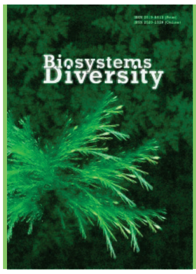

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An overview of the red-fleshed apple: History and its importance for horticulturists, gardeners, nurserymen, and consumers

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The present review summarizes the information on the botany, breeding, genetic features, cultivation, and nutraceutical values of red-fleshed apples. *Malus sieversii* var. *niedzwetzkyana* or Niedzwetzky's apple became widely known after the publication of Georg Dieck in the last XIX century. It is characterized by anthocyanin coloration of all organs. Another source of red flesh is the ancient variety 'Surprise', which differs from the Niedzwetzky's apple by a mutation in another gene. These two mutated genes, MYB10 and MYB110a, are located on chromosomes 9 and 17, respectively. Their expression correlated with the anthocyanin accumulation. In type 1 red-fleshed apples, which belong to the Niedzwetzky's apple progeny, the transcription factor MYB10 confers extensive anthocyanin accumulation in fruit flesh and skin, flowers, leaves, and stems. In type 2 red-fleshed apples, the 'Surprise' progeny, only the flesh is red, determined by the transcription factor MYB110a. A new combination *Malus domestica* f. *niedzwetzkyana* comb. nov. has been proposed for orchard apples, originated from Niedzwetzky's apple. The apple cultivars which are progeny of Niedzwetzky's apple and 'Surprise' apple can be placed to *Malus* Niedzwetzkyana Group and *Malus* Surprise Group, respectively. All red-fleshed cultivars of orchard apple can be grouped together into *Malus domestica* Red Flesh Group. Many dozens of new ornamental apple trees have been developed for of European and North American conditions, including the most famous red-flowered centennial apple varieties such 'Aldenhamensis', 'Lemoinei', 'Makamik', and 'Oekonomierat Echtermeyer'. Rootstocks 'MB', 'PB9', '54-118', '62-396' and others have become popular in nurseries for the propagation of dwarf and semi-dwarf apple trees thanks to their red leaves, which are useful when removing scion shoots from budded plants. In the F3-F4 and next generation, the new high-quality red-fleshed cultivars have been developed by crossing both Niedzwetzky's apple and 'Surprise' apple with the best orchard apple varieties. Marker-assisted breeding shows great promise for accelerating the development of new red-fleshed cultivars with outstanding traits. The use of the Redlove®, Red Moon®, Kissabel®, and Lucy™ apples brands will ensure the red-fleshed apples' best path to the consumer as well as the fruit quality and production volume of these novelties. Increasing the consumption of red-fleshed apples is essential for a healthy diet.

Keywords: *Malus domestica* f. *niedzwetzkyana*; *Malus* Niedzwetzkyana Group; *Malus* Surprise Group; anthocyanidins; apple classification; apple breeding; health benefit.

Introduction

Apple trees are one of the most important fruit crops in the world and are widely used in ornamental gardening. Among the numerous fruit and ornamental apple cultivars as well as rootstocks, varieties characterized by the red color of their leaves, flowers and fruits, including skin and flesh or only flesh, occupy a special place (Krüssmann, 1977; Wang et al. 2018). The vast majority of them are genetically related to the Central Asian taxon that was once considered a separate species called the Niedzwetzky's apple tree. There is also another ancestor of the red-fleshed apple, an ancient variety 'Surprise'. In the two centuries of human attention to red-fleshed apples, they have spread around the world. Ongoing molecular research has revealed many secrets about the color characteristics of these apples (Chagné et al., 2007, 2013; Nocker et al., 2012; Sato et al., 2017). New varieties of attractive, red-fleshed apples, rich in nutrients essential for a healthy diet becoming increasingly popular (Sadilova et al., 2006; Sato et al., 2017; Pomiferous, 2021).

Taxonomy and nomenclature of *–orchard apple tree with its main progenitor, including Niedzwetzky's apple tree

Philip Miller (Miller, 1754) established the genus *Malus* using the generic name *Malus* proposed by Tournefort (1700), while Carl Linnaeus (1753) combined apple and pear into a single genus *Pyrus*. The legitimacy of Miller's separation of *Malus* from *Pyrus* has been confirmed by modern taxonomists at the morphological and molecular levels (Robertson et al., 1991; Campbell et al., 2007; Takhtajan, 2009). Recently it has been proposed to reunite these genera by including *Malus* and many other related genera in *Pyrus* (Christenhusz et al., 2018). However, such a broad concept of *Pyrus* has not been supported (Aydın & Dönmez, 2019; Govaerts et al., 2024). *Malus* contains many taxa and cultivars of exceptional economic, ecological, aesthetic and other importance. Scientists have different estimates of the number of species, ranging from only eight major species, according to Likhonos (1983), to up 78 described wild species and 44 cultivated species, according to Ponomarenko (1986). Modern authors include in *Malus* 36 accepted species together with cultivated species (Volk et al., 2021; Govaerts et al., 2024). Other researchers, based on numerical analyses recognize 26 wild species in the genus (Li et al., 2022).

The correct binominal for the orchard, domesticated or cultivated apple tree has long been debated. Some authors proved the legitimacy of the name *Malus domestica* (Korban & Skirvin, 1984; Terpó, 1988), others *Malus sylvestris* (Kartesz & Gandhi, 1992), although both previous names are illegitimate and the cultivated apple should be called *Malus pumila* (Mabberley et al., 2001). The name *Malus pumila*, published in 1768, has priority over the name *Malus domestica*, which appeared in 1803, but the latter is common in horticultural practice and appears most frequently in literary sources. Therefore, Qian et al. (2010) proposed to conserve the name *Malus domestica*. The Nomenclature Committee for Vascular Plants, after considering this proposal, noted that numerous names have been published that do or might apply to the cultivated apple. The priority name is *Malus pumila* and it unambiguously applies to the cultivated apple. The fact that the correct name *M. pumila* is currently used by a minority of the scientific community is not a reason for suspending the rules to suppress it (Applequist, 2014). However, the General Committee (by a very narrow majority) referred the proposal back to the Nomenclature Committee for Vascular Plants, which in a second vote narrowly recommended the proposal be accepted after all (Wilson, 2017). The conserved name *M. domestica* is now used for orchard apple.

Malus sieversii from Central Asia clustered close to *M. domestica*, implying that, as previously thought, cultivated apples originated from *M. sieversii* (Harris et al., 2002; Cornille et al., 2014; Chen et al., 2021). Compared to *M. sieversii*, the fruits of orchard apple tree are larger, harder, and sweeter. In contrast, they are less acidic and much larger than those of *M. sylvestris* (Duan et al., 2017). Despite the similarities between *M. domestica* and *M. sieversii*, genetic evidence suggests that they can be genetically distinguished based on microsatellite markers (Gross et al., 2012). Nevertheless, according to The World Checklist of Vascular Plants (Govaerts et al., 2024). *Malus sieversii* and *M. niedzwetzkyana* are synonymized with *M. domestica*. Then progeny of Niedzwetzky's apple cultivated throughout the world can be treated as *M. domestica* f. *niedzwetzkyana* (Dieck) Mezhenskyj [*M. niedzwetzkyana* Dieck in Neuheiten-Off. Natl.-Arbor. Zöschen 1891: 16 (1891); *Pyrus niedzwetzkyana* (Dieck) Hemsley); *Pyrus malus* var. *niedzwetzkyana* (Dieck) Asch. & Graebn. in Syn. Mitteleur. Fl. 6(2): 78 (1906); *Malus pumila* var. *niedzwetzkyana* (Dieck) C. K. Schneid. in Ill. Handb. Laubholzk. 1: 716 (1906); *Malus sylvestris* var. *niedzwetzkyana* (Dieck) L. H. Bailey in Hortus Sec.: 457 (1941); *Malus sieversii* var. *niedzwetzkyana* (Dieck) Langenf. in Daildarznieciba 8: 15 (1971); *Malus sieversii* f. *niedzwetzkyana* (Dieck) Langenf. in Yablonya: 171 (1991)] under rules of International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al., 2018).

The orchard apple tree, which arose as a result of several events of interspecific hybridization (Cornille et al., 2012, 2014) and whose gene pool is constantly enriched by new genomes of other apple tree species, is characterized by significant intraspecific differentiation. However, the botanical hierarchy of intraspecific categories is difficult to apply to cultivated plants, which do not have a natural population structure. For them, a system was developed based on the category of cultivar and cultivar Group, the names of which are regulated by the International Code of Nomenclature for Cultivated Plants (Brickell et al., 2016). It is permissible to retain taxon epithets to denote cultivar epithets, so the cultivar name *M. pumila* 'Niedzwetzkyana' was formed based on of *M. pumila* f. *niedzwetzkyana*. However, its use in the genealogies of nothospecies and cultivars (Krüssmann, 1977; Fiala, 1994) is inappropriate, as it misleadingly suggests that only one cultivar, 'Niedzwetzkyana', was involved in numerous combinations of crosses (Pyshcholka & Mezhenskyj, 2023). The apple cultivars in the origin of which Niedzwetzky's apple participated can be placed to *Malus* Niedzwetzkyana Group and *Malus domestica* Niedzwetzkyana Group (Mezhenskyj, 2008; Mezhenskyj and & Mezhenska, 2021). 'Surprise' together with his progeny can be placed to *Malus* Surprise Group and *Malus domestica* Surprise Group. All red-fleshed cultivars of orchard apple can be grouped together into *Malus domestica* Red Flesh Group.

Several hybridogenous taxa have originated from *Malus sieversii* f. *niedzwetzkyana* were named, including *M. ×denboerii* (= *M. ioensis* × *M. ×purpurea*), *M. ×gloriosa* (= *M. pumila* var. *niedzwetzkyana* × *M. scheideckeri*), *M. ×moerlandsii* (= *M. ×purpurea* 'Lemoinei' × *M. sieboldii*), *M. ×purpurea* (= *M. ×atrosanguinea* × *M. pumila* var. *niedzwetzkyana*) (Krüssmann, 1977). Since many varieties have a multi-species origin and it is difficult to determine the parent species, it is now more optimal to use a combination of the generic name and the varietal epithet or the trade mark, e. g., *Malus* 'Lemoinei' or *Malus* Coralburst®.

Niedzwetzky's apple trees were cultivated in Kashgar, China where they were known as "Kisil alma" (red apple) because of the prevailing color of all their parts (Hemsley, 1904). At the same time, the cultivar "Kul'dzhinka" (meaning "from Ghulja/Kuldja") was under cultivation in Kazakhstan (Fedorov & Poletiko, 1954). Later, many group names and trademarks were proposed, such as Red- or Pink-flowered and Red- or Pink-fleshed apples, Moerlansdii group, Purpurea group, Redvein crabs, Rosybloom crabs, Rosetta™ series, Redlove® series, Red Moon® series, Kissabel® series, and Lucy™ apples.

Natural range and discovery of Niedzwetzky's apple

Nikolaj Vavilov (1930) suggested that the wild apples of Turkestan, which bear large fruits similar to the orchard apple, must have been the progenitor, believing that Central Asia is an ancestral home of the cultivated apple tree. Most apple species have small bird-distributed pomes, while only two species wild *M. sieversii* and cultivated *M. domestica* are characterized by the largest fruit. Therefore, *M. sieversii* tree was considered as the ancestor of cultivated apple (Likhonos, 1983). The application of molecular data analysis methods confirmed this hypothesis. The sequence analysis of the matK region of the chloroplast genome of *Malus* species and cultivars found two matK duplications, one in the series *Malus* and the other in most *M. domestica* cultivars and one *M. sieversii* accession. The occurrence of a shared 18-bp duplication in the cpDNAs of wild and cultivated apple supports the close relationship between them. A phylogeny based on the internal transcribed spacer (ITS) of nuclear ribosomal DNA shows that *M. domestica* cluster closely together *M. sieversii*, including a rare colored form *M. sieversii* f. *niedzwetzkyana* (Robinson et al., 2001; Harris et al., 2002). Data from the sequencing and assembly of the apple genome support the formation of the *M. domestica* gene pool from *M. sieversii* (Velasco et al., 2010).

The main part of the natural range of Niedzwetzky's apple is Ile Alatau, or Zailijskij Alatau as part of Western and Northern Tian Shan Mountain in Kazakhstan, and the mountains of Western and Northern Xinjiang, and Kashgar in China (Yuzepchuk, 1939; Dzhangaliev et al., 2003; Yan et al., 2008). *Malus sieversii* f. *niedzwetzkyana* had higher similarity to *M. sieversii* in China than in other countries (Yang et al., 2020). It is also distributed in Afghanistan, Kyrgyzstan, and Uzbekistan, according to CEPF – Critical Ecosystem Partnership Fund (www.cepf.net) and the IUCN Red List of Threatened Species (www.iucnredlist.org). Single individuals occur sparsely in the walnut and fruit forest zone. This endemic species was included in the Red Book of the USSR (Krasnaja…, 1975), the Red Book of Kazakhstan (Krasnaja…, 1981), and the Red Book of Kyrgyzstan (Red…, 2006) and was last assessed for the Red List of Threatened Species of the International Union for Conservation of Nature in 2007. It is listed as Critically Endangered – very rare species throughout its range, with individuals sporadically distributed in severely fragmented populations, by the International Union for Conservation of Nature. Although the range is large, the actual area occupied is very small. It is suffering continuing decline owing to multiple threats (The…, 2023). Consequently, ecologists treated Niedzwetzky's apple as a full species.

This apple tree became famous in Europe thanks to the German biologist George Dieck (1847–1925). His worldwide contacts and his own travels led to an increasing number of new and rarely cultivated woody plants. In 1874, he founded the Tree Nurseries of the Zöschen Estate. By 1890, the nurseries had reached their largest size with an area of 50 hectares and a stock of about 6,000 species, forms and varieties. Dieck also experimented with cross-breeding ornamental apples from East Asia. Since then, he has belonged to the group of well-known breeders who have been working on new ornamental apples since the end of the 19th century. Dieck worked closely with various botanists and dendrologists, as well as amateurs and enthusiasts, to obtain new species and varieties for his nurseries. One of his main goals was to constantly introduce new plants from all over the world to trade and science (Kümmel & Kiehne, 2009). Among other collectors, Dieck maintained contact with the court president and amateur naturalist Vladislav Efimovich Niedzwiecki (also spelled Niedzwetsky and Niedzwetzky) from Verny (now Almaty, Kazakhstan), who devoted his free time to studying the local flora. It is believed that Niedzwiecki sent the material from the apple tree that he discovered directly to Dieck, but according to Ponomarenko (1975), Niedzwiecki sent the scions and seeds to Yaroslav Nemetz, a pomologist in Vinnytsia (now Ukraine), who then forwarded this material to Dieck. Dieck (1891) named a new apple in honor of the collector. In the first publication, the collector's surname was written as Medwietzky. In the next edition of the seed catalogue, he corrected this spelling to *M. niedwietzkyana* (Dieck, 1893).

It did not take long for the new apple tree to expand all over the world. Thanks to the Nemetz, the red-fleshed apple tree has spread to Ukraine. Dieck donated specimens to the Späth nursery (Germany), and Niels Ebbesen Hansen imported it from the Späth nursery to the USA in the winter 1896–1897, but the plants froze out the next winter. During his 1897 expedition, he found red-fleshed apples in Turkestan and western China, collected many seeds, and met with Vladislav Niedzwiecki (Hansen, 1901). Niedzwetzky's apple is known to have borne fruit in Canon Ellacombe's Garden, Bitton (England) in 1901 and in Royal Gardens, Kew in 1904 (Hemsley, 1904) (Fig. 1a). The tree in New York Botanical Garden was secured by exchange with Royal Gardens, Kew in 1901 (Nash, 1921) (Fig. 1b). Niedzwetzky's apple was introduced into the USA by the Arnold Arboretum in 1896, collection unknown (Norrys, 1996). The Bureau of Plant Industry of USDA imported *Malus niedwietzkyana* in 1909 (Galloway, 1911).

It should be noted that in the mountainous regions of Talysh, Azerbaijan, red-fleshed apples have long been cultivated in the gardens of the local population (Fedorov & Poletiko, 1954). Ivan Michurin (1948), who already in 1900 used the Niedzwetzky's apple in his crosses, believed it a Caucasian semi-cultivated tree.

The 'Surprise' apple tree, an ancient variety with pink-fleshed apples, is believed to be related to the Niedzwetzky's apple tree. It has now been proven that 'Surprise' is not closely related to *Malus sieversii* f. *niedzwetzkyana* and that its red flesh color is caused by a different mutation (Sekido et al., 2010; Umemura et al., 2013). It had made its way from Eastern Europe to England and Germany by the early 1800s. It was reported to be growing in the London Horticultural Society Gardens (Catalogue, 1831) and appeared in North America the following decade via German immigrants who settled in the Ohio River Valley in the 1840's (Fishman, 1995).

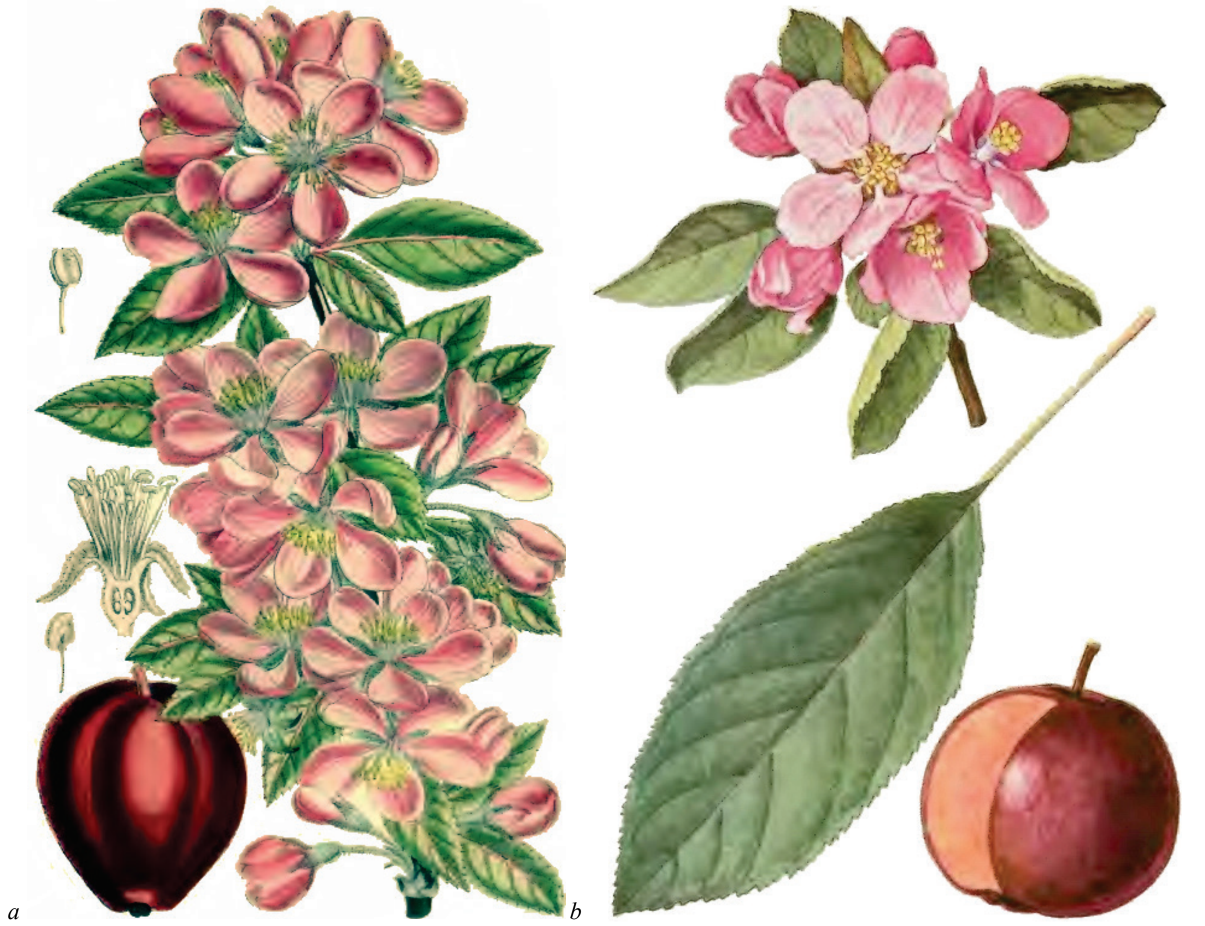

Fig. 1. First illustrations of *Malus sieversii* f. *niedzwetzkyana*: (*a*) as *Pyrus niedzwetzkyana* (Hemsley, 1904); (*b*) as *Malus niedzwetzkyana* (Nash, 1921)

Niedzwetzky's apple for the breeding of ornamental apples

In the whole range of flowering trees there is nothing more beautiful and effective than ornamental apples, especially red-flowered ones (Fig. 2a). In 1910, the Nursery Barbier & Cie of Orléans, France, offered a new ornamental apple tree to the trade (Grignan, 1910). It is an artificial ternary hybrid *M.* ×*atrosanguinea* (= *M. halliana* × *M. toringo*) × *M. sieversii* f. *niedzwetzkyana*. It combines abundant flowering of *M.* ×*atrosanguinea* with colored organs of Niedzwetzky's apple, attractive both in deep rosy-red flowers and dark vinous-red fruit because it was named *M. purpurea* (Rehder, 1920) (Fig. 2b). Another French nurseryman Victor Lemoine, Nancy, in 1922 developed 'Lemoine', one of the better red-blooming variety (Trees…, 2024). In the 1911 Barbier's apple tree was purchased by the Kew from its originator. Thanks to its high ornamental qualities, it quickly became very popular among gardeners and lovers of trees and shrubs. Soon two varieties were selected in England around 1920. Charles Eley from East Bergholt, Suffolk, UK selected 'Eleyi', and Vicary Gibbs, Aldenham House, Hertfordshire, UK raised 'Aldenhamensis'. The combination *M. scheideckeri* 'Exzellenz Theil' × *M. sieversii* f. *niedzwetzkyana* led to the creation of magnificent varieties, belonging to *M.* ×*gloriosa*. The first cultivar 'Oekonomierat Echtermeyer' was introduced in 1914 by Späth nursery, Berlin, Germany (Trees…, 2024). Its characteristic is widespreading canopy.

In the USA one of the goals of Hansen's breeding work at the South Dakota Agricultural Experiment Station was to develop ornamental crabapples by using his own introduction of *M. sieversii* f. *niedzwetzkyana*. Introduced in 1919, 'Red Tip' was raised from crossing the native American crab 'Elk River' × Niedzwetzky's apple. Its red-tipped young leaves make it an interesting tree from an ornamental standpoint. The best ornamental variety, 'Hopa', was developed in 1920 from Niedzwetzky's apple pollinated by *Malus baccata*. It is a striking sight when in bloom. Good for lawns and orchards, 'Redflesh' crabapple was introduced in 1928. It is the result of the pollination of Niedzwetzky's apple by 'Elk River'. In 1933, Hansen also developed a new series of red-flowered crabapples, 'Zaza', 'Zelma', and 'Zita', the parent of which is Siberian crab (Hansen, 1937, 1940). Isabella Preston at the Central Experimental Farm in Ottawa, Canada crossed Niedzwetzky's apple with the extremely hardy *M. baccata* for attractive and hardier hybrids in 1920. More than 100 seedlings were grown from artificially and naturally pollinated seed. By 1932 Preston had selected and named 15 of them after Canadian lakes (Anstey, 1986). They are a series of Rosybloom crab apples, including 'Amisk', 'Chilko', 'Cowichan', 'Makamik', 'Rosseau', 'Scugog', 'Simkoe', 'Sissipuk', 'Timiskaming', 'Wabiskaw'. Arie den Boer (1959) at the Waterworks Arboretum (now Den Boer Arboretum), Des Moines, Iowa created one of the world's largest collections of flowering crabapple trees. In the late 1930s, he developed 'Evelyn', originated as open-pollinated hybrid of *M. ioensis*, probably with *M. ×purpurea*. A new nothospecies name *M. ×denboerii* was applied for it (Krüssmann, 1977). His 'Purple Wave' has dark red-purple, single or with a few extra petals flowers, very dark purplish-green foliage, and dark purple fruit with a bloom. Many red-flowered apple varieties have been developed by John Fiala (1994) in USA. These are 'Buccaneer', 'Calvary', 'Cardinal's Robe', 'Cranberry Lace', 'Maria', 'Orange Crush', 'Purple Prince', and 'Wildfire'. A lot of new ornamental crab apples with red and red-purple flowers were developed by other breeders in the USA. These are 'Adams', 'Almey', 'Aros, 'Bailears', 'Branzam' (Brandywine®), 'Cheal's Weeping', 'Coppurple' (Perfect Purple™), 'Coral'(Coralburst®), 'Durleo' (Gladiator™), 'Fridlund' (Royal Gem™), 'Indian Magic', 'Indian Summer' 'JFS-KW5' (Royal Raindrops®), 'JFS KW139MX' (Ruby Dayze®), 'JFS-KW213MX' (Raspberry Spear®), 'JFS KW207' (Sparkling Sprite®), 'Malusquest' (Pink Sparkles®), 'Neville Copeman', 'Prairifire', 'Princeton Cardinal', 'Purple Prince', 'Scbrazam' (Scarlet Brandywine®), 'Shotizam' (ShowTime™), 'Velvetcole' (Velvet Pillar™) etc. 'Pink Cascade', 'Sutherland', 'Thunderchild', 'Royal Beauty', 'Royalty', and 'Rudolph' were originated in Canada (Trees…, 2024). The objectives of creating new varieties with better pink, red and deep purple flowers was to improve and diversify these and other ornamental traits, and to increase resistance to environmental factors (Jefferson, 1970).

a *b*

Fig. 2. Ornamental apple trees: *a* – diversity of the flowers (Mezhenskyj & Mezhenska, 2021); *b* – *Malus ×purpurea* (Mezhenskyj & Mezhenska, 2023)

In Europe and other parts of the world, intensive breeding work has also been carried out on new ornamental apple varieties. Simon Doorenbos, Public Parks in The Hague, The Netherlands crossed *M. ×purpurea* 'Lemoinei' with *M. toringo* before 1938. As a result of this hybridization, the nothospecies name *M. ×moerlandsii* was proposed for a new hybrid group. Initially 'Profusion' was introduced, and later in the following generations 'Edith', 'Liset' ('Lizette'), 'Nicoline', and 'Wies' (Grootendorst, 1964; Belder, 1984; Lombarts, 1984). Antoni Wróblewski in Kórnik, Poland, was engaged in the selection of *M. purpurea* seedlings in the years 1926–1938 and obtained several interesting varieties, named 'Hoser', 'Hedwigia' ('Jadwiga'), 'Kobendzi', 'Makowiecki', 'Sophia', 'Szafer, and 'Wierdakii' (Browicz & Bugała, 1952). In England, 'Barbara', 'Crimson Cascade', 'Harry Baker, and 'Neville Copeman' were developed, in France – 'Courtarou' (Coccinella®), and 'Diable Rouge', in the Netherlands – 'Mokum', in New Zealand – 'Bali', in Russia – 'Alaja Plakuchaja', 'Aurora', 'Gazonnaja', 'Karmen', 'Malinovka Dekorativnaja', and 'Vesna', in Ukraine 'Chorna Perlyna' and 'Oksana' (Mezhenskyj & Mezhenska, 2021, 2023). The above varieties vary in the size and red shades of the flowers and fruits, flowering and ripening times, and crown shape from upright to spreading and weeping. Columnar varieties of apples are also gaining in popularity (Havryliuk et al., 2022). The following varieties have a special columnar habit that is particularly suitable for small gardens. These are 'Laura', and 'Maypole' from England, Canadian 'Jefspire' (Purple Spire®), Belgian 'DvP Obel' (Red Obelisk™), Czech 'Rosalie' and 'Pomfital'. The last of these is a promising variety for fruit orchards.

Breeding of red-fleshed orchard apples

Ivan Michrin, Kozlov, Tambov region, Russia, first crossed the Niedzwetzky's apple with the popular Russian variety 'Antonovka' as well as 'Monstrosun' in 1900. Half of the hybrid seedlings grown from two hybrid pomes turned out to be red-leaved and the originator gave them names 'Azalija', 'Detskoe', 'Kagor', 'Paskhal'noe', 'Visant', and 'Rubinovoe' ('Yakhontovoe'). At the first fructification of hybrids, which took place in 1914, Michurin hybridized 'Rubinovoe' with his own varieties, which were derived from the crossing of European orchard apples with *M. prunifolia*. He continued such crosses in the following years for obtaining new varieties of apple trees with beautifully colored pulp. The second generation of hybrids began to bear fruit in 1923–1926. If some of the first-generation hybrids had fruits of mediocre taste, the new selections 'Bel'fler Puntsovyjj', 'Bel'fler Krasnyj', 'Bel'fler-rekord', 'Komsomolets' (Fig. 3b) and 'Krasnyj Shtandart' had fruit of improved quality. Their fruits of the winter ripening period, weighing 70–120 g had deep rose skin, pink to deep pink flesh, juicy, and sweet with pleasant acidity (Michurin, 1948). The third-generation hybrids with the participation of the best European varieties, used to further improve the quality of the fruit, began to bear fruit after the breeder's death.

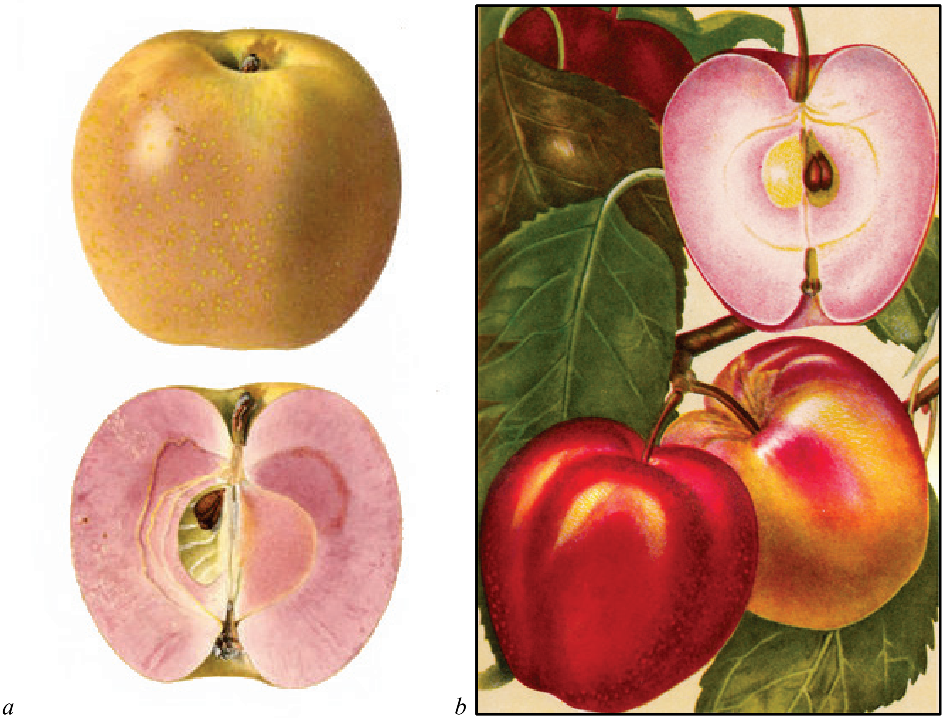

Fig. 3. First illustrations of red-fleshed apple varieties: *a* – *Malus* (Surprise Group) 'Surprise' F1 (Steadman, 1924); *b* – *Malus* (Niedzwetzkyana Group) 'Komsomolets' (Michurin, 1948)

Niels Hansen believed that Niedzwetzky's apple was a small red-fleshed apple without any promise as a table fruit. The hybrids and ornamental varieties between it and crabs are small-fruited, but Hansen's 'Redflesh' fruit makes excellent red preserves and red jelly. Cultivars of new series of red-fleshed crabapple 'Zaza', 'Zelma', and 'Zita' were both ornamental and useful for cooking into good red sauce (Hansen, 1937, 1940). Repeated crossing of Redvein crabs with an orchard apple tree improved the quality of the fruits of these hybrids. 'Almata', 'Ata', and 'Redflesh Winter Crab' developed from 'Redflesh' have a larger pome (Hansen, 1946). 'Almata' is a cross of ('Beautiful Arcade' × 'Fluke 38') × 'Redflesh'. Its fruit has a striking watermelon-red flesh, tart flavor. Makes excellent applesauce and can be used for pickling. Richard Wellington, in the New York Experiment Station, Geneva crossed *M. sieversii* f. *niedzwetzkyana* with 'Wolf River' in 1924. A new variety named 'Redfield` has first fruit in 1935. Its fruit was larger Niedzwetzky's apple, but it was valued as an ornamental (Brooks & Olmo, 1997).

Unlike Michurin and Hansen, who used natural *M. sieversii* f. *niedzwetzkyana*, Albert Ether began breeding red-flavored apples based on a pink-fleshed 'Surprise' (Fig. 3a). Around 1900, he planted an experimental apple orchard in Ettersburg, California, USA, to conduct a variety trial that would become the genetic basis for his own breeding program. 'Surprise' became the progenitor of a whole new class of varieties with pink flesh. By 1928, he developed two pink-fleshed apples 'Redflesh Winter Banana' and 'Pink Pearl'. Among the offspring of 'Surprise' from controlled and open pollination, about 30 selections were selected ranging in skin color from almost transparent to almost solid red, and including intermediate specimens with green, yellow, blushed and striped exteriors. Size also ranged from very small to very large, and ripening dates also vary from late June to late November. 'Pink Pearl' was patented and introduced in 1945. It is a beautiful fruit with a robust flavor, suitable for desserts, salads or sauces (Fishman, 1995). The progeny of *M. sieversii* f. *niedzwetzkyana*, and *M. baccata* × *M. sieversii* f. *niedzwetzkyana* are susceptible to diseases such as apple scab and fire blight (Jefferson, 1970). However, hybridization with other *Malus* species has been exploited to create new cultivars with superior qualities for industrial nutraceutical production from fruit, including disease resistance, yield, and degree of anthocyanin accumulation (Nocker et al., 2012).

In 1970–1980, Ram Fishman, Greenmantle Nursery, Garberville, California explored the old Ether's orchard together his neighbor's neglected gardens and selected some of excellent varieties. These were named Blush Rosette™, Christmas Pink®, Grenadine®, Pink Parfait®, Pink Pearmain®, Rubaiyat®, and Thornberry®. These seven selects along with Ether's two varieties, form a distinct class of apple called the Rosetta™ Series. The time of ripeness of their fruits is late September to late November under the California climate. The flesh of the apples is pink to deep pink, with a firmer and juicier texture (Fishman, 1995). In the early 1960s, an apple tree was accidentally found in an abandoned orchard in Oregon, which is a progeny of 'Surprise'. Known as 'Airlie Red Flesh' ('Mountain Rose', Hidden Rose®), this late-suppressing variety has a greenish-yellow skin and bright pink to red crisp juicy flesh with a well-balanced flavor.

During World War II, the red-fleshed apple tree was introduced from Ukraine to Germany. This was either a local form or one of the varieties of the Michurin selection was grown in Germany under the name 'Rote Mond' and patented as 'Weirouge' in 1997 (Sadilova et al., 2006; Pomiferous, 2021). Baya® Marisa is the result of Michael Neumüller's crossing of the 'Weirouge' with the 'Kreuzung' (a tasteful 'Zuchtklon 166') and is released by the Bavarian Fruit Center, Hallbergmoos. The Baya® Marisa fruit has an attractive flesh color and is a pleasure to bite into thanks to its crisp texture and delicious taste, whereas all previous varieties have a very tart taste (Fig. 4a). Through breeding, it has been found that the female parent has a greater proportion of red-fleshed progeny than the male parent (Neumüller & Dittrich, 2017). Markus Kobelt, Lubera Nurseries of Buchs, Switzerland develop several sweet-tart, red-fleshed apples during the early 2000s. It took nearly 20 years of experimenting with crossing red-fleshed varieties with white-fleshed 'Royal Gala' and 'Braeburn' apples until the first red-fleshed apple of the series Redlove hit the market in 2009. This series includes Redlove® Circe, Redlove® Calypso, Redlove® Era, Redlove® Jedermann's, Redlove®

Lollipop, Redlove® Odysso, and Redlove® Sirena (Pomiferous, 2021). The fruit is red on the outside and inside, with a white line in the middle. Appreciated as a fresh-eating apple for its balanced tartness and sweetness, it is also useful for baking, jellies, and juice. The trees are resistant to scab.

In Japan, red-fleshed apple breeding has been carried out since 1989. This was prompted by the fact that most Japanese consumers peel apples before eating them. Removing the apple skin, which is rich in red pigments with antioxidant activity, reduces the value of the fruit. Therefore, in an effort to preserve the health benefits, breeding has begun to create varieties with red flesh rich in anthocyanins. 'Pink Pearl' and its progeny 'Irodori' and 'JPP35' were used to produce new red-fleshed cultivars, including *M. domestica* (Surprise Group) 'Enbu', 'HFF33', 'HFF60', 'Kurenainoyume', 'Moonrouge', 'Nakano no Kirameki', 'Nakano Shinku', 'Rose Pearl', 'Ruby Sweet', and other (Sekido et al., 2010; Matsumoto et al., 2016, 2018).

A tree fruit varieties management company Proprietary Variety Management (PVM) has tested two varieties of red-flesh apples 'Howell TC2' and 'Howell TC3' developed by apple breeder Bill Howell, Prosser, Washington, USA. These apple trees originated as a result of an open pollination of 'Airlie Red Flesh' by tastier 'Honeycrisp' in 2001. Considered to be of exceptional quality, crisp, juicy, and sweet-tart with berry notes flavor, these hybrids will be distributed under the names Lucy™ Glo and Lucy™ Rose. As more trees are planted, Lucy™ apples will become more widely available, and new varieties will be introduced.

Three new red-fleshed apples commercially released under the names Kissabel® Jaune ('Y102'), Kissabel® Orange ('Y101'), and Kissabel® Rouge ('R201') were developed in Seiches-sur-le-Loir, France by Valérie Fouillet in cooperation with the Ifored, an international consortium of apple growers. They were registered by International Fruit Obtention in 2016–2018. All three apple varieties were bred for their pigmented flesh coloring. Both cultivars 'Y102' and 'Y101' are derived from a controlled cross of 'Golden Delicious' × 'SJ109' in 2006. Their color of skin is accordingly dark orange-yellow and red-orange. The apple of a third cultivar 'R201' originating from a cross 'MNR33S1A51 × 'Galaxy' in 2006 has dark purple brown skin and red flesh. There are also other pink and red-fleshed cultivars developed in Seiches sur le Loir, which Ifored plans to use to expand the line. Red Moon® is a new brand for a series of two red-flesh apples developed by Jean-Luc Carrières, Montcuq, Lot, France in collaboration with Escande Nursery, Saint-Georges, France and Italian varietal management enterprise KVM. Niedzwetzky's apple is the ancestor of these 'RM-1' ('Red Moon') and 'RS1' ('Red Sun') with red flesh that were discovered in 2001 (Gasic et al., 2001).

In New Zealand, at the Institute for Plant and Food Research Limited (formerly HortResearch) breeders have been working to develop new red varieties since 1998. The red-fleshed accessions belong to two distinct phenotypes, crossed with high-quality cultivars and advanced selections that have white flesh. The best red-fleshed seedlings of F1 families were used for developing new hybrid populations to find selections with superior eating quality (Volz et al., 2009; Chagné et al., 2013). In addition, the scientists pinpointed the gene that controls anthocyanins and developed genetic markers to quickly identify seedlings with red fruits without the need to grow the trees. Sequencing the apple genome revealed targets for desirable traits. Using technologies such as CRISPR, scientists began to edit genes. Genetic modification isolated the gene needed in Niedzwetzky's apple to combine the red colored flesh with the size and sweetness of the 'Royal Gala' orchard apple (Espley et al., 2013; Volz et al., 2013).

Recently, many of the new red-fleshed apple varieties appearing on supermarket shelves are not only patented or registered for plant breeder's rights, but also trademarked and managed as legally protected brands. In many cases, the commercializing organizations are trademarking and marketing their varieties under a single umbrella brand instead of assigning a single trademark or brand name to a single registered variety. These include brands such as cited above Redlove®, Lucy™, Kissabel®, and Red Moon® (Huang & Carpenter, 2022).

a b

Fig. 4. Some fruit cultivars of the Malus Niedzwetzkyana Group: (a) 'Marisa'; (b) 'Dr. Campbell's' (Mezhenskyj & Mezhenska, 2023)

Niedzwetzky's apple for breeding clonal rootstock and usage of these rootstocks

Valentin Budagovskij, Michurinsk, Fruit and Vegetable Institute, Russia, hybridized a Paradise apple, which is used as a dwarf rootstock, with Michurin's 'Krasnyj Shtandart', creating a red-pigmented dwarf rootstock 'Paradizka Budagovskogo', or 'PB9'. He further involved in crosses the Siberian crabs to increase its winter hardiness. As result several popular rootstocks were developed. They are dwarf rootstock '62-396', and semi-dwarf '54-118', or 'B118, as well as the series '57-146', '57-

233', '57-469', '57-490', '57-491', '54-545'and other. A new super dwarf rootstock 'Malysh Budagovskogo' or 'MB' was created by crossing 'PB9' with a complex hybrid '13–14' derived from *M. domesica* × *M. prunifolia* × *M. baccata* (Budagovskij, 1974; Potapov et al., 1990).

In the process of growing grafted apple cultivars in the nursery, a labor-intensive operation is removing scion shoots from budded plants. Red-leaved scion shoots, as opposed to the typical green shoots, are easy to distinguish from the shoots of the grafted variety. In addition to its direct uses as a rootstock for grafting varieties, fruits and leaves of red-leaved rootstocks can be used as raw material. These hybrids with high content of antioxidants in fruits may be promising for planting orchards for raw material purposes. Their fruits can be used to make compotes with a high antioxidant content. Some of the clonal rootstocks are suitable for the production of raw fruit, while others are more suitable for ornamental purposes. During the production of planting stock, nurseries generate a significant amount of plant waste annually in the form of non-standard shoots in the nursery and cut parts of rootstocks in the nursery. Apple plant material production waste – rejected non-standard shoots of red leaf clonal rootstocks – can serve as an alternatively available source of natural, environmentally safe food colorants.

Role of the MYB10 and MYB110a transcription factor genes

Malus sieversii f. *niedzwetzkyana* is a color mutant of *M. sieversii* (Ponomarenko, 1975). It differs from *M. sieversii* in having a single major color gene. The red pigmentation of all parts of the plant is caused by the action of this homozygous, dominant gene in the plant (Lewis & Crane, 1938; Trebuschenko, 1939; Reim et al., 2006). This form may simply be the result of a particular set of alleles coming together by chance in seedlings because multiple genes probably influence the location and intensity of anthocyanin pigmentation in the species (Juniper & Mabberley, 2019). Nikolaj Vavilov (1935) noted that the presence or absence of anthocyanin coloration is an alternative characteristic "in almost all plants, in all species". According to Vasilchenko (1963), under the name of Niedzwetzky's apple trees peculiar color deviations observed in all or most apple trees of Central Asia were artificially united. One of the collection accessions named Niedzwetzky's apple according to the results of the isoperoxidase assay appeared to be closer to the *M. sylvestris* than the *M. sieversii* (Grushin & Ivakin, 1989). Thus, anthocyanin mutants of the apple tree may not be related to *M. sieversii* f. *niedzwetzkyana*. An anthocyanin pigmentation of flesh inherited from 'Surprise' is thought to be controlled by a single dominant gene under the influence of "modifier" genes. The effect of these modifiers could be seen in the wide spectrum of color intensity varying from pale pink through rose pink and even, in a few cases, purplish or "beet" red (Fishman, 1995).

Anthocyanin concentration is an important determinant of the color of many fruits, including apples. Apples usually have white flesh and green, yellow or red skin, meaning that the accumulation of anthocyanins in these fruits is limited to the skin in some varieties. The red skin accumulates anthocyanins in response to developmental, hormonal, and light signals (Ubi et al., 2006). In the plants the anthocyanin biosynthesis is controlled at the level of transcription. The proteins of a large gene family, the MYB genes, read and interpret the genetic information in the DNA. The transcription factor MYB1 is responsible for the accumulation of anthocyanins in apple skin. Their expression correlated with the skin anthocyanin accumulation induced by ultraviolet-B irradiation and low temperature treatment. Another transcription factor, MYB10, an allele of MYB1 co-segregates with the red flesh and leaf phenotypes (Takos et al., 2006; Ban et al., 2007). It is located on linkage group 09 of the apple genome. This locus results in increased MYB10 transcript levels and subsequent ectopic accumulation of anthocyanins throughout the red-fleshed apples (Chagné et al., 2007; Espley et al., 2007, 2009).

However, there are apple phenotypes in which red-flesh cortex is associated with enhanced expression of MYB110a, a paralog of MYB10. This gene homologous to MYB10 is located on linkage group 17. Linkage groups/chromosomes 9 and 17 are highly colinear and arose from a whole-genome duplication event during the evolution of the Maloideae subfamily (Velasco et al., 2010; Chagné et al., 2013; Umemura et al., 2013). These two types of red color of the flesh, determined by different genes, are named type 1, inherent in the Niedzwetzky's apple tree, and type 2, inherent in the progeny of 'Surprise' (Volz et al., 2009; Würdig et al., 2014; Neumüller & Dittrich, 2017). In type 1 red flesh apples, MYB10 confers extensive anthocyanin accumulation throughout the plant, including fruit flesh and skin, flowers, leaves, and stems. In type 2 apples, only the flesh is red, and other organs are the same color as those of common orchard apple trees that bear white-fleshed fruit. Therefore, fruits with yellow skin and red flesh are only associated with the MYB110a genotype. MYB10 and MYB110a are expressed early and late in the fruit maturation process, respectively (Hamada et al., 2015). Würdig et al. (2014) believe type 2 red-fleshed apple phenotype seems to be more useful for breeding. An attempt to combine both functional MYB10 and MYB110a in one apple genotype was unsuccessful. It was suggested that some sort of breeding depression must have occurred (Hamada et al., 2015).

The promoter region of MYB10 has six MYB binding motifs in tandem, whereas other MYB1 alleles have a single MYB binding motif at the promoter (Espley et al., 2009). Therefore, MdMYB10 and other MdMYB1 alleles are known as R6 and R1 MYBs, respectively. If the R6 promoter is assigned to red-flesh and red-leaved progeny of *M. sieversii* f. *niedzwetzkyana*, then red-flesh and green-leaved apples derived from 'Surprise' have only the R1 promoter (Sekido et al., 2010; Nocker et al., 2012). Many orchard apple cultivars with highly pigmented skin exhibit internal pigmentation, but this has typically been subtle and mostly confined to the cell layers underlying the epidermis. It is explained by intercellular diffusion or trafficking of anthocyanin biosynthetic intermediates, enzymes, or regulatory factors such as MYB10 that are normally restricted to the skin. A few cultivars also exhibited pigmentation within the vasculature, a feature that may also result from ectopic expression of such factors. The red-fleshed trait depends on R6, but the presence of the MYB10 R6 is neither sufficient nor required for this trait in all apple genotypes. There are apple cultivars that contained the R6 element yet did not develop significant pigmentation. In addition, many R6-containing cultivars produce fruit exhibiting various internal coloration patterns and intensities, and this was not obviously related to whether R6 is apparently heterozygous or homozygous. The activity of the R6 allele of MdMYB10 is extensively modified by genotype (Nocker et al., 2012). Wang et al. (2017) indicated that there are R1R1 homozygous genotypes with white-flesh phenotype, R6R1 heterozygous genotypes with red-flesh phenotype, and R6R6 homozygous genotypes with dark red flesh apples in the hybrid population between *M. sieversii* f. *niedzwetzkyana* cultivar and white-flesh cultivar of *M. domestica*. The red-flesh phenotype is determined by the R6 repeat sequence of the MYB10 promoter.

The tandem motif in MYB10 of apple positively regulates its own expression, which results in an abundance of MYB10 and anthocyanin accumulation in many different organs. In contrast, the molecular mechanisms that regulate MYB110a expression are unclear (Honda & Moriya, 2018). Transcriptome analyses showed that flavonoid metabolism might be involved in stress responses in red-fleshed apple (Wang et al., 2015). There are flavonoid-related genes encoding R2R3-MYB transcription factors, MYB12 and MYB22. The expression patterns of MYB12 and MYB22 directly correlated with those of leucoanthocyanidin reductase and flavonol synthase, respectively (Wang et al., 2017).

Red-flesh apple polyphenols and health benefits

The apple tree is one of the most widely grown and economically important fruit crops in temperate regions. Apples are an important source of flavonoids and other nutrients in the human diet (Wang et al., 2018). The 19th century adage "An apple a day keeps the doctor away" is particularly relevant in the modern era of health and wellness. As noted by Hyson (2011) "exposure to apples and apple products has been associated with beneficial effects on the risk, markers, and etiology of cancer, cardiovascular disease, asthma, and Alzheimer's disease". Recent research suggests that apple products may also be beneficial for cognitive decline in older adults, diabetes, obesity, bone health, and pulmonary and gastrointestinal function. These benefits are often attributed to the high antioxidant content. The apples, including peel and flesh have an antioxidant activity thanks to vitamin C and polyphenolic antioxidants, including anthocyanins (Hertog et al., 1993; Wolfe et al., 2003; Toufektsian et al., 2008).

The main classes of polyphenols in apple are the hydroxycinnamic acids, flavonols, chalcones, catechins, procyanidins and anthocyanidins (Tsao et al., 2003). Nearly half of the polyphenols in whole apples are found in the peel, and the peel contains essentially all of the flavonols and anthocyanins. However, consumers eat much less of the apple skin than the flesh. Therefore, apple varieties with red flesh are of great importance for increasing human intake of flavonoids to maintain health (Wang et al., 2018; Yuste et al., 2022).

Anthocyanin gene expression in MYB10 'Royal Gala' apple tissue shows a significant increase for five cyanidin glycosides, of which cyanidin-3-galactoside was the most abundant. Total average anthocyanin concentrations in apple tissue rose up to 20-fold. MYB10 over-expression also increased concentrations of quercetin-3-galactoside flavonoid up to a 10-fold and a threefold increase in proanthocyanidins. The immediate precursors of proanthocyanidins, catechin and epicatechin, were also increased, two and threefold, respectively (Espley et al., 2013). However, highly anthocyanic red-fleshed apples have accelerated ripening and an increased incidence of internal browning flesh disorder (Espley et al., 2019).

Red-fleshed apples are a novelty and therefore considered to be more attractive to consumers and contain more health beneficial compounds (Würdig et al., 2014). Market research has found consumers are willing to pay significant price premiums for fruit with novel colors and tastes, as well as added health benefits. Apples are rich source of phenolic compounds exhibiting a strong antioxidant activity. The potential of anthocyanidins to provide protection against oxidative damage is well known (Tsao et al., 2003; Wojdyło et al., 2008; Rupasinghe et al., 2010). Anthocyanin concentrations in red-fleshed apples are considerably higher than for common red-peeled apples (Sadilova et al., 2006). However, flavanol polymers induce the taste of bitterness and the tactile sensation of astringency that can be unpleasant (Lesschaeve & Noble, 2005). Therefore, the breeding challenge is to create varieties that are rich in anthocyanins and have an improved flavor on par with the best dessert apples, unless they are intended for processing. Although the high content of polyphenols impairs the taste of fresh apples, these fruits are good raw materials for processing and blending, such as 'Dr. Campbell's' apple (Fig. 4b).

Flavonoid metabolism in red apple depends on genotype and environmental factors. Higher levels of flavonoids in the fruit can reduce fruit quality by creating a more astringent taste. Increasing the anthocyanin content can lead to the accumulation of malic acid (Wang et al., 2018). The study by Volz et al. (2014) suggests that the progress that could be made in breeding for individual polyphenols (except anthocyanin) is variable and depends on the polyphenol group to which the individual compound belongs. With the exception of catechin, all other peel and flesh flavanols had low heritabilities, and thus breeding progress for altered composition of these compounds would be slow. For all other polyphenols, the heritabilities were moderate to high, so that good breeding progress should be possible. Furthermore, the high genetic correlations between individual polyphenols within a polyphenol class would mean that selection for a single polyphenol would generally mean a concurrent change in the concentration of polyphenols within the same class. Another study of cultivars, which share a common MYB110a allele with different color intensities in their cortex, revealed that not only cyanidin-3-galactoside, but also chlorogenic acid and epicatechin are the dominant phenolic compounds in type 2 red-fleshed cultivars, except for a red-fleshed lineage with a white cortex. Bioinformatic analysis further revealed that cultivars with deep red flesh accumulated caffeic acid and procyanidin B2, whereas cultivars with pale red flesh accumulated catechin and epicatechin (Sato et al., 2017).

Conclusion

Data on the origin, study, selection, and use of red-flowered and red-fleshed apples are presented in this review. The progeny of Niedzwetzky's apple and 'Surprise' apple, which contain the genome of other *Malus* species, are characterized by extreme variability of red flowers and fruits. The increased content of anthocyanins in the organs of these trees is caused by two mutated genes, the action of which is being further studied in genomic and proteomic studies. Ornamental red-flowered varieties with different habitus are best suited for landscaping, and red-leaved rootstocks are very convenient for nursery cultivation. Currently, there are many red-fleshed cultivars available for both processing and fresh consumption. Due to their significant amount of anthocyanidins and other high antioxidant flavonoids, these pomes are needed in the human diet. Recent high-quality cultivars have been registered as trademarks and are grown in significant quantities. The next step in breeding is to improve high flavonoid apples to increase their sweetness, excellent flavor, high crispness with longer storage, good transport and different ripening times.

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References

Anstey, T. H. (1986). One hundred harvests: Research branch, Agriculture Canada, 1886–1986. Minister of Supply and Services Canada, Ottawa.

Applequist, W. L. (2014). Report of the Nomenclature Committee for Vascular Plants: 66. Taxon, 63(6), 1358–1371.

Aydın, Z. U., & Dönmez, A. A. (2019). Taxonomic and biogeographic notes on the genus *Pyrus* L. (Rosaceae): A new record and a new synonym, with data on seed morphology. Plant and Fungal Research, 2(1), 2–8.

Ban, Y., Honda, C., Hatsuyama, Y., Igarashi, M., Bessho, H., & Moriguchi, T. (2007). Isolation and functional analysis of a MYB transcription factor gene that is a key regulator for the development of red coloration in apple skin. Plant Cell Physiology, 48, 958–970.

Belder, J. (1984). S. G. A. Doorenbos: Leven en werk. Dendroflora, 1984, 15–54.

Boer, A. F. D. (1959). Ornamental crab apples. American Association of Nurserymen, Washington.

Brickell, C. D., Alexander, C., Cubey, J. J., David, J. C., Hoffman, M. H. A., Leslie, A. C., Malécot, V., & Jin, X. (Eds.). (2016). International code of nomenclature for cultivated plants. Scripta Horticulturae. 9th ed. International Society of Horticultural Science, Leuven.

Brooks, R. M., & Olmo, H. P. (1997). Register of fruit and nut varieties. 3rd ed. ASHS Press, Alexandria.

Browicz, K., & Bugała, W. (1952). Nowe odmiany *Malus purpurea* Rehd. Otrzymane w Kórniku przez A. Wróblewskiego. Acta Societatis Botanicorum Poloniae, 21, 719–724.

Budagovskij, V. I. (1974). Mezhvidovaja gibridizatsija v rode *Malus* Mill. pri vyvedenii klonovykh podvoev jabloni [Interspecific hybridization of the *Malus* Mill. variety for breeding clonal stocks]. In: Morozov, A. V., Stepanov, S. N., Sokol, P. F., & Kovalev, K. G. (Eds.). Papers of Soviet scientists presented to the XIX International Congress on Horticulture (Warsaw, PPR). Kolos, Moscow. Pp. 20–23 (in Russian).

Campbell, C. S., Evans, R. C., Morgan, D. R., Dickinson, T. A., & Arsenault, M. P. (2007). Phylogeny of subtribe Pyrinae (formerly the Maloideae, Rosaceae): Limited resolution of a complex evolutionary history. Plant Systematics and Evolution, 266(1–2), 119–145.

Catalogue of the fruits cultivated in the garden of the Horticultural Society of London (1831). 2nd ed. W. Nicol, London.

Chagné, D., Carlisle, C. M., Blond, C., Volz, R. K., Whitworth, C. J., Oraguzie, N. C., Crowhurst, R. N., Allan, A. C., Espley, R. V., Hellens, R. P., & Gardiner, S. E. (2007). Mapping a candidate gene (MdMYB10) for red flesh and foliage colour in apple. BMC Genomics, 8, 212.

Chagné, D., Lin-Wang, K., Espley, R. V., Volz, R. K., How, N. M., Rouse, S., Brendolise, C., Carlisle, C. M., Kumar, S., De Silva, N., Micheletti, D., McGhie, T., Crowhurst, R. N., Storey, R. D., Velasco, R., Hellens, R. P., Gardiner, S. E., & Allan, A. C. (2013). An ancient duplication of apple MYB transcription factors is responsible for novel red fruit-flesh phenotypes. Plant Physiology, 161, 225–239.

Chen, P., Li, Z., Zhang, D., Shen, W., Xie, Y., Zhang, J., Jiang, L., Li, X., Shen, X., Geng, D., Wang, L., Niu, C., Bao, C., Yan, M., Li, H., Li, C., Yan, Y., Zou, Y., Micheletti, D., Koot, E., Ma, F., & Guan, Q. (2021). Insights into the effect of human civilization on *Malus* evolution and domestication. Plant Biotechnology Journal, 19, 2206–2220.

Christenhusz, M. J. M., Fay, M., & Byng, J. W. (Eds.). (2018). The global flora. 4. Special edition, Glovap Nomenclature. 1. Plant gateway, Bradford.

Cornille, A., Giraud, T., Smulders, M. J. M., Roldán-Ruiz, I., & Gladieux, P. (2014). The domestication and evolutionary ecology of apples. Trends in Genetics, 30(2), 57–65.

Cornille, A., Gladieux, P., Smulders, M. J. M., Roldán-Ruiz, I., Laurens, F., Le Cam, B., Nersesyan, A., Clavel, J., Olonova, M., Feugey, L., Gabrielyan, I., Zhang, X. G., Tenaillon, M. I., & Giraud, T. (2012). New insight into the history of domesticated apple: Secondary contribution of the European wild apple to the genome of cultivated varieties. PLoS Genetics, 8(5), e1002703.

Dieck, G. (1891). *Malus nedwietzkyana* m. i. l. Neuheiten-Offerte des National-Arboretums zu Zöschen bei Merseburg, 1891. E. Karras, Halle. P. 16.

Dieck, G. (1893). *Malus niedwietzkyana*. Neuheiten-Offerte des National-Arboretums zu Zöschen bei Merseburg, 1892/93. E. Karras, Halle. P. 18 (in German).

Duan, N., Bai, Y., Sun, H., Wang, N., Ma, Y., Li, M., Wang, X., Jiao, C., Legall, N., Mao, L., Wan, S., Wang, K., He, T., Feng, S., Zhang, Z., Mao, Z., Shen, X., Chen, X., Jiang, Y., Wu, S., Yin, C., Ge, S., Yang, L., Jiang, S., Xu, H., Liu, J., Wang, D., Qu, C., Wang, Y., Zuo, W., Xiang, L., Liu, C., Zhang, D., Gao, Y., Xu, Y., Xu, K., Chao, T., Fazio, G., Shu, H., Zhong, G. Y., Cheng, L., Fei, Z., & Chen, X. (2017). Genome re-sequencing reveals the history of apple and supports a two-stage model for fruit enlargement. Nature Communication, 8, 249.

Dzhangaliev, A. D., Salova, T. N., & Turekhanova, P. M. (2003). The wild fruit and nut plants of Kazakhstan. Horticultural Reviews, 29, 305–371.

Espley, R. V., Bovy, A., Bava, C., Jaeger, S. R., Tomes, S., Norling, C., Crawford, J., Rowan, D., McGhie, T. K., Brendolise, C., Putterill, J., Schouten, H. J., Hellens, R. P., & Allan, A. C. (2013). Analysis of genetically modified red-fleshed apples reveals effects on growth and consumer attributes. Plant Biotechnology Journal, 11, 408–419.

Espley, R. V., Brendolise, C., Chagné, D., Kutty-Amma, S., Green, S., Volz, R., Putterill, J., Schouten, H. J., Gardiner, S. E., Hellens, R. P., & Allan, A. C. (2009). Multiple repeats of a promoter segment causes transcription factor autoregulation in red apples. Plant Cell, 21, 168–183.

Espley, R. V., Hellens, R. P., Puterill, J., Stevenson, D. E., Kutty-Amma, S., & Allan, A. C. (2007). Red colouration in apple fruit is due to the activity of a MYB transcription factor, MdMYB10. Plant Journal, 49, 414–427.

Espley, R. V., Leif, D., Plunkett, B., McGhie, T., Henry-Kirk, R., Hall, M., Johnston, J. W., Punter, M. P., Boldingh, H., Nardozza, S., Volz, R. K., O'Donnell, S., & Allan, A. C. (2019). Red to brown: An elevated anthocyanic response in apple drives ethylene to advance maturity and fruit flesh browning. Frontiers in Plant Sciences, 10, 1248.

Fedorov, A. F., & Poletiko, O. M. (1954). Apple tree genus – *Malus* Mill. In: S. Y. Sololov (Ed.). Derev'ja i kustarniki SSSR [Trees and shrubs of USSR]. AN SSSR, Moscow, Leningrad. Vol. 3. Pp. 414–458 (in Russian).

Fiala, J. L. (1994). Flowering crabapples. Timber Press, Portland.

Fishman, R. (1995). Albert Etter and the pink-fleshed daughters of surprise. Fruit Gardener, 27, 3.

Galloway, B. T. (1911). Seeds and plants imported during the period from October 1 to December 31, 1909: Inventory no. 21; nos. 26048 to 26470. Bulletin of the Bureau of Plant Industry, 205, 1–282.

Gasic, K., Preece, J. E., & Karp, D. (2020). Register of new fruit and nut cultivars list 50. HortScince, 55(7), 164–1201.

Govaerts, R., Nic Lughadha, E., Black, N., Turner, R., & Paton, A. (2024). The world checklist of vascular plants, a continuously updated resource for exploring global plant diversity. Scientific Data, 8, 215.

Grignan, G. T. (1910). *Malus floribunda purpurea*. Revue Horticole, 82, 539.

Grootendorst, H. J. (1964). *Malus* – sierappels [*Malus* – ornamental apples]. Dendroflora, 1, 3–15 (in Dutch).

Gross, B. L., Henk, A. D., Forsline, P. L., Richards, C. M., & Volk, G. M. (2012). Identification of interspecific hybrids among domesticated apple and its wild relatives. Tree Genetics and Genomes, 8, 1223–1235.

Grushin, A. A., & Ivakin, A. P. (1989). Sistematicheskoe polozhenie *Malus niedzwetzkyana* (Rosaceae) po dannym izuchenija izoperoksidaz [Systematic position of *Malus niedzwetzkyana* (Rosaceae) based on isoperoxidases investigation]. Botanicheskij Zhurnal, 74(2), 189–193 (in Russian).

Hamada, Y., Sato, H., Otagaki, S., Okada, K., Abe, K., Matsumoto, S., & Flachowsky, H. (2015). Breeding depression of red flesh apple progeny containing both functional MdMYB10 and MYB110a_JP genes. Plant Breeding, 134(2), 239–246.

Hansen, N. E. (1901). Ornamentals for South Dakota. Research Bulletins of the South Dakota Agricultural Experiment Station, 72, 1–206.

Hansen, N. E. (1927). Plant introductions. Research Bulletins of the South Dakota Agricultural Experiment Station, 224, 1–68.

Hansen, N. E. (1937). Fruits, old and new and northern plant novelties. Research Bulletins of the South Dakota Agricultural Experiment Station, 309, 1–16.

Hansen, N. E. (1940). New hardy fruits for the northwest. Research Bulletins of the South Dakota Agricultural Experiment Station, 339, 1–31.

Hansen, N. E. (1946). Northern plant novelties for 1945. Agricultural Experiment Station Horticulture Pamphlets, 8, 1–4.

Harris, S. A., Robinson, J. P., & Juniper, B. E. (2002). Genetic clues to the origin of the apple. Trends in Genetics, 18(8), 426–430.

Havryliuk, O., Kondratenko, T., Mazur, B., Kutovenko, V., Mazurenko, B., Voitsekhivska, O., & Dmytrenko, Y. (2022). Morphophysiological peculiarities of productivity formation in columnar apple varieties. Agronomy Research, 20(1), 148–160.

Hemsley, W. B. (1904). *Pyrus niedzwetzkyana*. Curtis's Botanical Magazine, 130, 7975.

Hertog, M. G. L., Feskens, E. J. M., Hollman, P. C. H., Katan, M. B., & Kromhout, D. (1993). Dietary antioxidant flavonoids and risk of coronary heart disease: The Zutphen Elderly study. Lancet, 342, 1007–1011.

Huang, X. C., & Carpenter, V. (2022). Intellectual property and commercializing red-fleshed apples. Rénwén shèhuì kēxué lùncóng,12, 195–207.

Hyson, D. A. (2011). A comprehensive review of apples and apple components and their relationship to human health. Advances in Nutrition, 2(5), 408–420.

Jefferson, R. M. (1970). History, progeny, and locations of crabapples of documented authentic origin. National Arboretum Contribution, 2, 1–107.

Juniper, B. E., & Mabberley, D. J. (2019). The extraordinary story of the apple. Kew Publishing, Kew.

Kartesz, J. T., Gandhi, K. N. (1992). Nomenclatural notes for the North American Flora. XI. Phytologia, 73, 124–136.

Korban, S. S., & Skirvin, R. M. (1984). Nomenclature of the cultivated apple. HortScience, 19, 177–180.

Krüssmann, G. (1977). Handbuch der Laubgehölze. 2. Paul Parey, Berlin, Hamburg.

Kümmel, F., & Kiehne, S. (2009). Georg Dieck (1847–1925) – ein bedeutender Dendrologe des 19. Jahrhunderts aus Mitteldeutschland. Schlechtendalia, 19, 1–26.

Lesschaeve, I., & Noble, A. C. (2005). Polyphenols: Factors influencing their sensory properties and their effects on food and beverage preferences. The American Journal of Clinical Nutrition, 81(suppl.), 330–335.

Lewis, D., & Crane, M. B. (1938). Genetical studies in apples. II. Journal of Genetics, 37, 119–128.

Li, J.-C., Liu, J.-Q., & Gao, X.-F. (2022). A revision of the genus *Malus* Mill. (Rosaceae). European Journal of Taxonomy, 853, 1–127.

Likhonos, F. D. (1983). *Malus* Mill. – apple. In: Likhonos, F. D., Tuz, A. S., & Lobachev, A. Y. (Eds.). Kul'turnaja flora SSSR. XIV. Semechkovye (yablonja, grusha, ajva) [Flora of cultivated plants. XIV. Pome fruits (apple, pear, quince)]. Kolos, Moscow (in Russian).

Linnaeus, C. (1753). Species plantarum. 1. Lars Salvius, Stockholm.

Lombarts, P. (1984). *Malus*: sierappels. Dendroflora, 21, 39–62.

Mabberley, D. J., Jarvis, C. E., & Juniper, B. E. (2001). The name of the apple. Telopea, 9(2), 421–430.

Matsumoto, K., Maeda, H., Fujita, T., Sato, S., & Shiozaki, Y. (2016). Apple breeding programs at Hirosaki University, Japan: Yellow skin, red flesh, and large size. Acta Horticulturae, 1127, 29–34.

Matsumoto, S., Li, T., Otagaki, S., Li, Y., & Bai, S. (2018). Efficient breeding and cultivation of type 2 red-fleshed apple cultivars using a search system for suitable apple cultivar combination. Horticultural Plant Journal, 4(6), 219–225.

Mezhenskyj, V. M. (2008). Hrupy dekoratyvnykh sortiv i form vydiv rody yablunia (*Malus* Mill, Rosaceae) [Groups of ornamental cultivars and forms of species of the genus *Malus* Mill. (Rosaceae)] Scientific Bulletin of the Bila Tserkva National Agrarian University, 54, 98–101 (in Ukrainian).

Mezhenskyj, V. M., & Mezhenska, L. O. (2021). Chervonokvitkova yablunia v kolektsii Natsionalnoho universytetu bioresursiv i pryrodokorustuvannia Ukrainy [Red-flowered apple tree in the collection of the National University of Life and Environmental Sciences of Ukraine]. Ukrainian Journal of Forest and Wood Science, 12(4), 72–82 (in Ukrainian).

Mezhenskyj, V. M., & Mezhenska, L. O. (2023). Henetychni resursy plodovykh i dekoratyvnykh roslyn [Genetic resources of fruit and ornamental crops]. Part 1. Lira-K, Kyiv (in Ukrainian).

Michurin, I. V. (1948). Sochinenija [Works]. 1–4. OGIS; Sel'khozgiz, Moscow (in Russian).

Miller, P. (1754). The gardeners dictionary. 4th ed. 2. John Rivingston & James Rivingston, London.

Nash, G. V. (1921). *Malus niedzwetzkyana*. Addisonia, 6, 23–24.

Neumüller, M., & Dittrich, F. (2017). Breeding for type 1 red-fleshed apple varieties: Using the red-fleshed apple variety as female parent yields a higher percentage of red-leafed seedlings. Acta Horticulturae, 1172, 241–244.

Nocker, S. van, Berry, G., Najdowski, J., Michelutti, R., Luffman, M., Forsline, P., Alsmairat, N., Beaudry, R., Nair, M. G., & Ordidge, M. (2012). Genetic diversity of red-fleshed apples (*Malus*). Euphytica, 185, 281–293.

Norrys, R. A. (Ed.). (1996). Plant inventory No. 204, part II. USDA, Agricultural Research Service, Beltsville.

Ponomarenko, V. V. (1975). Cho takoe *Malus pumila* Mill? [What is *Malus pumila* Mill?]. Botanicheskij Zhurnal, 60(11), 1574–1586 (in Russian).

Ponomarenko, V. V. (1986). Obzor vidov roda *Malus* Mill. [A review of the species of the genus *Malus* Mill.]. Proceedings on Applied Botany, Genetics and Breeding, 106, 16–27 (in Russian).

Potapov, V. A., Lebedev, V. M., & Guseva, N. N. (1990). Opisanie i kharakteristika rajonorovannykh i perspektivnykh zymostojkikh slaboroslykh podvoev jabloni Plodoovoshhnogo instituta im. I. V. Michurina [Description and characterization of zoned and promising winter-hardy low-growing apple rootstocks of the I. V. Michurin Fruit and Vegetable Institute]. In: Zimostojkie slaboroslye klonovye podvoji jabloni [Winter-hardy and low-growing clonal rootstocks]. Michurinsk. Pp. 6–23 (in Russian).

Pyshcholka, D. V., & Mezhenskyj, V. M. (2023). Yablunia Sivarsa Nedzvetskiieva v dekoratyvnomu sadivnytstvi, rozsadnytstvi ta plodivnytstvi [Niedzwetzky's ap-

ple in ornamental gardening, nursery and fruit growing]. In: Ethnobotanical traditions in agronomy, pharmacy and garden design: Proceeding of VI International Scientific Conference. National Dendrological Park "Sofiivka", Uman'. Pp. 229–235 (in Ukrainian).
Qian, G.-Z., Liu, L.-F., & Tang, G.-G. (2010). Proposal to conserve the name *Malus domestica* against *M. pumila*, *M. communis*, *M. frutescens*, and *Pyrus dioica* (Rosaceae). Taxon, 59(2), 650–652.
Rehder, A. (1920). New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum. Journal Arnold Arboretum, 2(1), 42–64.
Reim, S., Flachowsky, H., Michael, M., & Hanke, M. V. (2006). Assessing gene flow in apple using a descendant of *Malus sieversii* var. *sieversii* f. *niedzwetzkyana* as an identifier for pollen dispersal. Environmental Biosafety Research, 5(2), 89–104.
Robertson, K. R., Phipps, J. B., Rohrer, J. R., & Smith, P. G. (1991). A synopsis of genera in Maloideae (Rosaceae). Systematic Botany, 16, 376–394.
Robinson, J. P., Harris, S. A., & Juniper, B. E. (2001). Taxonomy of the genus *Malus* Mill. (Rosaceae) with emphasis on the cultivated apple, *Malus domestica* Borkh. Plant Systematic and Evolution, 226(1–2), 35–58.
Rupasinghe, H. P. V., Huber, G. M., Embree, C., & Forsline, P. L. (2010). Red-fleshed apple as a source for functional beverages. Canadian Journal of Plant Science, 90(1), 95–100.
Sadilova, E., Stintzing, F. C., & Carle, R. (2006). Chemical quality parameters and anthocyanin pattern of red-fleshed Weirouge apples. Journal of Applied Botany and Food Quality, 80(2), 82–87.
Sato, H., Otagaki, S., Saelai, P., Kondo, S., Shiratake, K., & Matsumoto, S. (2017). Varietal differences in phenolic compounds metabolism of type 2 red-fleshed apples. Scientia Horticulturae, 219, 1–9.
Sekido, K., Hayashi, Y., Yamada, K., Shiratake, K., & Matsumoto, S. (2010). Efficient breeding system for red-fleshed apple based on linkage with S3-RNase allele in 'Pink Pearl'. HortScience, 45(4), 534–537.
Steadman, R. C. (1924). Apple from seedling of the Surprise cultivar. USDA Pomological Watercolor Collection, Beltsville.
Takhtajan, A. L. (2009). Flowering plants. Springer, Berlin.
Takos, A. M, Jaffě, F. W, Jacob, S. R, Bogs, J., Robinson, S. P., & Walker, A. R. (2006). Light-induced expression of a MYB gene regulates anthocyanin biosynthesis in red apples. Plant Physiology, 142, 1216–1232.
Terpó, A. (1988). *Malus* Miller. In: Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M., & Webb, D. A. (Eds.). Flora Europaea. Vol. 2. Pp. 66–67. Cambridge University Press, Cambridge.
Toufektsian, M.-C., de Lorgeril, M., Nagy, N., Salen, P., Donati, M. B., Giordano, L., Mock, H. P., Peterek, S., Matros, A., Petroni, K., Pilu, R., Rotilio, D., Tonelli, C., de Leiris, J., Boucher, F., & Martin, C. (2008). Chronic dietary intake of plant-derived anthocyanins protects the rat heart against ischemia-reperfusion injury. The Journal of Nutrition, 138, 747–752.
Tournefort, J. P. (1700). Institutiones rei herbariae [Institutions of the herbal matter]. 1. Typographia Regia, Paris (in Latin).
Trebuschenko, P. D. (1939). Nasledovanie antotsianovoj okraski u jabloni [Inheritance of anthocyanin coloration in apple-tree]. Doklady AN SSSR, 23(9), 935–939 (in Russian).
Tsao, R., Yang, R., Young, J. C., & Zhu, H. (2003). Polyphenolic profiles in eight apple cultivars using high-performance liquid chromatography (HPLC). Journal of Agricultural and Food Chemistry, 51, 6347–6353.
Turland, N. J., Wiersema, J. H., Barrie, F. R., Greuter, W., Hawksworth, D. L., Herendeen, P. S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T. W., McNeill, J., Monro, A. M., Prado, J., Price, M. J., & Smith, G. F. (Eds.). (2018). International code of nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Glashütten: Koeltz Botanical Books.
Ubi, B. E., Honda, C., Bessho, H., Kondo, S., Wada, M., Kobayashi, S., & Moriguchi, T. (2006). Expression analysis of anthocyanin biosynthetic genes in apple skin: Effect of UV-B and temperature. Plant Science, 170, 571–578.
Umemura, H., Otagaki, S., Wada, M., Kondo, S., & Matsumoto, S. (2013). Expression and functional analysis of a novel MYB gene, MdMYB110a_JP, responsible for red flesh, not skin color in apple fruit. Planta, 238, 65–76.
Vasilchenko, I. G. (1963). Novye dlja kultury vidy jabloni [New species of apple trees for cultivation]. Izdatel'stvo AN SSSR, Moscow, Leningrad (in Russian).
Vavilov, N. I. (1930). Wild progenitors of the fruit trees of Turkistan and the Caucasus and the problem of the origin of fruit trees. Reports and Proceedings of the 9th International Horticultural Congress. Royal Horticultural Society, London. Pp. 271–286.
Vavilov, N. I. (1935). The law of homological series in hereditary variability. In: Vavilov, N. I. (Ed.). Teoreticheskie osnovy selektsii rastenij [Theoretical foundations of plant breeding]. Vol. 1. Pp. 75–128. Selkhozgiz, Moscow, Leningrad (in Russian).
Velasco, R., Zharkikh, A., Affourtit, J., Dhingra, A., Cestaro, A., Kalyanaraman, A., Fontana, P., Bhatnagar, S. K., Troggio, M., Pruss, D., Salvi, S., Pindo, M., Baldi, P., Castelletti, S., Cavaiuolo, M., Coppola, G., Costa, F., Cova, V., Dal Ri, A., Goremykin, V., Komjanc, M., Longhi, S., Magnago, P., Malacarne, G., Malnoy, M., Micheletti, D., Moretto, M., Perazzolli, M., Si-Ammour, A., Vezzulli, S., Zini, E., Eldredge, G., Fitzgerald, L. M., Gutin, N., Lanchbury, J., Macalma, T., Mitchell, J. T., Reid, J., Wardell, B., Kodira, C., Chen, Z., Desany, B., Niazi, F., Palmer, M., Koepke, T., Jiwan, D., Schaeffer, S., Krishnan, V., Wu, C., Chu, V. T., King, S. T., Vick, J., Tao, Q., Mraz, A., Stormo, A., Stormo, K., Bogden, R., Ederle, D., Stella, A., Vecchietti, A., Kater, M. M., Masiero, S., Lasserre, P., Lespinasse, Y., Allan, A. C., Bus, V., Chagné, D., Crowhurst, R. N., Gleave, A. P., Lavezzo, E., Fawcett, J. A., Proost, S., Rouzé, P., Sterck, L., Toppo, S., Lazzari, B., Hellens, R. P., Durel, C.-E., Gutin, A., Bumgarner, R. E., Gardiner, S. E., Skolnick, M., Egholm, M., Van de Peer, Y., Salamini, F., & Viola, R. (2010). The genome of the domesticated apple (*Malus ×domestica* Borkh.). Nature Genetics, 42(10), 833–839.
Volk, G. M., Cornille, A., Durel, C.-E., & Gutierrez, B. (2021). Botany, taxonomy, and origins of the apple. In: Korban, S. S. (Ed.). The apple genome. Springer Nature Switzerland AG, Cham. Pp. 19–32.
Volz, R. K., Kumar, S., Chagné, D., Espley, R., McGhie, T. K., & Allan, A. C. (2013). Genetic relationships between red flesh and fruit quality traits in apple. Acta Horticulturae, 976, 363–368.
Volz, R. K., Mcghie, T. K., & Kumar, S. (2014). Variation and genetic parameters of fruit colour and polyphenol composition in an apple seedling population segregating for red leaf. Tree Genetics and Genomes, 10, 953–964.
Volz, R. K., Oraguzie, N. C., Whitworth, C. J., How, N., Chagné, D., Carlisle, C. M., Gardiner, S. E., Rikkerink, E. H. A., & Lawrence, T. (2009). Red flesh breeding in apple: Progress and challenges. Acta Horticulturae, 814, 337–342.
Wang, N., Jiang, S., Zhang, Z., Fang, H., Xu, H., Wang, Y., & Chen, X. (2018). *Malus sieversii*: The origin, flavonoid synthesis mechanism, and breeding of red-skinned and red-fleshed apples. Horticulture Research, 5, 70.
Wang, N., Xu, H., Jiang, S., Zhang, Z., Lu, N., Qiu, H., Qu, C., Wang, Y., Wu, S., & Chen, X. (2017). MYB12 and MYB22 play essential roles in proanthocyanidin and flavonol synthesis in red-fleshed apple (*Malus sieversii* f. *niedzwetzkyana*). Plant Journal, 90(2), 276–292.
Wang, N., Zheng, Y., Duan, N., Zhang, Z., Ji, X., Jiang, S., Sun, S., Yang, L., Bai, Y., Fei, Z., & Chen, X. (2015). Comparative transcriptomes analysis of red- and white-fleshed apples in an F_1 population of *Malus sieversii* f. *niedzwetzkyana* crossed with *M. domestica* 'Fuji'. PLoS One, 10(7), e0133468.
Wilson, K. L. (2017). Report of the general committee: 18. Taxon, 66(3), 742–744.
Wojdyło, A., Oszmiański, J., & Laskowski, P. (2008). Polyphenolic compounds and antioxidant activity of new and old apple varieties. Journal of Agricultural and Food Chemistry, 56, 6520–6530.
Wolfe, K., Wu, W., & Liu, R. H. (2003). Antioxidant activity of apple peels. Journal of Agricultural and Food Chemistry, 51, 609–614.
Würdig, J., Flachowsky, H., Höfer, M., Peil, A., Eldin Ali, M. A. M. S., & Hanke, M.-V. (2014). Phenotypic and genetic analysis of the German *Malus* germplasm collection in terms of type 1 and type 2 red-fleshed apples. Gene, 544(2), 198–207.
Yan, G., Long, H., Song, W., & Chen, R. (2008). Genetic polymorphism of *Malus sieversii* populations in Xinjiang, China. Genetic Resources and Crop Evolution, 55(1), 171–181.
Yang, M., Che, S., Zhang, Y., Song, W., Yan, G., & Yu, W. (2020). *Malus niedzwetzkyana* (Dieck) Langenf. transcriptome comparison and phylogenetic analysis with *Malus sieversii* (Ledeb) Roem. Genetic Resources and Crop Evolution, 67(3), 313–323.
Yuste, S., Ludwig, I. A., Romero, M.-P., Motilva, M.-J., & Rubió, L. (2022). New redfleshed apple cultivars: A comprehensive review of processing effects, (poly)phenol bioavailability and biological effects. Food and Function, 13, 4861–4874.
Yuzepchuk, S. V. (1939). Apple tree genus – *Malus* Mill. In: Komarov, V. L. (Ed.). Flora SSSR [Flora of USSR]. Vol. 9. Pp. 357–372. Izdatel'stvo AN SSSR, Moscow, Leningrad (in Russian).
Takhtajan, A. L. (Ed.). (1975). Krasnaja kniga. Dikorastushhie vidy flory SSSR nuzhdajushhiesja v okhrane [Red book. Wild species of the USSR flora that need protection]. Nauka, Leningrad (in Russian).
Bykov, B. A. (Ed.). (1981). Krasnaja kniga Kazakhskoj SSR. Chast' 2. Rastenija [Red book of Kazakh SSR. Part 2. Plants]. Nauka of Kazakh SSR, Alma-Ata (in Russian).
Davletkeldiev, A. A. (Ed.) (2006). Kyzyl kitebi Kyrgyz Respyblikasynyn [Red data book of Kyrgyz Republic]. State Agency on Environment Protection and Forestry under the Government of Kyrgyz Republic; Institute for Biology and Pedology of National Academy of Sciences of Kyrgyz Republic; Ecological Movement "Aleine" of Kyrgyzstan, Bishkek (in Kyrgyz, Russian, and English).