



# Botany, Taxonomy, and Origins of the Apple

# 2

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## Abstract

Apples are important from both a cultural and nutritional standpoint. The fruit produced from the cultivated apple, *Malus × domestica* Borkh., is grown in temperate regions throughout the world. Ornamental crabapple trees represent other *Malus* species and are generally valued for their landscape properties rather than their fruits. Genetic analyses of apple cultivars and species have revealed domestication pathways, pedigree relationships, as well as data that guide genebank collection management practices. Molecular information is also critical for breeding programs that are using new techniques to identify novel genetic combinations with

enhanced biotic and abiotic stress resistance as well as desirable fruit quality and production traits. This chapter includes information about wild apple species, origins of cultivated apples, genetic assessments, as well as some basic information about tree phenology, architecture, and propagation methods.

## 2.1 Introduction

*Malus* spp., belonging to the family Rosaceae, includes approximately 61 apple wild species and hybrids, traditionally taxonomically organized based on key morphological distinctions (Qian et al. 2006), and a single cultivated species, *Malus × domestica* Borkh. Worldwide, apples are one of the most economically important fruit crops (Bramel and Volk 2019). Fruit from *M. × domestica* is harvested for fresh consumption, cider, and processing uses, while other species of *Malus* are cultivated as either rootstocks or ornamentals. Wild *Malus* species are primarily found in temperate climates throughout much of the northern hemisphere, with China as a primary center of origin (Juniper and Maberley 2006). *Malus × domestica* is proposed to have originated primarily from its progenitor, *M. sieversii*, which is native to Central Asia and Western China (Harris et al. 2002; Cornille et al. 2015, 2019).

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## 2.2 Wild *Malus* Species and Hybrids

Most *Malus* species have a haploid genome with 17 chromosomes originating from genome duplication (Daccord et al. 2017). However, there is a range in genome size and ploidy among and within species (Höfer and Meister 2010; Chagné et al. 2015). Most dessert apple cultivars are either diploid or triploid, while wild species of *Malus* may be diploid, triploid, or tetraploid. *Malus* genera have been subdivided into eight sections, likely corresponding to their geographic origins (Fig. 2.1, Table 2.1).

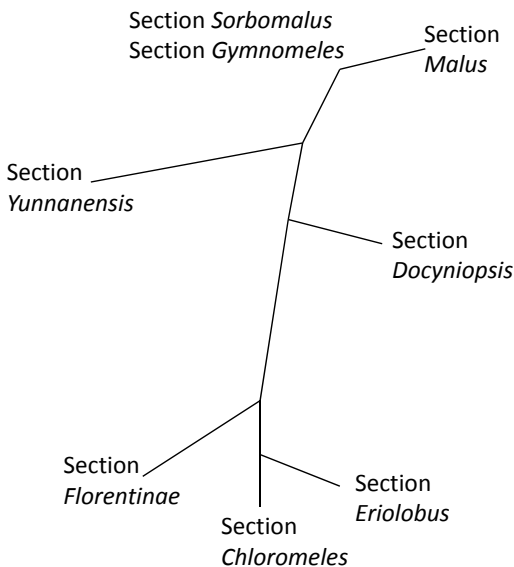
Section *Malus* includes the cultivated apple, *M. × domestica*, along with its primary crop relatives including *M. sieversii* (Ledeb.) M. Roem., *M. orientalis* Uglitzk., and *M. sylvestris* Mill., as well as a number of other related species (Table 2.1). These three species, as well as *M. prunifolia* (Willd.) Borkh., share regions of nuclear and chloroplast sequences with *M. × domestica* (Fig. 2.2; Velasco et al. 2010; Nikiforova et al. 2013; Volk et al. 2015). Moreover, microsatellite, or simple sequence repeats (SSRs), markers have revealed that *M. × domestica* and *M. sieversii* form distinct genetic

groups, with *M. × domestica* being a panmictic group (Cornille et al. 2012). Assessments of the wild apple genetic diversity using microsatellite markers have compared diversity among and within sampling locations in Kazakhstan (*M. sieversii*), the Caucasus region (*M. orientalis*), and Europe (*M. sylvestris*). It is found that the three wild species form distinct genetic groups in Eurasia but are only weakly genetically differentiated from each other (Richards et al. 2009; Cornille et al. 2013, 2015; Volk et al. 2008). Furthermore, data suggest that there is substantial gene flow among populations and species. These findings support the existence of wild *Malus* populations that are highly outcrossing (Richards et al. 2009) and that range contractions may have occurred during glacial periods in Europe (Cornille et al. 2013).

Sections *Sorbomalus*, *Gymnomeles*, and *Yunnanensis* are comprised of wild species native to China and the Far East (Fig. 2.1 and Table 2.1, USDA 2020; Zhi-Qin 1999; Volk et al. 2015; Yu 1988). An exception is *M. fusca* (Raf.) C.K. Schneid. (Section *Sorbomalus*), which is native to the western coast of North America, and it is suggested to have arrived in North America across the Bering Strait (Qian et al. 2006; Robinson et al. 2001; Routson et al. 2012).

Section *Docyniopsis* includes the only tropical apple species, *M. doumeri* (Bois) A. Chev., that grows in the wild in Southern China, and as far south as Vietnam. Moreover, *M. leiocalyca* S.Z. Huang and *M. tschonoskii* (Maxim.) C.K. Schneid. have also been assigned to this section (Robinson et al. 2001).

Each of sections *Florentinae* (*M. florentina* (Zucc.) C.K. Schneid., native to Southern Europe) and *Eriolobus* (*M. trilobata* (Poir.) C.K. Schneid., native to the Middle East and Southern Europe) has a single species. These are deemed as likely European relict species (Qian et al. 2008) that share common ancestries with North American *Malus* species in Section *Chloromeles* (Fig. 2.1, Forte et al. 2002). Ancestors of the species within Sections *Florentinae*, *Eriolobus*, and *Chloromeles* may have inhabited the northern landmass in the Cretaceous Period when current North America and Europe have been in



**Fig. 2.1** Relationships among sections of *Malus* based on chloroplast sequence data of *Malus* as adapted from Volk et al. (2015) and Robinson et al. (2001)

**Table 2.1** Sections of *Malus*\*

|   |
|---|
| <b><i>Malus</i> Mill. Sect. <i>Malus</i></b>            |
| <i>Malus chitralensis</i> Vassilcz                      |
| <i>Malus crescimannoi</i> Raimondo                      |
| <i>Malus</i> × <i>domestica</i> (Suckow) Borkh          |
| <i>Malus muliensis</i> T.C. Ku                          |
| <i>Malus orientalis</i> Uglitzk                         |
| <i>Malus prunifolia</i> (Willd.) Borkh                  |
| <i>Malus sieversii</i> (Ledeb.) M. Roem                 |
| <i>Malus spectabilis</i> (Aiton) Borkh                  |
| <i>Malus sylvestris</i> (L.) Mill                       |
| <i>Malus zhaojiaoensis</i> N.G. Jiang                   |
| <b><i>Malus</i> Mill. Sect. <i>Sorbomalus</i></b>       |
| <i>Malus fusca</i> (Raf.) C.K. Schneid                  |
| <i>Malus kansuensis</i> (Batalin) C.K. Schneid          |
| <i>Malus komarovii</i> (Sarg.) Rehder                   |
| <i>Malus sargentii</i> Rehder                           |
| <i>Malus toringo</i> (Siebold) de Vriese                |
| <i>Malus toringoides</i> (Rehder) Hughes                |
| <i>Malus transitoria</i> (Batalin) C.K. Schneid         |
| <i>Malus zumi</i> (Matsum.) Rehder                      |
| <b><i>Malus</i> Mill. Sect. <i>Gymnomeles</i></b>       |
| <i>Malus baccata</i> (L.) Borkh                         |
| <i>Malus halliana</i> Koehne                            |
| <i>Malus hupehensis</i> (Pamp.) Rehder                  |
| <i>Malus mandshurica</i> (Maxim.) Kom. Ex Skvortsov     |
| <i>Malus sikkimensis</i> (Wenz.) Koehne ex C.K. Schneid |
| <i>Malus spontanea</i> (Makino) Makino                  |
| <b><i>Malus</i> Mill. Sect. <i>Yunnanensis</i></b>      |
| <i>Malus honanensis</i> (Rehder)                        |
| <i>Malus ombrophila</i> Hand.-Mazz                      |
| <i>Malus prattii</i> (Hemsl.) C.K. Schneid              |
| <i>Malus yunnanensis</i> C.K. Schneid                   |
| <b><i>Malus</i> Mill. Sect. <i>Docyniopsis</i></b>      |
| <i>Malus doumeri</i> (Bois) A. Chev                     |
| <i>Malus leiocalyca</i> S.Z. Huang                      |
| <i>Malus tschonoskii</i> (Maxim.) C.K. Schneid          |
| <b><i>Malus</i> Mill Sect. <i>Florentinae</i></b>       |
| <i>Malus florentina</i> (Zucc.) C.K. Schneid            |
| <b><i>Malus</i> Mill Sect. <i>Eriolobus</i></b>         |
| <i>Malus trilobata</i> (Poir.) C.K. Schneid             |

(continued)

**Table 2.1** (continued)

|  |
|--|
| <b><i>Malus</i> Mill. Sect. <i>Malus</i></b>       |
| <b><i>Malus</i> Mill. Sect. <i>Chloromeles</i></b> |
| <i>Malus angustifolia</i> (Aiton) Michx            |
| <i>Malus coronaria</i> (L.) Mill                   |
| <i>Malus ioensis</i> (Alph. Wood) Britton          |

\*This list is based on information collected from USDA (2020), Robinson et al. (2001), and Qian et al. (2006, 2008)

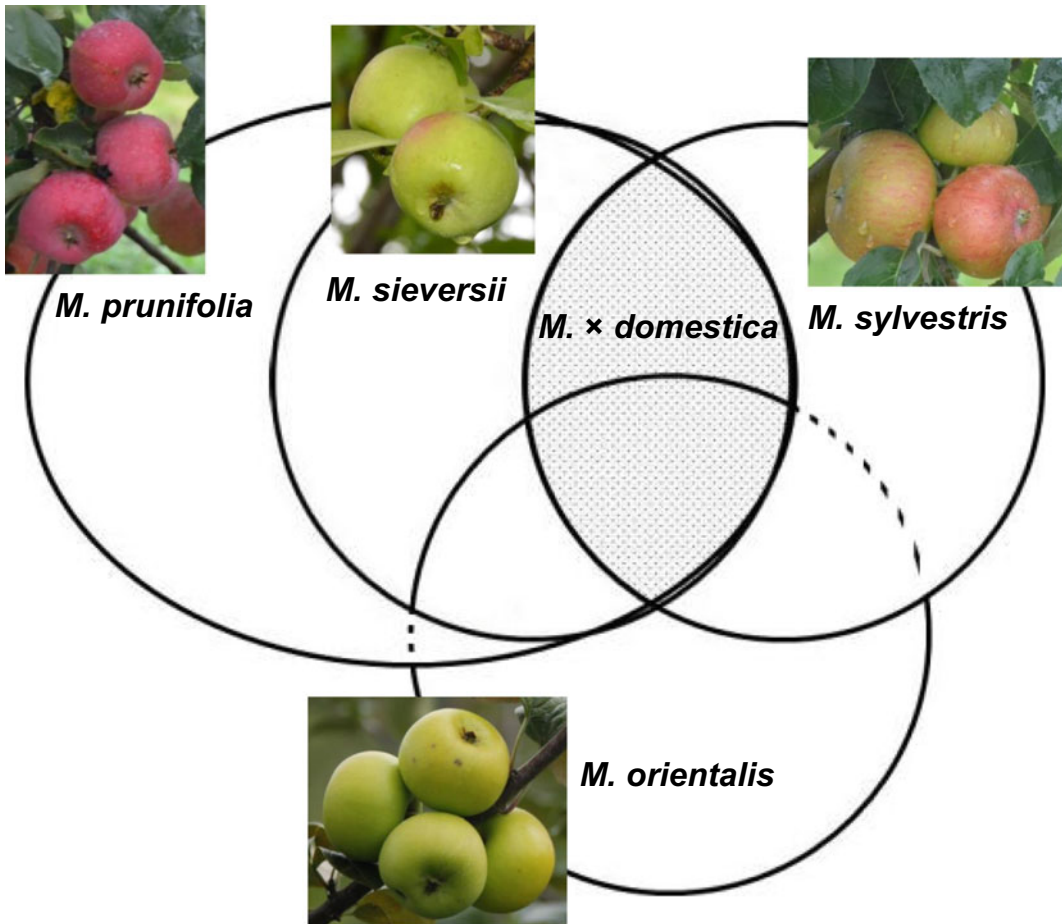
close proximity, and have then diverged when these continents have separated (Forte et al. 2002).

Section *Chloromeles* consists of *M. coronaria* (L.) Mill., *M. angustifolia* (Aiton) Michx., and *M. ioensis* (Alph. Wood) Britton, these are found in eastern North America. Moreover, these appear to be the most distant species from *M. × domestica* and from Sections *Malus* and *Sorbomalus* based on assessments of chloroplast sequence data (Lo and Donoghue 2012; Robinson et al. 2001; Volk et al. 2015).

Most research on *Malus* focuses heavily on the cultivated, consumed apple. While dessert apples have sweet fruit, crabapples represent their counterparts, wherein fruit is bitter, acidic, and in terms of human edibility, unappealing. The term crabapple could be used to describe nearly all species other than *M. × domestica* species. Generally, crabapples bear smaller fruit, although fruit size varies significantly (Cornille et al. 2014). In general, crabapple fruit size ranges from 10 to 50 mm (USDA 2020). Although poor in fruit quality, crabapples have a significant economic impact, particularly as ornamentals (Fiala 1994). Additionally, they are planted in commercial orchards as pollinizers. Many ornamental crabapples are either specific selections from *Malus* wild species or have developed as hybrids between two *Malus* species, as *Malus* species are interfertile/cross-compatible (Table 2.2).

## 2.3 Cultivar Origins

Desirable apple trees have been originally identified in their native settings. The first drivers of the domestication of apple are most probably



**Fig. 2.2** Relationships among *Malus × domestica* and primary crop wild relatives based on chloroplast sequence data (adapted from Volk et al. 2015)

fruit size and organoleptic traits (Yao et al. 2015; Duan et al. 2017). *Malus × domestica* is proposed to have arisen from the progenitor species *M. sieversii* (native to Western China, Kazakhstan, and other Central Asian countries). Wild *M. sieversii* trees exhibit a wide range of fruit diversity (Fig. 2.3), and these may have served as original sources for domestication events in China and Russia, as well as for western cultivars. Then, during its journey along the Silk Routes through the Caucasus region (native to *M. orientalis*) and Europe (native to *M. sylvestris*), *M. sieversii* underwent several hybridization events with local wild apples (Fig. 2.4; Cornille et al. 2019; Duan et al. 2017; Gao et al. 2015; Luby 2003; Peace et al. 2019). When Greeks and

Romans brought apples into Europe, about 1,500 years ago, *M. sieversii* was introgressed to *M. sylvestris*, the European crab apple (Cornille et al. 2012, 2014, 2019).

During its journey along the Silk Routes, desirable *M. × domestica* trees were vegetatively propagated locally to preserve desirable genetic combinations. Traits that were especially favored included lower acidity and higher sugar content, thus resulting in numerous cultivars with sweet or sub-acid fruits (Duan et al. 2017; Ma et al. 2018). Domestication, and recent breeding efforts, also changed fruit metabolic compositions and lowered levels of phenolic compounds influencing astringency, bitterness, and color (Lea and Arnold 1978; Sanoner et al. 1999; Khan

**Table 2.2** Taxonomy of *Malus* interspecific hybrids and progenitor species as listed in GRIN-Global (USDA 2020)

| Taxon                             | Proposed parentage  |
|-----------------------------------|---|
| <i>M.</i> × <i>adstringens</i>    | <i>M. baccata</i> × <i>M. pumila</i>                                    |
| <i>M.</i> × <i>arnoldiana</i>     | <i>M. baccata</i> × <i>M. floribunda</i>                                |
| <i>M.</i> × <i>asiatica</i>       | <i>M. sieversii</i> × <i>M. baccata</i>                                 |
| <i>M.</i> × <i>astracanica</i>    | <i>M. prunifolia</i> × <i>M. pumila</i>                                 |
| <i>M.</i> × <i>atrosanguinea</i>  | <i>M. halliana</i> × <i>M. toringo</i>                                  |
| <i>M.</i> × <i>dawsoniana</i>     | <i>M.</i> × <i>domestica</i> × <i>M. fusca</i>                          |
| <i>M.</i> × <i>gloriosa</i>       | <i>M.</i> × <i>scheideckeri</i> × <i>M. pumila</i><br>'Niedzwetzkyana'  |
| <i>M.</i> × <i>hartwigii</i>      | <i>M. baccata</i> × <i>M. halliana</i>                                  |
| <i>M.</i> × <i>magdeburgensis</i> | <i>M. pumila</i> × <i>M. spectabilis</i>                                |
| <i>M.</i> × <i>micromalus</i>     | <i>M. spectabilis</i> × <i>M. baccata</i>                               |
| <i>M.</i> × <i>moerlandsii</i>    | <i>M.</i> × <i>purpurea</i> × <i>M. toringo</i>                         |
| <i>M.</i> × <i>platycarpa</i>     | <i>M.</i> × <i>domestica</i> × <i>M. coronaria</i>                      |
| <i>M.</i> × <i>purpurea</i>       | <i>M.</i> × <i>atrosanguinea</i> × <i>M. pumila</i><br>'Niedzwetzkyana' |
| <i>M.</i> × <i>robusta</i>        | <i>M. baccata</i> × <i>M. prunifolia</i>                                |
| <i>M.</i> × <i>scheideckeri</i>   | <i>M. floribunda</i> × <i>M. prunifolia</i>                             |
| <i>M.</i> × <i>soulardii</i>      | <i>M. ioensis</i> × <i>M. pumila</i>                                    |
| <i>M.</i> × <i>sublobata</i>      | <i>M. prunifolia</i> × <i>M. toringo</i>                                |
| <i>M.</i> × <i>xiaojinensis</i>   | <i>M. toringoides</i> × <i>M. kansuensis</i>                            |

et al. 2014), particularly as fruits were increasingly used for fresh and dessert consumption, in contrast to making alcoholic ciders. In Europe, Russia, and China, particular offsprings were named as cultivars and propagated.

Some apple cultivars are likely to be from the Roman period, including 'Annurca' and 'Decio'. Moreover, there are many examples of Old-World apple cultivars, such as 'Winter Pearmain' (the year 1200), 'Calville Blanc d'Hiver' (1598), 'Court Pendu Plat' (1613), 'Blenheim Orange' (1740), 'Antonovka' (1826), and 'Yellow Transparent' (1850) (Fig. 2.5).

Apple seeds and trees moved along as Europeans migrated to North America. Apple seeds were planted throughout North America, and in some cases, seedling trees were named, propagated, and thereafter referred to as cultivars. The plethora of seedling apple trees and hundreds of cultivars that were named led to the designation of North America as a likely secondary center of origin for apple cultivars. Early North American apple cultivars included 'Roxbury Russet' (1600), 'Rhode Island Greening' (1650), and 'Esopus Spitzenburg' (1735). Interestingly, molecular marker-based pedigree inferences identified pedigrees of cultivars derived from North American seedling trees (Muranty et al. 2020). For example, 'Esopus Spitzenburg' was found to be directly derived from the French cultivar 'Reinette Franche' (1510). By the mid-1800s, the most popular apple cultivar in the USA was 'Ben Davis', a cultivar identified from a North American seedling in about 1800 (Fig. 2.6).

Centuries of domestication, selection, and propagation have resulted in a wide range of genetic diversity among apple cultivars. Some have bitter, phenolic traits desirable for hard cider production. Other cultivars have a wide range of fruit shapes and skin color, including stellar shape (e.g., 'Api Etoilée'), ribbed apple (e.g., 'Calville Blanc d'Hiver'), fully russeted fruit (e.g., 'Renetta Grigia di Torriana'), or burgundy-colored apple mutants (e.g., 'Bravo'<sup>TM</sup>). Furthermore, new cultivars have enhanced biotic and/or abiotic stress resistance, as well as tree architectures that lend themselves to modern horticultural practices, including automated harvesting. Modern cultivars may also have an extremely long fruit shelf-life, particularly when stored under controlled atmosphere conditions (Stanger et al. 2018). In addition, modern cultivars and production practices result in high crop loads (i.e., number of fruits per tree), thus necessitating fruit thinning to avoid biennial bearing. Another innovation for breeding programs is the identification and use of wild apple species carrying desirable genes and alleles for disease resistance. For example, *M. floribunda* '821' is a source for Vf (*Rvi6*) apple scab





**Fig. 2.3** Diversity of fruits collected from *Malus sieversii* trees growing at the USDA National Plant Germplasm System Apple Collection (Peggy Greb, USDA Image Gallery)

resistance allele for several commercial cultivars (Janick 2002).

Today, there are many well-known apple cultivars that are sold as specialty cultivars around the world, including those from Europe ('Cox's Orange Pippin'), Russia ('Antonovka', 1826), Japan ('Fuji', 1930s), Australia ('Granny Smith', 1868), New Zealand ('Braeburn', 1952; 'Gala', 1930s), and the USA ('Golden Delicious', 1914; 'Red Delicious', 1880; 'Honeycrisp', 1991) (Fig. 2.7). Surprisingly, many of these well-known apple cultivars have been identified as chance seedlings or bred decades or even hundreds of years ago. Breeding programs continue to select for improved disease resistance and stress tolerance, fruit quality, and storage characteristics (Laurens et al. 2010).

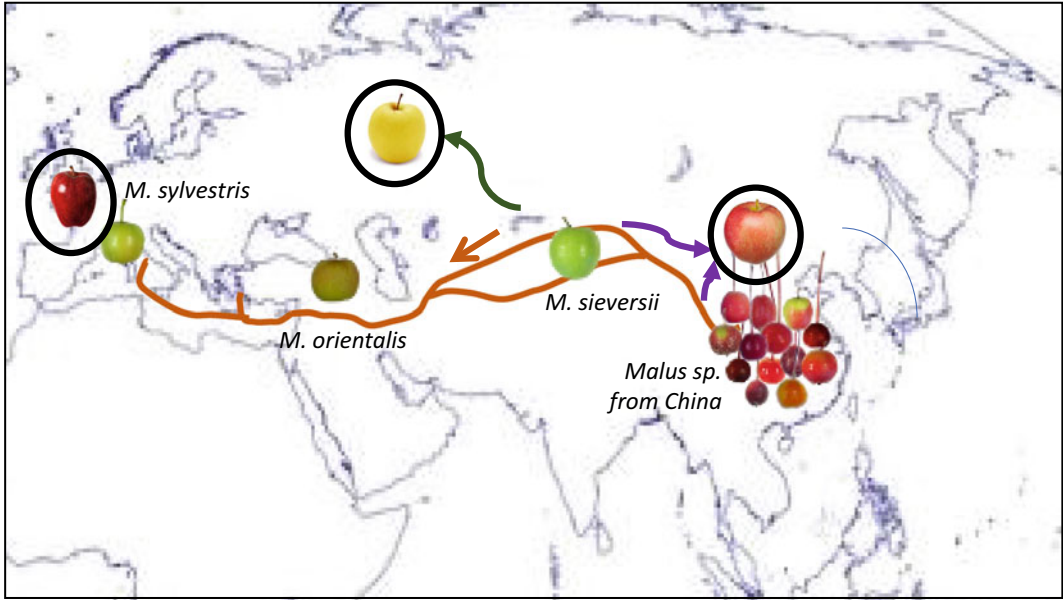
Sometimes apple trees spontaneously mutate, and these mutations result in the observable

change(s) that can be maintained following clonal propagation. These "sports" of a cultivar are nearly identical genetically to the original cultivar and are usually not detected using most genetic techniques. Sport variation ranges from mild to extreme. For example, 'Red Delicious' has a series of sports with various fruit red color pigmentation/or patterns, and 'Sargeant Russet Golden' is a russeted sport mutant of 'Golden Delicious' (Fig. 2.8; Gross et al. 2012). Another form of observed mutations, chimeras, is most often visible as sectional variations in apple fruit coloration. However, such chimeras are generally not maintained during clonal propagation.

## 2.4 Genetic Characterization

Genetic characterization of apple cultivars has long been grounded in the so-called pomological descriptions, based on accurate phenotypic observations of various fruit and tree traits (Juniper and Mabberley 2006). In his 'Dictionnaire de Pomologie', A. Leroy cites the first classifications performed by Greek writers such as Théophraste who subdivided Greek apple cultivars into six types according to their phenology or fruit taste (Leroy 1873). In modern times, biochemical analyses have been used to characterize sets of apple cultivars in addition to morphological traits. However, such biochemical analyses are more geared for purposes of description rather than classification.

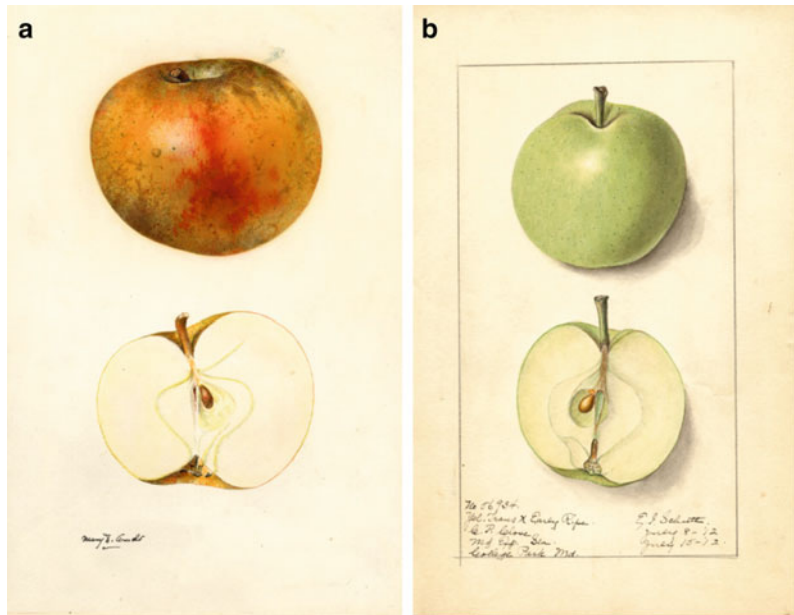
Genetic characterization of apple cultivars began with isozyme analyses in the 1980s and 1990s (Weeden and Lamb 1985; Menendez et al. 1986; Korban and Bournival 1987; Battle et al. 1995). Subsequently, analyses of microsatellite/SSR markers have led to the collection and species diversity assessments, as well as for use in genetic fingerprinting for cultivar identity analyses. These markers can also be used to determine cultivar/genotype trueness-to-type, as well as identify duplications and sport-families within collections. Assessments have been performed for national apple genebank collections in France, the UK, the USA, and elsewhere (Lassois et al. 2016; Hokanson et al. 2001; Gross

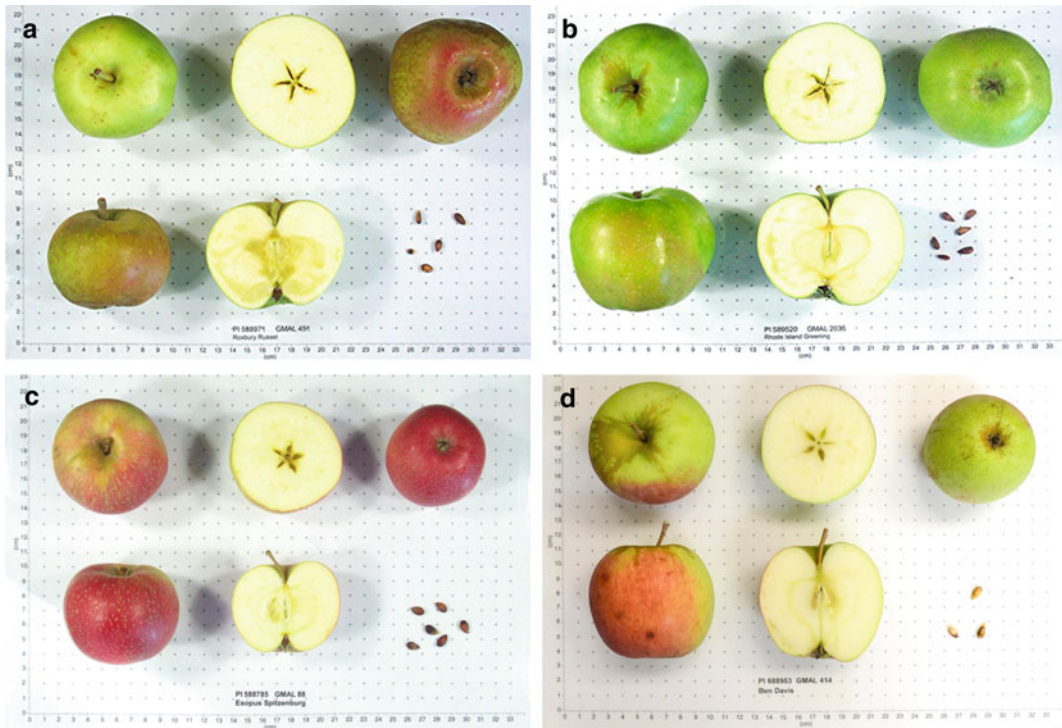


**Fig. 2.4** Proposed routes of *Malus* domestication, with circled fruit denoting likely domestication lineages. Orange-colored arrows denote domestication routes of apples of European ancestry, while Black-colored arrows

denote domestication route of apples in Russia, and Purple-colored arrows denote domestication of apples in East Asia

**Fig. 2.5** Watercolor paintings of apple fruits from Old World apple cultivars. **a** ‘Blenheim Orange’, United Kingdom, 1740; and **b** ‘Yellow Transparent’, Russia, 1850 (National Agricultural Library 2020)





**Fig. 2.6** Fruits of historic North American apple cultivars. **a** ‘Roxbury Russet’ (1600 AD); **b** ‘Rhode Island Greening’ (1650 AD); **c** ‘Esopus Spitzenburg’ (1735 AD); and **d** ‘Ben Davis’ (1800 AD) (USDA 2020)

et al. 2012; Ordidge et al. 2018). Microsatellite assessments of collections have also facilitated international collection comparisons (Evans et al. 2011; Urrestarazu et al. 2016).

Genebank collections serve as reference sets of known cultivars to aid in the identification of historic fruit trees on public and private lands (Routson et al. 2009; Lassois et al. 2016; Magby et al. 2019). Recently, single nucleotide polymorphism (SNP) arrays and genomic sequencing have rapidly advanced our capacity to determine pedigree relationships, pursue marker-based selection breeding programs, and target specific cultivars/genotypes with alleles of particular interest to breeding programs (Cornille et al. 2019; Peace et al. 2019; Ordidge et al. 2018; Muranty et al. 2020; Howard et al. 2017; Baumgartner et al. 2016). The most frequently cited apple SNP arrays are the International RosBREED SNP Consortium (IRSC) Illumina Infinium 8K SNP array (Chagné et al. 2012), the

Illumina Infinium 20K SNP array (Bianco et al. 2014), and the Affymetrix Axiom 487K SNP array (Bianco et al. 2016).

## 2.5 Tree Phenology and Architecture

Self-rooted apple trees grow to heights ranging between 2 and 20 m and have juvenile periods ranging between 4 and 12 years (Fischer 1994). Juvenility is a significant challenge for breeding and genetic research in apples. An early bearing can be induced by grafting seedling trees onto dwarfing rootstocks (Fazio et al. 2014). Transgenic approaches can drastically shorten generation cycles to 1 year or less (Flachowsky et al. 2011).

In general, inflorescences develop on first-year fruiting shoots (i.e., 2-year-old wood), brindles (medium shoots), or spurs (compact

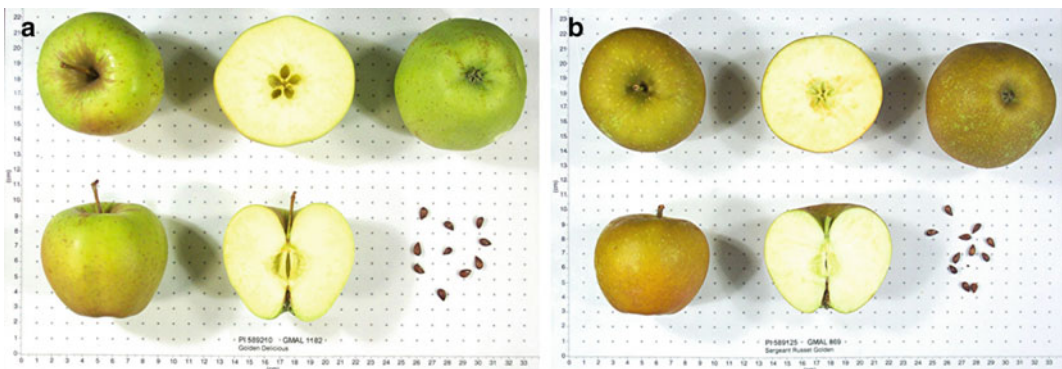




**Fig. 2.7** A fruit display of internationally known cultivars of ‘Golden Delicious’, ‘Gala’, ‘Granny Smith’, and ‘Red Delicious’ apples (Scott Bauder, USDA Image Gallery)

shoots). Bourse shoots (short vegetative shoots) develop proximally from the inflorescence meristem and terminate in vegetative or inflorescence buds (Costes et al. 2006). Floral bud development is initiated after full-bloom when terminal meristems either remain vegetative or commit to flowering (Foster et al. 2003). The development of floral primordia is influenced by genetic, physiological, and environmental factors (Koutinas et al. 2010). Flowers develop from inflorescences (consisting of 5–7 flowers) with a distinctive king flower. Flowers are complete, typically arranged with five petals, ranging from white to red in color. *Malus* trees are either deciduous or semi-deciduous with an alternate leaf arrangement. Leaves are typically serrulate elliptical to ovate. Fruit is a pome ranging from 3 to 12 cm in diameter, usually with five carpels, a red, yellow, or green exocarp, and typically a white mesocarp. The persistent calyx may be open or closed, pedicle length is typically 1.5 cm but ranges from 0.5 to 4.0 cm (USDA 2020).

Growth habits of apple trees can be classified into distinct categories based on the positioning of fruits and branches, with columnar and weeping representing the two extremes. High-



**Fig. 2.8** Fruits of **a** ‘Golden Delicious’ and **b** ‘Sargeant Russet Golden’, a russeted sport of ‘Golden Delicious’ (USDA 2020)

density planting favors more compact columnar and spur types to maximize production and sustainability. The genetic characteristics that contribute to distinct architectural traits have been identified (Kenis and Keuleman 2007; Segura et al. 2009; Okada et al. 2020).

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## 2.6 Propagation

Wild *Malus* trees propagate by seeds that are often spread by animals. *Malus* species, including *M. × domestica*, are self-incompatible (Igc et al. 2008). They exhibit gametophytic self-incompatibility, which is determined by the multigenic *S*-locus with two major components (Kubo et al. 2010; Pratas et al. 2018). One of these two components is a pistil specificity *S*-RNase that inhibits pollen tube growth from self-pollen, and the second consists of *S*-pollen specificity F-box proteins that recognize and degrade non-self *S*-RNases (Kubo et al. 2010; Pratas et al. 2018).

Due to self-incompatibility, apple trees must be pollinated by a different cultivar/genotype as a pollen source. Therefore, seeds collected from these fruits are hybrids, and if germinated, they grow into seedlings that are not true-to-type to their maternal parent as they are highly heterozygous. A notable exception is when seeds are derived asexually from maternal tissues and are true-to-type through apomixis. Apomixis is observed in *Malus* species, including *M. hupehensis* (Pamp.) Rehder and *M. toringo* (Siebold) de Vriese.

Cultivar-specific allelic combinations are maintained through asexual propagation techniques, with grafting as the most common propagation method. Either dormant or summer buds are budded/grafted onto rootstocks, thereby resulting in a two-genotype compound tree system, consisting of a combination of a rootstock (below-ground) and a scion cultivar (above-

ground) (Fig. 2.9). This clonal propagation method dates back approximately 4000 years ago (Zohary 2000), and it has been used for centuries to maintain identities of unique apple selections. Remarkably, ‘Winter Pearmain’ fruit consumed today has the same genetic profile as that of fruit grown in 1200 AD. In some cases, somatic mutations may accumulate as a result of asexual propagation methods, but the rate(s) of incidence of such mutations has not been well documented.

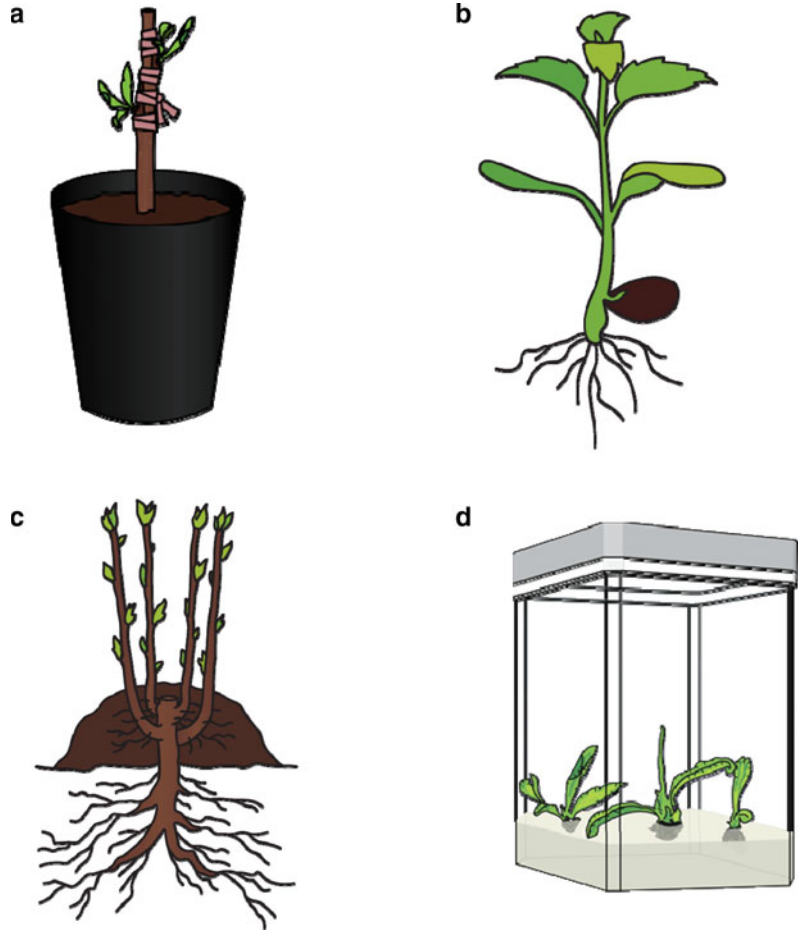
Until the mid-1800s, rootstocks were derived from seeds, and germinating seedlings were grown simply for use in the vegetative propagation of scion cultivars. Modern apple clonal rootstocks have transformed apple production worldwide, as these have been selected for particular desirable traits that they confer to scions, including disease resistance and dwarfing, fruit quality, tree habit, nutrient assimilation, and tolerance to biotic and abiotic stress (Marini and Fazio 2018; also see Chap. 6 in this volume). Modern rootstocks are vegetatively propagated using mound layering or in vitro tissue culture systems (Fig. 2.9, Teixeira da Silva et al. 2019).

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## 2.7 Conclusions

*Malus* species have critical importance in world agriculture, yet the genetic relationships among wild species, their contributions to apple domestication, and cultivar pedigrees are currently under investigation and will be elucidated. Genomic approaches are being used to assess the diversity of wild species, as well as those of important and desirable cultivars. These wild species and targeted cultivars are critical for current and future breeding efforts to enhance nutritional content, productivity, resistance to various biotic and abiotic stress, as well as sustainably of apple produced for future generations.

**Fig. 2.9** Illustrations of *Malus* propagation methods. **a** Grafting; **b** seedling (derived sexually or by apomixis); **c** mound layering; and **d** in vitro tissue culture



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