur (Syn. Schwaikheimer 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 Grievex 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        |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year | Classification | Assumed parentage (if available) | Profile No. | Sample provenance from collection | Reference(s) |
|-----|---------------------------------|--------|------------------|------|----------------|---------------------------------|------------|----------------------------------|--------------|
| 322 | Lureprec (LUB A0905) [Circe®/Redlove®] | 2n     | Switzerland      | 2009 | Recent         | Weirouge(C) × Series Re        | 830        | LAG, LB                          | 41; 54       |
| 323 | Luressweet [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         | Fraerotacher × 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 | Malus floribunda 821            | 2n     | Japan            | n.a.    | M. floribunda  | –                  | 3          | FEM                              | 33           |
| 347 | Mantet                           | 2n     | Canada           | 1928    | Old            | Tetofsky × unknown     | 816        | NFC, SLU                         | 43           |
| 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 (CC) | 842            | BSA, NFC                          | 26; 38         |
| 349 | Marielle (Riky 2000) [Lola®]    | 2n     | Netherlands       | 2007     | Recent          | (Gloster × Meiprinces) × Elstar$^{(C)}$ | 498            | HG, LB                            | 41; 54         |
| 350 | Mariella (ACW 06375)            | 2n     | Switzerland       | 1982     | Recent          | Maigold × Arlet (CC)                  | 577            | HG, LB                            | 52             |
| 351 | Martina                         | 2n     | Switzerland       | 1970     | Recent          | Kids Orange × Idared (CC)             | 631            | LB, UB                            | 6              |
| 352 | Martini                         | 2n     | Germany           | 1875     | Historic        | Cox Orange × unknown (? )             | 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 Parmäne (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 Scharlachsämmling$^{(NC)}$ × 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 Renette × unknown         | 17             | AGES, KN                          | 25             |
| 366 | Minneiska [Sweetango®]          | 2n     | USA               | 2005     | Recent          | Honeycrisp × Minnewashta$^{(C)}$      | 508            | HG, LB                            | 41; 56         |
| 367 | Minnewashta [Zestar®]           | 2n     | USA               | 1997     | Recent          | State Fair × MN 1691                  | 522            | LB; parent to Minneiska           | 56             |
| 368 | Mio                             | 2n     | Sweden            | 1932     | Old             | Worcester Parmäne$^{(C)}$ × Oranie    | 837            | NFC, SLU                          | 25             |
| 369 | MM.101                          | 2n     | UK                | 1950     | Rootstock       | Northern Spy$^{(C)}$ × unknown        | 343            | BSA, EMR                          | 29             |
| 370 | MM.102                          | 2n     | UK                | 1950     | Rootstock       | Northern Spy$^{(C)}$ × unknown        | 344            | BSA, EMR                          | 29             |
| 371 | MM.104                          | 2n     | UK                | 1950     | Rootstock       | Northern Spy × M.2 (CC)               | 346            | BSA, EMR                          | 29; 50         |
| 372 | MM.105                          | 2n     | UK                | 1950     | Rootstock       | Northern Spy$^{(C)}$ × unknown        | 347            | BSA, EMR                          | 29             |
| 373 | MM.106                          | 2n     | UK                | 1950     | Rootstock       | Northern Spy × M.1 (CC)               | 284            | BSA, EMR                          | 29; 50         |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year | Classification | Assumed parentage (if available) | Profile No. | Sample provenance from collection | Reference(s) |
|-----|---------------------------------|--------|-------------------|------|---------------|-------------------------------|------------|-----------------------------------|--------------|
| 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 × unknown        | 551        | BSA, EMR                         | 29          |
| 376 | MM.111                          | 2n     | UK                | 1950s| Rootstock     | Northern Spy × 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 | Neveson [Sonya®]                | 2n     | New Zealand       | 1996 | Recent        | Gala × Red Delicious (NC)     | 68         | LB, UB                           | 39; 56      |
| 386 | Nicogreen [Greenstar®]          | 2n     | Belgium           | 2001 | Recent        | Delcor × 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 × Braebum (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 (CC), 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 Muskatrenette     | 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      | Wagener 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 × Ouva        | 765        | FEM, LB                          | 41; 56      |
Table 2 (Continued)

| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample presence from collectione | Reference(s)f |
|-----|---------------------------------|--------|-------------------|-------|-----------------|----------------------------------|-------------|----------------------------------|---------------|
| 401 | Orleans Renette                 | 3n     | France (?)        | 1776  | Historic        | Golden Reinette x 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 x Jonala                | 303         | LB; parent to Orion               | 38; 54        |
| 405 | Pamyat Syubarovoj               | 2n     | Russia            | 1992  | Recent          | –                                 | 663         | LB, UB                            | 54           |
| 406 | Parfum d’Eût                    | 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 | Pfaffenhof 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          | Undine/C x Helios (CC)            | 739         | FEM, UB                           | 26           |
| 412 | Pigeon de Jerusalem (Syn. Roter Wintertaubenapfel) | 2n | France | Late 1600s (?) | Historic | – | 936 | JL, NFC | 25 |
| 413 | Pikant                          | 2n     | Germany           | 1962  | Recent          | Undine/C x Kalco                 | 815         | BSA, SLU                          | 26           |
| 414 | Pikkolo                         | 2n     | Germany           | 1993  | Recent          | Clivia x Tumanga/C                | 989         | BSA, NFC                          | 25           |
| 415 | Pilot                           | 2n     | Germany           | 1962  | Recent          | Clivia x Undine/C                 | 208         | KN, LB                            | 26           |
| 416 | Pimona                          | 2n     | Germany           | 1962  | Recent          | Clivia x Undine/NC                | 813         | BSA, SLU                          | 26           |
| 417 | Pingo                           | 2n     | Germany           | 1995  | Recent          | Undine/C x Bancroft (CC)          | 734         | FEM, OKR                          | 26           |
| 418 | Pink Pearl                      | 2n     | USA               | 1944  | Old             | –                                 | 1032        | ACW, BV                          | 51           |
| 419 | Pinova                          | 2n     | Germany           | 1965  | Recent          | Undine/C x Golden Delicious/C     | 207         | FEM, KN, LB, UB                   | 26           |
| 420 | Pirella [Pino®]                 | 2n     | Germany           | 1992  | Recent          | Golden Delicious x Alkmene (CC)   | 996         | FEM, UB                           | 41; 54       |
| 421 | Piros                           | 2n     | Germany           | 1963  | Recent          | Helios x Apollo (CC)              | 724         | FEM, OWL                          | 26           |
| 422 | Plumac (Kotabarù) [Koru®]       | 2n     | New Zealand       | 2010  | Recent          | Fuji/NC x Braeburn/C              | 722         | 2LB                               | 56           |
| 423 | Pohorka                         | 2n     | Slovenia          | 1960  | Recent          | Cox Orange x Ontario (CC)         | 602         | KOB, NFC                          | 49           |
| 424 | Pomme Violette                  | 2n     | France            | 1628  | Historic        | –                                 | 919         | JL, NFC                           | 25           |
| 425 | Pomo Ruseneite                  | 2n     | Italy, Veneto     | n.a.  | Historic (local) | –                                 | 1070        | 2VA                               | 35           |
| 426 | Prem A17 [Smitten®]             | 2n     | New Zealand       | 2010  | Recent          | A045R13T007 x A020R02T167         | 586         | CReSO, LB                         | 56           |
| 427 | Prem A280 [Sweetie®]            | 2n     | New Zealand       | 2005  | Recent          | Braeburn x Royal Gala (CC)        | 511         | FEM, LB                           | 41; 56       |
| 428 | Priam (370-16)                  | 2n     | USA and France    | 1956  | Recent          | PRI 14-126 x Jonathan/C           | 697         | JL, UB                            | 26; 43       |
| 429 | Prima (Co-op 2)                 | 2n     | USA               | 1960  | Recent          | –                                 | 393         | KN, NFC                           | 26; 43       |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenance from collectione | 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 Preußen      | 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      | 1766  | Historic        | –                               | 572         | BSA, KOB, NFC                     | 25            |
| 438 | Rafzubin [Rabinette®]           | 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 Papelou                 | 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: Malus floribunda   | 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: Antonowa | 723         | FEM, UB                           | 26            |
| 450 | Reinette Clochard               | 2n     | France           | Mid 1800s | Historic              | –                               | 695         | JL, NFC, UB                       | 25            |
| 451 | Reinette d'Armorique            | 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: Malus pumila | 759         | BSA, UB                           | 26; 43        |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenance from collectione | Reference(s)f |
|-----|--------------------------------|--------|-------------------|-------|----------------|---------------------------------|------------|-----------------------------------|--------------|
| 456 | Releta                         | 2n     | Germany           | 1984  | Recent         | –                               | 771        | BSA, UB                           | 43           |
| 457 | Remo                           | 2n     | Germany           | 1984  | Recent         | James Grieve® × F3: Malus floribunda | 397        | KN, VA                            | 12; 26; 54   |
| 458 | Remura                         | 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 Bihorel            | 2n     | France            | 1859  | Historic       | –                               | 1042       | ACW, TR                           | 6            |
| 461 | Resi                           | 2n     | Germany           | 1992  | Recent         | Clivia × scab 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® × F3: Malus floribunda   | 737        | FEM, UB                           | 26; 43       |
| 464 | Rewena                         | 2n     | Germany           | 1988  | Recent         | (Cox Orange × Geheimrat Dr. Oldenburg) × F3: Malus floribunda | 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 Netherland | 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 Sondergleichen × 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. Steirishe Schafnase) | 2n | Austria | Around 1800 | Historic | – | 279 | HG, KN, ZASS | 8 |
| 476 | Rote Sternmenette              | 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 Eiserapfel               | 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 | Classification | Assumed parentage (if available) | Profile No. | Sample provenance from collection | Reference(s) |
|-----|---------------------------------|--------|-------------------|------|----------------|----------------------------------|------------|----------------------------------|--------------|
| 481 | Roter Jungfemapfel              | 2n     | Austria (?)       | Before 1800 | Historic | – | 27 | AGES, KN, KOB | 8 |
| 482 | Roter Rosmarinapfel             | 2n     | Austria           | 1839 | Historic | – | 363 | LB, MSPP | 45 |
| 483 | Roter Stettiner                 | 3n     | Germany           | 1776 | Historic | – | 251 | LB, OWL | 25 |
| 484 | Roter Trierscher Weinapfel      | 2n     | Germany           | 1872 | Historic | – | 70 | BOKU, KOB, ZASS | 17 |
| 485 | Roter von Simonffii             | 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 | Rünsé                           | 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   | PR1 1235 × Golden Delicious (C) | 587 | CReSO, FEM | 25; 39 |
| 497 | Sauergnauch                     | 2n     | Switzerland       | 1800s | Historic | – | 456 | BOKU, KN, RW | 49 |
| 498 | Schmalprinz                     | 2n     | Germany           | Before 1941 | Old | – | 1072 | KOB, TR | 38 |
| 499 | Schmidtberger Renette           | 2n     | Austria           | Around 1832 | Historic | – | 94 | AGES, KN, LB, ZASS | 25 |
| 500 | Schneiderapfel                  | 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 Herrenhut           | 2n     | Germany           | 1880 | Historic | – | 612 | KOB, NFC | 49 |
| 503 | Schöner aus Pontoise            | 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 Wiltshire           | 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 |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year | Classification<sup>a</sup> | Assumed parentage (if available)<sup>b</sup> | Profile No.<sup>c</sup> | Sample provenance from collection<sup>d</sup> | Reference(s)<sup>f</sup> |
|-----|----------------------------------|--------|-------------------|------|------------------|---------------------------------|-----------------|---------------------------------|-----------------|
| 509 | Sciearly [Pacific Beauty®]       | 2n     | New Zealand       | 1993 | Recent           | Gala×Splendour (CC)              | 509             | LB, UB                          | 12; 54          |
| 510 | Scifresh [Jazz®]                 | 2n     | New Zealand       | 1997 | Recent           | Gala×Braeburn (CC)              | 417             | HG, LB                          | 41; 54          |
| 511 | Scired [Pacific Queen®]          | 2n     | New Zealand       | 1993 | Recent           | Gala×Splendour (CC)              | 510             | LB, UB                          | 12; 54          |
| 512 | Sciros [Pacific Rose®]           | 2n     | New Zealand       | 1989 | Recent           | Gala×Splendour (CC)              | 524             | LB, UB                          | 12; 54          |
| 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            | 2n     | USA               | Before 1972 | Recent |                      |                   | 986             | 2UB                            | 56 (mentioned as parent cultivar) |
| 515 | Senshu                           | 2n     | Japan             | 1978 | Recent           | Jonathan×Golden Delicious (CC)   | 981             | 3UB                            | 54              |
| 516 | Septer                           | 2n     | Netherlands       | After 1952 | Recent |                      |                   | 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; 54          |
| 519 | Shinagold                        | 2n     | n.a.              | n.a. | Recent           | –                               | 732             | LB, PEM                         | 57              |
| 520 | Shinano Gold [yello®]            | 2n     | Japan             | 1996 | Recent           | Golden Delicious×Senshu (CC)     | 419             | LB, NES, OJE, SKS                | 41; 54          |
| 521 | Siebenkant                       | 2n     | Austria           | n.a. | Historic?        | Seedling Minister von Hammerstein (?) | 295         | BOKU, KN, ZASS                   | 14              |
| 522 | Signe Tillisch                   | 2n     | Denmark           | 1866 | Historic         | Weißer Winterkalvi×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             | CRSeO, LB, SKS                   | 56              |
| 525 | Sinta                            | 2n     | Canada            | 1955 | Recent           | Golden Delicious<sup>c</sup>×Grimes Golden<sup>NC</sup> | 982             | NFC, UB                         | 25              |
| 526 | Sir Prize (Co-op 5)              | 3n     | USA               | 1975 | Recent           | Doud Golden Delicious<sup>4n</sup>×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<sup>c</sup> | 805             | BOKU, BSA                       | 38              |
| 530 | Sonnenwirtsapfel                  | 3n     | Germany           | 1932 | Old              | Geflammert Kardinal×unknown (?)  | 777             | BSA, KOB, TR                    | 17              |
| 531 | Spartan                           | 2n     | Canada            | 1926 | Old              | McIntosh×Red Delicious (CC)      | 385             | KN, NFC                         | 25; 39          |
| 532 | Spätblühender Taffet              | 2n     | Germany           | 1872 | Historic         | –                               | 240             | AGES, KN, NFC                   | 43              |
Table 2 (Continued)

| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year | Classificationa | Assumed parentage (if available)c | Profile No. | Sample provenance from collectiond | 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 (CPRO133) [Allure®]      | 2n     | Netherlands      | 2014 | Recent          | Golden Delicious (C) × 1980-015-047| 484        | HG, LB                            | 3              |
| 536 | SQ159 (CPRO159) [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 Maschanzer         | 2n     | Austria (?)      | Before 1800 | Historic    | –                                 | 78         | AN, BOKU, HG, KN, OKOS, SGB       | 8; 47          |
| 541 | Steirischer Passamaner         | 2n     | Austria (?)      | 1891 | Historic        | –                                 | 861        | 2OKOS                             | 8 (p. 230); 47 |
| 542 | Steina Lohmann (= Korbiniantsapfel) | 2n | Germany        | 1841 | Historic        | –                                 | 117        | BVC, JL, RW                       | 44             |
| 543 | Straualdts Goldpørmæne (Syn. Neue Goldpørmæne) | 2n | Germany | 1905 | Old | Goldpørmæne (C) × Parkers Pepping (NC) | 312 | KOB, NFC, RW | 25; 49 |
| 544 | Summerfree                     | 2n     | Italy            | 1998 | Recent          | Golden Delicious (C) × PRI 1956-6  | 474        | LB, VA                            | 23             |
| 545 | Summerred                      | 2n     | Canada           | 1961 | Recent          | Summerland × unknown              | 380        | KN, NFC                           | 26             |
| 546 | Sunset                         | 2n     | UK               | 1933 | Old             | Cox Orange × James Grieve (CC)     | 850        | NFC, TR                           | 32; 40         |
| 547 | Suntan                         | 3n     | UK               | 1956 | Recent          | Cox Orange × Königlicher Kurzstiel | 762        | BSA, JL, NFC                      | 25; 32         |
| 548 | Süßer Pfaffenpapf              | 2n     | Switzerland      | 1850 | Historic        | –                                 | 754        | KOB, RW                           | 6              |
| 549 | Talimi                         | 2n     | Italy, Veneto    | n.a. | Historic (local) | –                                 | 1074       | 2VA                               | 36             |
| 550 | Telamon (Syn. Waltz)           | 2n     | UK               | 1976 | Recent          | McIntosh, Wijcik × Golden Delicious (CC) | 997 | NFC, UB | 25 |
| 551 | Thurgauer Weinapfel            | 2n     | Switzerland      | 1860 | Historic        | Fraurotacher × unknown (?)         | 622        | ACW, KOB, TR                      | 49             |
| 552 | Tiroler Maschanzer             | 2n     | Austria          | n.a. | Historic (local) | –                                 | 860        | HG, SGB                           | 47             |
| 553 | Tiroler Spitzlederer           | 2n     | Italy, South Tyrol | 1855 | Historic       | –                                 | 174        | KN, LB, MSPP, NFC                 | 25             |
| 554 | Tobiasler                      | 2n     | Switzerland      | 1805 | Historic        | –                                 | 1040       | ACW, NFC                          | 25             |
| 555 | Topaz                         | 2n     | Czech Republic   | 1991 | Recent          | Rubin (C) × Vanda                  | 140        | KN, LB                            | 41; 54         |
| 556 | Trajan (Syn. Polka)            | 2n     | UK               | 1976 | Recent          | McIntosh, Wijcik × Golden Delicious (CC) | 829 | NFC, SLU | 25 |
| No. | Cultivar name [Trademark name®] | Ploidy | Country of origin | Year | Classification | Assumed parentage (if available) | Profile No. | Sample provenance from collection | Reference(s) |
|-----|---------------------------------|--------|-------------------|------|---------------|----------------------------------|------------|-----------------------------------|--------------|
| 558 | Transparent aus Croncels | 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 | Delcort (C) × Liberty (NC) | 491 | LB, VA | 41; 54 |
| 561 | Tuscan (Syn. Bolero) | 2n | UK | 1976 | Recent | McIntosh, Wijcik × Greensleves (CC) | 827 | NFC, SLU | 25 |
| 562 | UEB 26002 [Mars®] | 2n | Czech Republic | 2005 | Recent | Topaz × Golden Delicious (CC) | 501 | FEM, LB | 54 |
| 563 | UEB 32642 [Opal®] | 2n | Czech Republic | 2001 | Recent | – | 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 | ACW, NFC | 43 |
| 566 | Ustertafel | 2n | Switzerland | 1760 | Historic | – | 543 | ACW, RW, TR | 6 |
| 567 | Van Mons Renette | 2n | Belgium | 1821 | Historic | – | 950 | JI, TR | 44 |
| 568 | Vernade (Syn. Versane) | 2n | France | 1948 | Old | – | 940 | JI, NFC | 25 |
| 569 | Vésna | 2n | Czech Republic | 1996 | Recent | – | 778 | BSA, FEM | 54 |
| 570 | Vista Bella | 2n | USA | 1956 | Recent | – | 900 | ACW, BS, NFC | 25 |
| 571 | Wagener Apfel | 2n | USA | 1791 | Historic | – | 257 | KOB, LB, NFC | 25 |
| 572 | Wealthy | 2n | USA | Around 1861 | Historic | – | 802 | JI, NFC, SLU | 25; 49 |
| 573 | Weidner's 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 | Weiße Griesapfel | 2n | Austria | 1800s | Historic | – | 378 | HG, KN | 38 |
| 577 | Weiße Klapfapfel | 2n | Russia | Early 1800s | Historic | – | 98 | AN, HG, KN, ZASS | 25 |
| 578 | Weiße Rosmarin | 2n | Italy, South Tyrol | Early 1800s | Historic | – | 294 | AGES, BOKU, LB | 25 |
| 579 | Weiße Winterkalvill | 2n | France | 1596 | Historic | – | 249 | BOKU, KN, MSPP | 43 |
| 580 | Weiße Wintertoffetapfel | 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 | Welschbrunner | 3n | Austria | 1825 | Historic | – | 55 | KN, KOB | 49 |
| 584 | Wettriner 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 | Yeara | Classificationb | Assumed parentage (if available)c | Profile No.d | Sample provenance from collectione | Reference(s)f |
|-----|---------------------------------|--------|-------------------|-------|----------------|-------------------------------|-------------|----------------------------------|----------------|
| 586 | Wilstedter                       | 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 | Xeleven [Swing®]                 | 2n     | France            | 2018    | Recent         | –                             | 728         | LB, PEM                           | 55             |
| 593 | YXI                              | 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         | Elstar × Delcorf (CC)           | 518         | LB, VA                            | 41; 56         |
| 598 | Zarya Alatau                     | 2n     | Belenus           | 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             |

n.a. not available; 2n diploid; 3n triploid

a The 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

b Scion 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
c Information 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
d Each 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
e The 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

f Each 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, Bartha-Pichler et al. (2005); 7, Bernkopf (2011); 8, Bernkopf et al. (2003); 9, Bosch (2006); 10, Bosch (2017); 11, Bounous (2006); 12, Brown and Maloney (2003); 13, Evans et al. (2011); 14, Gasser (2020); 15, Hampon and Kemp (2003); 16, Hartmann (2003); 17, Hartmann (2015); 18, Jacobsen (2014); 19, Larsen et al. (2017); 20, Lassois et al. (2016); 21, Lenol (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, Neri (2004); 29, NIAB-EMR (2016); 30, Oberhofer (2007); 31, Orange (2019); 32, Ordidge et al. (2018); 33, Perazzolli et al. (2014); 34, Petzold (1984); 35, Provincia di Vicenza (2005a); 36, Provincia di Vicenza (2005b); 37, Ramos-Cabrer et al. (2007); 38, Rolff (2001); 39, Salvi 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, Szalay et al. (2009); 49, Votteler (2014); 50, Webster and Wertheim (2003); 51, Whealy and Thuente (2001); 52, Widmer et al. (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 |
|-----|---------|-------------|---------------------------|-----------------|------------------|-----|---------------|
|     | CH01c06 | WellRED D4  | 0.8                       | 146–190         | 19 (17)          | 0.774 | 8             |
|     | CH02b10 | WellRED D2  | 1.0                       | 107–155         | 18 (18)          | 0.897 | 2             |
|     | CH03a04 | WellRED D4  | 0.4                       | 86–134          | 20 (20)          | 0.845 | 5             |
|     | CH01d08 | WellRED D4  | 0.7                       | 238–294         | 20 (19)          | 0.750 | 15            |
|     | CH01f02 | WellRED D4  | 0.3                       | 160–228         | 27 (27)          | 0.856 | 12            |
|     | CH02d12 | WellRED D2  | 0.6                       | 169–223         | 23 (22)          | 0.764 | 11            |
|     | CH02h11a| WellRED D3  | 0.8                       | 98–130          | 12 (12)          | 0.791 | 4             |
|     | CH01c06 | WellRED D4  | 0.9                       | 125–209         | 32 (31)          | 0.897 | 2             |
|     | CH02c02a| WellRED D3  | 0.6                       | 233–259         | 12 (12)          | 0.821 | 15            |
|     | CH02c11a| WellRED D4  | 0.52                      | 210–268         | 20 (19)          | 0.879 | 10            |
|     | CH01h01a| Cy5          | 0.25                      | 102–146         | 17 (17)          | 0.831 | 17            |
|     | CH01f07a| WellRED D3  | 0.3                       | 173–205         | 16 (16)          | 0.840 | 10            |
|     | CH02d08a| 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

This list is based on the database of validated profiles (Liebhard et al. 2002). 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.

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 genotypic data of the target cultivar or to import a list of cultivars from an Excel file comprising three columns...
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) in order to achieve an alignment with the here presented dataset (compare Supplementary Table S6).

**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 |
|-----------|------------------|
| CH01h02   | –3 (163–199); –2 (>202) |
| CH02c09   | 0                 |
| CH02c11   | –1                |
| CH01h01   | –2 (104–128); –3 (>131) |
| CH02d08   | –1 (209–233); 0 (>244) |

**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 $2.6 \times 10^{-30}$, to $3.4 \times 10^{-19}$, to $8.8 \times 10^{-10}$, and to $5.0 \times 10^{-8}$ 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 $5.8 \times 10^{-11}$ and $9.3 \times 10^{-4}$, 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,
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, and 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 ‘Lombarts 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 inversed. 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 × 10⁻⁴ 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 reduced 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 spurts 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 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.

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