CHAPTER 11

PHYLOGENETIC CONNECTIONS BETWEEN REPRESENTATIVES OF THE GENUS AMELANCHIER MEDIK

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ABSTRACT

Within the frames of retrospective discourse, the information concerning breeding value of a representative of the genus *Amelanchier* Medik. — for national pomiculture, decorative gardening, and pharmacy – is integrated. This article characterizes their: biological peculiarities, ecological adaptiveness, palatability traits and cooking qualities of their fruits, their availability for drying and processing, namely preparing juices, syrups, jams, candied fruit jellies, comfiture, and also fruit wine. The effectiveness of using Juneberry for phytomeliorative is mentioned, some ethnobotanical aspects are discussed. Data about chromosome numbers and the geographical origin of the genus *Amelanchier* representatives cultivated in Ukraine and their closest congeners from the family *Rosaceae* Juss. are cited. Controversial questions of the genus *Amelanchier* system were discussed from the classical and molecular genetic approaches. The results of phylogenetical and molecular genetic researches made by scientists of different countries offer a possibility to specify the systematic position of the genus *Amelanchier* representatives of the family *Rosaceae* Juss. grown in Ukraine, and to place them temporarily in a big subfamily *Amygdaloideae* Arn., which combines the former subfamilies *Amygdaloideae*, *Spiraeoideae*, and *Maloideae*, tribe – *Maleae* Small, subtribe – *Malinae* Rev.

11.1 INTRODUCTION

Among the decisive premises of successful conservation of biotic diversity (biodiversity), and the enrichment of local diversity of any plant, including representatives of the genus *Amelanchier* Medik. under certain conditions, one should determine their systematic position, ascertainment of geographical origin and peculiarities of phylogenetical connections on the interfamily and interspecies levels. Such information will be favorable to scientifically ground a planning of their introduction, prevention from invasion, and also create sources of outgoing material to conduct their breeding.

According to the classification of Armen Takhtadzhan [1], representatives of the genus *Amelanchier* (Juneberry) belong to the family *Rosaceae*, subfamily *Pyroideae* (former *Maloideae*), tribe *Maleae*.

In Ukraine, representatives of the genus *Amelanchier* are considered unconventional for growing, but interest in Juneberry and many other promising, but currently undervalued plants (mostly known to a narrow range of wildlife lovers) increases with increasing population welfare. First of all, it is referred to the species *Hippophae* L. (sea buckthorn), *Lonicera* L. (honeysuckle), *Sorbus* L. (mountain ash) and *Viburnum* L. (viburnum), which, now together with Juneberry, are gaining more popularity due to the decorativeness, and high taste, remedial, and dietic qualities of their fruits [2, 3].

Juneberry is a very flexible and unpretentious plant. In the culture, and as well as in the natural state, it grows in the form of a large shrub, sometimes a tree. It can be used as an ornamental, nectareous, phyto-reclamative, and medicinal plant. It is valued as a fast-growing, fast-fetal, and perennial fruit crop. It has a number of other benefits. According to the degree of resistance to unfavorable conditions, Juneberry is a unique plant. It has a great tolerance to winter conditions. The plant itself is capable of withstanding temperatures of 40–50° C below zero, and the flowers that blossomed – to minus 5–7°C [2, 4, 5].

Juneberry successfully grows on the soils of different mechanical makeups and acidity. It thrives on the rather moisty light soil, sometimes even on the marshy ones. At the same time, it withstands drought well and can grow on rocky and sandy dry areas. However, it can't withstand poorly drained clay soils with low humus content [2, 5].

Juneberry is a photophilous plant, but it can grow in the shade. Burmistrov [5] mentions an interesting biological feature of young Juneberry plants (under 5 years), that it has an ability to withstand relatively intense shading. Juneberry plants are distinguished by being sufficiently fast growing and by the age of ten they reach their full development. Duration of the yielding period for the bush is 60–70 years (some shoots can grow up to 15 years) [5, 6].

Juneberry is a hermaphrodite plant, outcrossing (self-fertilizes rarely). The Juneberry can berry on last years' shoots even if it had a single area that was self-fertilized [3–5]. It starts to berry rather early, it produces crops in 3–4 years. It is characterized by annual and abundant berrying, which reaches 3–5 kg from wild-growing bushes of 5 years, and up to 10–12 kg from 10 or more year-old ones [4, 5].

A positive feature of Juneberry is that diseases rarely affect it. Sometimes, there can be powdery mildew, fruit rot, leaf blight, and leaf rust. However, many pests willingly settle on it. Among them are: the green apple aphid (*Aphis pomi* Deg.), the apple blossom weevil (*Anthonomus pomorum* L.), the garden chafer (*Phyllopertha horticola* L.), caterpillars of different species of butterflies (*Operophtera brumata* L., *Euproctis chrysorrhoe* L., *Orgyia antiqua* L., *Dasychira pudibunda* L., *Acronicta tridens* (Den. and Schiff.), *Melanchra persicariae* L.), leaf-rolling moths of the genus *Pandemis,* and others. Forming the complex of phytophages of this genus takes place mainly due to broad polyphages and olygophages connected primarily with apples, hawthorns and some other representatives of *Maleae* [6–8]. Besides, sparrows, thrushes, and robins like juneberries, so it is sometimes necessary to scare these birds to preserve the harvest [6, 7].

Juneberries are sweet, exquisitely tender, and very useful. Their sugar content is 8–12% with a prevalence of fructose and glucose; organic acids 0.4–0.7 (preferably apple); tannins and dyes 0.5–0.8; 1.5–2.5% of pectin; 0.4–0.7 mg/100 g of carotene; 35–45 of vitamin C, from 7 to 12 mg/100 g of vitamin B_2, 0.2–1.0 mg/100 g of provitamin A; to 100 mg/100 g to anthocyanins; among these trace constituents, there is also copper, lead, and cobalt. Beta-sitosterol can also be found in them. It is a substance that helps to reduce cholesterol, and coumarins, which are characterized by an anti-sclerotic effect [2, 4, 9]. Its fruit – in the fresh, dried, frozen, and processed form – is consumed. Juice, syrup, wine, liqueur, jam, confiture, jelly, and marmalade can be prepared. While processing juneberries, other berries (e.g., black currant) can be mixed together, but only 300 grams of sugar per 1 kg of fruit is used (due to the high sugar content of juneberries). A peculiarity of freshly picked juneberries is the fact that they are very difficult to squeeze juice from, but if they are left for about a week, then 70% of juice, from the total mass, accumulates in them [6].

The value of the Juneberry fruit as a fine, raw material for producing fruit wines was first emphasized by the academician V.V. Pashkevych who initiated introducing juneberry into the Ukrainian culture. It was V.V. Pashkevych who launched its plantation while establishing an arboretum in the territory of modern NDP "Sofiyivka" NAS of Ukraine, now known as Pashkevich Arboretum [5, 10].

The fruit of Juneberry dries quickly in the bright sun, as well as, in the home dryers and, by its appearance, are similar to raisins – dried berries of seedless grape cultivars. Fruits that have just ripened contain more vitamin C and are better for freezing and conservation; completely ripe fruits contain more sugar and can be used to make juice and wine. While cooking wine, the juice is fermented without adding sugar. The wine has a pleasing savor, nice dark-ruby color, and its strength is 8–10° [6].

Juneberry, as a fruit crop, is grown on the industrial scale in the USA and Canada. Accordingly, much attention is paid to the breeding work. There are cultivars grown for fruit: 'Beaverlodge,' 'Bluff,' 'Buffalo,' 'Elizabeth,' 'Idaho Giant,' 'JB30,' 'Killarney,' 'Lee № 3,' 'Moonlake,' 'Sturgeon,' 'Thiessen,' 'Thiessen RS,' 'Timm' and so on, and also cultivars, which combine its high productivity and quality with decorative value: 'Altaglow,' 'Gypsy,' 'Honeywood,' 'Martin,' 'Nelson,' 'Northline,' 'Parkhill,' 'Pembina,' 'Regent,' 'Smoky,' 'Success' and so on. There are purely ornamental cultivars: 'Altaglow,' 'Autumn Brilliance,' 'Autumn Sunset,' 'Ballerina,' 'Carleton,' 'Cumulus,' 'Fergi,' 'Forest Prince,' 'Helvetia,' 'Hollandia,' 'Jennybelle,' 'Lustre,' 'Prince Charles,' 'Prince William,' 'Princess Diana,' 'Rainbow Pillar,' 'Reflection,' 'Robin Hill,' 'Silver Fountain,' 'Tradition,' 'White Pillar,' etc. Among them there are representatives of the different species: *A. alnifolia*, *A. bartramiana*, *A. canadensis*, *A. laevis*, *A. spicata*, *A. stolonifera*, and a number of interspecies and hybrids between other species [6, 11, 12].

Juneberry, as an ornamental plant, is suitable for the arboretums, Dendrological parks, and settlement gardening. It is possible to form alleys, delicate hedges (well-tolerated to a cut), Juneberry is effective in group plantings and solitaires. It gives off a pleasing effect when placed in the background of other plants or along buildings. At the same time, due to the abundant frondescence, blossoming and fruiting Juneberry plants are ornamental throughout the year. In spring, at the time of blossoming, its inflorescences are light and delicate against the background of the young leaves, and its white and cream-colored flowers have a light pleasant scent. In early summer, because it is still ripening, the fruit is first green. Then, on the one side of the little fruit, there is a pink erubescence and the ripe fruit is usually blue and purple, but the color can vary from cream to almost black. The juneberries' leaves display a special decorativeness throughout the growing season: when blooming, they are white-tomentose, later – green, green-gray, green-red, in autumn – yellow, orange, red, purple. In winter Juneberry shoots can be graphically distinguished above the snow cover [5, 6, 12]

During blossoming, Juneberry is eagerly visited by bees; providing them with an early spring honey gathering (lots of pollen and little nectar) and in gardens it attracts them to other fruit crops, thus increasing their productivity [13–15].

Juneberry is used for fixing gullies and eroded slopes. While phytomelioration of recreational and devastated forest areas, it can even be used as an attractive factor for forming forest environment [14, 16]. It is recommended that Juneberry be planted in multifunctional shelter belts, namely in forest shelter and snow shelter belts along railways or highways. It can also be planted in different rows and tiers of wind belts as an orchard-protecting belt that would protect field crops from winds – both dry and hot, as well as, help capture snow and use its meltwater better. Under its protection, currants, gooseberries, raspberries, strawberries, and others can be grown, while simultaneously being capable of capturing snow. If fruit crops need protection from the winter cold, the location in areas that are blown by the wind does not matter for Juneberry (due to its high degree of frost hardiness). Besides, heavy beds of Juneberry as orchard-protecting belts are a great place for nesting insectivorous birds [4–6, 7, 17]. Also, according to A.D. Burmistrov, the offer to plant Juneberry on the edge of the garden is not devoid of practical sense. During the Juneberry fruiting, which lasts about a month, its non-simultaneous ripening coincides with the time of fruiting strawberries, black currants, and sometimes, cherries. Because of this, attacks from birds (starlings, blackbirds) on these baseline fruit cultures are strongly reduced [5].

Juneberry wood is solid and resilient; with gray, reddish or reddish-brown color with slightly visible beams and annual rings. It has a silky surface; it can be easily bent and polished. It doesn't have a timber industry value because of the small diameter. In the past Juneberry wood was used for making ramrods and canes. It is perfectly suited for wickerwork, industrial and domestic and art objects; delicate holders for climbing plants can be made of it [14, 18, 19].

Juneberry fruits are used with the purpose of treatment for atherosclerosis (due to the content of beta-sitosterol, which is an antagonist of cholesterol); for different diseases of the gastrointestinal tract (as an astringent); for the prevention of hypo-and avitaminosis C and B (as multivitamin remedy). Tincture of Juneberry flowers is used as antihypertensive and cardiotonic remedy. Decoction of the rind and leaves has astringent and coating properties and is used for the prevention of gastrointestinal diseases and for septic wounds epulosis [9, 17].

A synonymous name for Juneberry was given to name to the City of Saskatoon – the largest in the Canadian province of Saskatchewan. It is derived from "mis-sask-quah-toomina," which is how the aboriginal inhabitants called the most wide-spread, local berries [20].

The importance of plants is proved by the fact that the Indian tribes distinguished between 8 individual species based on morphological differences in the plants. Juneberry flowers and fruits were used in ceremonial rites, and the beginning of harvest was celebrated by solemn feasts. Some tribes believed that even the first humans were created from Juneberry bushes [20].

Juneberry was widely used in the everyday life of the aboriginal inhabitants, and subsequently of the first settlers. Fruits were one of the staple foods, and often the only kind of fruit in sufficient quantity. They were consumed fresh, cooked, and dried. They were part of the ethnic dishes – pemykan. Young cut shoots, dried fruits, and leaves were used for making drinks and treatment remedies for children, adults, and animals. Arrows and household tools were made from Juneberry solid wood [20].

The value of the genus *Amelanchier* representatives and some problems concerning their classification, especially their place in the family, led to an active search for phylogenetic connections between cultivated species and close families.

11.2 MATERIALS AND METHODOLOGY

Considering the importance of the problem of the starting material for breeding and taking into account the data obtained from the analysis of experimental and theoretical studies performed in different countries over a long historical period by scientists from different scientific schools [1, 4, 11, 12, 20–28, 33–42], the attempt to generalize available information is made. In this study the quota sampling method was used, which allowed to eliminate dubious publications using the criteria in peer-reviewed publication citing and giving priority to research that is carried out by international programs. Works on the domestication of the genus *Amelanchier* and their nearest families published in different years, were analyzed, summarized [3, 9, 12, 20–34] and supplemented with the results of our study in the preparing process of the article.

11.3 RESULTS AND DISCUSSION

11.3.1 THE ORIGIN OF THE GENUS NAME AMELANCHIER AND ETNOBOTANICHNI ASPECTS OF THE SPECIES EPITHETS

Genus *Amelanchier* Medik. (Juneberry) was described in 1789 by Friedrich Casimir Medicus [35], a German botanist and physician, director of the botanical garden in Mannheim. One of the first records about the plant dates back to the year 1581 [36]. However, before singling out *Amelanchier* as a separate genus (probably due to the similarity of its morphological features) Joseph Pitton de Tournefort referred its species to the genus *Mespilus* [37] and Carl Linnaeus – to the genus *Chionanthus* [38].

The origin of the international name genus *Amelanchier* have several versions that are associated with taste or size of the fruit. According to one that is presented in a botanical dictionary by M.I. Annenkov edited in 1878 [39], the name *Amelanchier* is derived from the Greek words melea – apple and anchein – astringe, due to the astringent flavor of the fruit. According to another version, A.I. Poyarkova, while describing the genus in the flora of the USSR, associates the name with Provencal *amelanche*, which indicates the honey taste of the fruit [21].

The version proved by Caden and Terentyeva [40] also explains the origin of the plant name from the Provencal amelanche, but as a fruit name of only one type of Juneberry, such as *Amelanchier vulgaris* Moench. Referring to a number of sources, they suggest a Celtic origin of the word *Amelanchier*. Besides, the genus *Amelanchier* species are characterized by a large number of epithets that indicate their popularity and are usually associated with morphological features, habitat characteristics, fruit taste, etc.

Thus, among the common American names of Juneberry species, G.N. Jones names: serviceberry, sarviceberry, sarvis, maycherry, june-berry, shadblow, shadbush, shadberry, shadblossom, shadflower, shad-wood, sugar pear, wild pear, lancewood, boxwood, Canadian medlar [41]. In Canada Juneberry is known as saskatoon, originating from the Indian mis-sask-quah-too-min [5].

Attention is drawn to ethnobotanical and symbolic aspects of the genus *Amelanchier* application by indigenous peoples of North America, emphasizing the value of the plant. G.N. Jones [41] gives an interesting interpretation of certain species epithets of American Juneberry species by associating them with the botanical characteristics and value of the plant for the indigenous population. Thus, the name Juneberry is stipulated by ripening fruit in early summer (from the month name June); in the eastern United States the names shadblow, shadberry, shadblossom, shadflower and shadwood are stipulated by the period of blossoming plants in early spring, which is an indicator of the breeding beginning of the shad run (river herring), which begins spawning migration from oceanic salt into fresh water rivers; the names lancewood and boxwood are stipulated by the use of dense wood as a part of tools (handle).

According to the botanical dictionary by M.I. Annenkov [39], the genus *Juneberry* is called in Polish – Swidośliwka, in Czech – Muchownik, in Serbian – Grašac, Irga, in German – Fluhbirne, Beermispel, Felsenbirnbaum, in French – Amelanchier, in English – The Medlar. The dictionary of Ukrainian scientific and vernacular names of vascular plants compiled by Yuri Kobiv [42] suggests names – sadova irha and irha.

11.3.2 THE SYSTEMATIC POSITION OF THE GENUS AMELANCHIER

The genus *Amelanchier* in classical phylogenetic, as well as in the molecular phylogenetic (cladistic) classification system of plants, is defined as a component of the family Rosaceae Juss. of the range *Rosales* Bercht. et J. Press. [1, 43–45].

The family Rosaceae is quite a large family of angiosperms, comprising about 90–110 genera and 2000–4828 species [43, 45–49], which averages about 100 genera and 3000 species [31].

Numerous "microspecies" are distinguished in many genera of Rosaceae, morphological differences between which are slight (e.g., details of pubescence), but they are considered stable. Microspecies appear in groups where free interbreeding in populations is limited because of apomixis spread or other reasons. Therefore, if counting microspecies, the number of Rosaceae species can significantly increase [49].

Traditionally, on the basis of differences, mainly in fruit morphology and in basic chromosome numbers, the family Rosaceae were separated into 4 subfamilies: Spiraeoideae (Meadowsweet) – fruit – hose, rarely capsule, basic chromosome numbers 8 and 9; Rosoideae (Rose) – coccus, aggregate fruit, aggregate-accessory fruit, the hypanthium often takes part in the fruit formation, basic chromosome numbers 7, 9, rarely 8; Maloideae (Apple) – fruit – apple, basic chromosome number 17; Prunoideae (Plum) – fruit – drupe, basic chromosome number 8 [46, 47]. Other authors, depending on the occurrence of stipules, calyx structure, hypanthium, gynoecium, fruit, and other signs in the family Rosaceae distinguish from 3 to 12 subfamilies [43].

The genus *Amelanchier,* since the times of Adolf Engler (1903) [45], was defined within the subfamily Pomoideae (later Maloideae):

Division – Embryophyta siphonogama
Subdivision – Angiospermae
Classis – Dicotyledoneae
Subclassis – Archichlamydeae
Ordo – Rosales
Subordo – Rosineae
Familia – Rosaceae
Subfamilia – Pomoideae
Genus – Amelanchier.

Formed at the beginning of the last century [32], synopsis of the genera of the subfamily Maloideae as a part of the family Rosaceae with certain deviations [34] in his near-classical state is supported by many authors [22, 23, 30, 50] (Figure 11.1).

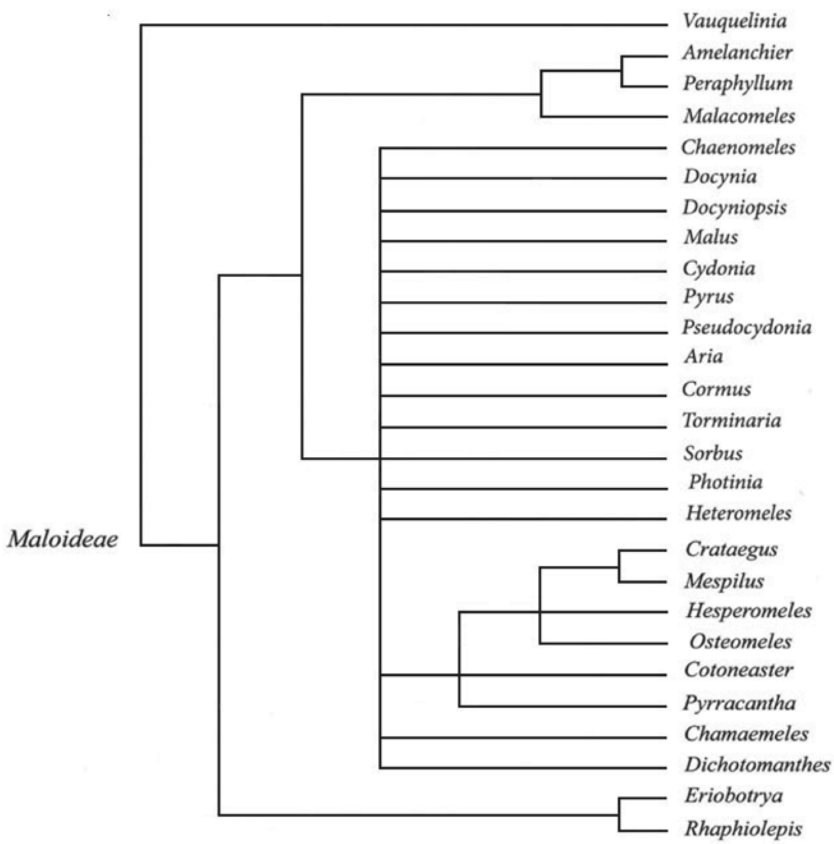

FIGURE 11.1 Simplified cladogram of the subfamily Maloideae (according to Aldasoro J.J. et al., 2005 [22] as amended [51]).

However, more evidences are provided concerning the revision of the family Rosaceae appropriateness on regrouping subfamilies, supertribes, tribes, subtribes, some genera and species with the simultaneous elimination of the subfamily Maloideae [24, 26, 31, 51].

The revision of the family Rosaceae was supported by Armen Takhtajan, who suggested a new version of flowering plants system, revised according to the latest results of molecular phylogenetics in the book "Flowering Plants" reissued in 2009 [1].

Armen Takhtajan highlights subfamily Pyroideae (formerly Maloideae) in the family Rosaceae, combining in it 27 genera in 4 tribes, defining the genus *Amelanchier* among the families of the tribe Maleae (Table 11.1):

TABLE 11.1 The Synopsis of the Pyroideae Genera (formerly Maloideae) by Armen Takhtajan (2009) [1]

Tribus	Genus
Kageneckieae	*Kageneckia*
Lindleyieae	*Vauquelinia*; *Lindleya*
Maleae	*Photinia* (у тому числі *Stranvaesia*); *Heteromeles*; *Eriobotrya*; *Rhaphiolepis*; *Sorbus*; *Chamaemespilus*; *Aronia*; *Amelanchier*; *Pyrus*; *Malus*; *Eriolobus*; *Peraphyllum*; *Docynia*; *Cydonia*; *Pseudocydonia*; *Chaenomeles*
Crataegeae	*Cotoneaster*; *Malacomeles*; *Chamaemeles*; *Pyracantha*; *Crataegus*; *Mespilus*; *Hesperomeles*; *Osteomeles*

Accordingly, the systematic position of the genus *Amelanchier,* according to Armen Takhtajan's system [1], appears as follows:

Divisio – Magnoliophyta
Classis – Magnoliopsida (Dicotyledons)
Subclass – Rosidae
Superordo – Rosanae
Ordo – Rosales
Familia – Rosaceae
Subfamilia – Pyroideae (Maloideae*)*
Tribus – Maleae
Genus – Amelanchier.

According to the analysis of subfamilies from the family Rosaceae, performed by a group of scholars of different universities in the USA, Canada and Sweden after six nuclear (18S, gbssi1, gbssi2, ITS, pgip, ppo) and four chloroplastic (matK, ndhF, rbcL, and trnL-trnF) segments of DNA sequences [24, 26, 31], only the subfamily Rosoideae (Juss.) Arn. turned out monophyletic, with the basic chromosome number x=7 or 8, except for the tribe Dryadeae (x=9). Instead the subfamilies Prunoideae and Maloideae in the traditional sense were paraphyletic, and Spiraeoideae – polyphyletic group. On this basis, the rank of the first two subfamilies is proposed to reduce to the tribe and together with the other related tribes to combine into one monophyletic (in a very broad sense) subfamily Spiraeoideae C. Agardh, with x=8, 9, 15 or 17. Therefore, the supertribe Pyrodae Camp., Ev., Morg. et Dick. with the tribe *Pyreae* Baill.

were included to the subfamily Spiraeoideae (x=17, with the exception of the genus *Vauquelinia* Correa ex Humb. Et Bonpl. with x=15), the subtribe of which Pyrinae absorbed most of the genera of the subfamily *Maloideae*, including the genus *Amelanchier*.

This extension of the subfamily Spiraeoideae enabled us to determine the systematic position of the genus *Amelanchier* within the family Rosaceae as follows [24, 51, 52]:

Familia – Rosaceae Juss.
Subfamilia – Spiraeoideae C. Agardh
Supertribus – Pyrodae Camp., Ev., Morg. et Dick.
Tribus – Pyreae Baill.
Subtribus – Pyrinae Dumort.
Genus – *Amelanchier* Medik.

However, there appeared to be a need to change the name of the subfamily Spiraeoideae due to the inclusion of the former subfamily Amygdaloideae to the newly formed subfamily Spiraeoideae. The fact is that under the International Code of Nomenclature for algae, fungi, and plants updated in 2011 [53] the taxon names must correspond to the earliest published name, so the priority name for the subfamily, which combines Spiraeoideae, Maloideae and Amygdaloideae is the name Amygdaloideae; for the tribe Pyreae – name Maleae Small; for the subtribe Pyrinae – name Malinae Rev. (Article 19.5, ex. 5).

While comparing the systematic position of the genus *Amelanchier* Medik., according to the different classification systems of plants different in time of creation and research level, the change in view on genus' phylogenetic connections can be partially traced (Table 11.2).

Herewith, the relative stability of the genus *Amelanchier* positiom within the major taxa of higher ranks should be noted. The range of fluctuations in the number of accepted species within the genus *Amelanchier* is quite wide: from 6 to 33 [30, 55], and with infraspecific taxa to 37 [48]. The number of Latin species names used by different authors is nearly ten times as much. Most of these names, which are now considered to be unresolved, have: unplaced and unassessed names, synonyms [48], provisionally accepted names, infraspecific taxa [56], interspecific hybrids, or misapplied names.

TABLE 11.2 The Systematic Position of the Genus *Amelanchier* Medik. According to Different Plant Classification Systems

Taxon	Classification systems of plants		
	Engler, 1903 [45]	**Takhtajan, 2009 [1]**	**APG III (2009) [53, 54].**
Division	Embryophyta siphonogama	Magnoliophyta	–
Subdivision	Angiospermae	–	–
Classis	Dicotyledoneae	Magnoliopsida (Dicotyledons)	–
Subclassis	Archichlamydeae	Rosidae	–
Superordo	–	Rosanae	–
Ordo	Rosales	Rosales	Rosales
Subordo	Rosineae	–	–
Familia	Rosaceae	Rosaceae	Rosaceae
Subfamilia	Pomoideae	Pyroideae (Maloideae)	Amygdaloideae
Tribus	–	Maleae	Maleae
Subtribus	–	–	Malinae
Genus	Amelanchier	Amelanchier	Amelanchier

A complex taxonomy of the genus is explained by morphological variation features of vegetative and generative organs, a large number of divergent and intermediate forms, polyploidy, hybridization, and a tendency to apomixis, causing the so-called occurring of agamospecies [57] and determining some taxonomic difficulties.

Generalized data on the genus *Amelanchier* taxonomy combine 279 names (including infraspecific). Of these 243 scientific plant names of species, 28 (11.5%) are accepted species names, 93 (38.3%) unassessed names, and 122 (50.2%) are synonyms [48].

We can assume that the ancestors of the genus *Amelanchier* modern species emerged by the end of the Cretaceous period of the Mesozoic era, or the beginning of the Paleogene period of the Cenozoic era, when there was a relatively rapid modernization of the flowering plants genus structure. So in the Eocene floras, most species can be classified within contemporary families. So, it is quite natural that certain fossilized footprints of *Amelanchier* are found in western North America, namely in the deposits of the Eocene period (48–50 million years ago) [58]. During the Neogene, in the arid regions of North America, a kind of "Madro-*Tertiary*" flora was formed, a detailed study of which [59] showed genus *Amelanchier* among other typical representatives of the fossil flora.

11.3.3 EVOLUTION DIRECTIONS OF THE GENUS AMELANCHIER

Adaptive radiation and hybridization are distinguished among the determinative evolution directions of the genus [24]. Thus, adaptive radiation most likely is caused by the formation of fleshy fruit and is related to vital functions of animals.

The conception about the growing importance of endozoochory during the process of fouling symphycarpous fruit aggregating by floral tube (apples formation), is also supported by Armen Takhtajan [60].

In general, the hypothesis about the origin of the subfamily Pyroideae (formerly Maloideae) shows the connection of this group with common ancestors of the most ancient subfamily Spiroideae. At the same time, they are close to Rosoideae according to the type of fruit-apples structure, as well as *Prunoideae*, as woody plants have a similar leaf shape, type of inflorescence, and structure of sepals and petals [47].

It should also be mentioned that the representatives of Pyroideae (Maloideae) have a basic chromosome number x=17 [61, 62].

Most of the other representatives of the Rosaceae family are characterized by a much lower number of chromosomes x=7, 8, or 9. That's why the logical assumption about the polyploid origin of chromosome number Pyroideae (Maloideae) was made. According to C.D. Darlington and A.A. Moffett (1930), Pyroideae (Maloideae) appeared from Rosoideae and is a triple trisomic tetraploid (x=7+7+3=17). In other words, it would double the number of chromosomes (all seven) with the addition of one more chromosome from three different pairs in one of the ancient specimens of Rosaceae with haploid set x=7 (very common chromosome number in the family Rosaceae) [51, 63].

However, the probability of triple trisomy is significantly lower than of amphidiploidy, so more followers supported the hypothesis of K. Sax (1931), who believed that Pyroideae (Maloideae) are alloploids arising out of doubling the number of chromosomes in hybrids between distant ancestors of two distant generic types. According to his view, this could be representatives of the subfamilies *Prunoideae*, which has a basic chromosome number *x*=8 and Spiroideae – with x=9, the uniting of which has put modern Pyroideae (Maloideae) x=17 chromosomes in a common genome [51, 61].

In those times, quoting Stebbins (1950), Armen Takhtajan [60] expressed an opinion that taking into account the data of cardiology and morphology of the flower, the most probable explanation for the origin of Pyroideae (Maloideae) is based on the fact that Pyroideae (Maloideae) is diploidizated polyploid arising out as a result of an ancient hybridization between Spiroideae and Rosoideae, which explains the basic haploid number of this subfamily *x*=17.

The fact of mainly bivalent chromosomes conjugation of Pyroideae (Maloideae) [61] gives ground to define the representatives of this subfamily as functional diploids. Although one can find tetraploid (68 chromosome) species (including the genus *Amelanchier*) near the diploid 2*n*=34 in the subfamily [46, 51, 62], the proportion of functional diploids in Pyroideae (Maloideae) prevails, and it is much larger than in other subfamilies of Rosaceae [25].

The results of the research released at the beginning of the 21st century, which were carried out at comparing the DNA sequences of the subfamily Pyroideae (Maloideae) and a large number of other representatives of the family Rosaceae, shake the prestige of these hypotheses [24, 26, 31].

The analysis of the obtained materials on the genomes similarity of the subfamily Pyroideae (Maloideae) specimens and the genus *Gillenia* from the subfamily Spiraeoideae, gave good reasons to believe that probably the genus *Gillenia* is the closest relative to the apple. All nuclear and chloroplast cladograms show that the genus *Gillenia* is invariably manifested as a sister group to *Pyroideae* (*Maloideae*). Taking into consideration that *Gillenia* has a less number of chromosomes (*x*=9) than all Pyroideae (*Maloideae*) (*x*=17), the authors assumed that the genom of Pyroideae (Maloideae) was formed monophyletic as a result of autopolyploidy of the genus *Gillenia* representatives from *x*=9 to *x*=18 and subsequent aneuploidy (nullisomy) to the current number of chromosomes *x*=17. Thus, the basic chromosome number *x*=17 is common to all Pyroideae (Maloideae) and some Spiraeoideae (*Kageneckia* and *Lindleya*), although *Vauquelinia* representatives have x=15, which may become a reason of a system revision [27].

Flow cytometry data [64] also showed the similarity of the genomes Pyroideae (Maloideae) and *Gillenia*. The comparative analysis of the characteristics of female and male gametophytes *Gillenia* and seven genera representatives of the subfamily (*Chaenomeles*, *Cotoneaster*, *Crataegus*, *Mespilus*, *Photinia*, *Rhaphiolepis* and *Sorbus*) confirmed the similarity of Pyroideae (Maloideae) and *Gillenia* floral development [29].

Admitting evidences of monophyletic nullisomic origin of the subfamily Pyroideae (Maloideae) representatives one has to explain the facts of mainly bivalent conjugation of their chromosomes by a prolonged evolution, in the process of which during interspecies hybridization and polyploidization within common ancestral group with *Gillenia* took place. Such course of events is more likely than the gradual formation of a functional diploid from an autoaneuploid that perhaps arose out of an autotetraploid because of its nullisomy.

These assumptions were confirmed as a result of summarizing data of collinearity (the order of location) analysis of genes along each of the 17 chromosomes of the apple. Working according to a united international program, 86 scientists from Italy, France, New Zealand, Belgium and the United States have examined the chromosomes of the genome sequence of the apple 'Golden Delicious' [33].

They showed similar collinearities between large segments of chromosomes 3 and 11, 5 and 10, 9 and 17, 13 and 16, and between short segments of chromosomes 1 and 7, 2 and 7, 2 and 15, 4 and 12, 12 and 14, 6 and 14, 8 and 15, about which they reported in a joint publication. They found that relatively not long ago, less than 50 (approximately 30–45) million years ago, there was a spontaneous duplication (autoreduplication) of the 9 chromosome ancestor genome of the apple with subsequent loss of the eighteenth chromosome and forming 17 chromosome karyotype of modern apples (Figure 11.2).

Herewith, the first chromosome of the apple ancestor donated genetic material to 5 and 10 chromosomes of apple trees, respectively 3 and 11 chromosomes intergraded from the second chromosome, 9 and 17 – from the third one, 13 and 16 – from the fourth one, and 4, 6, 12 and 14 chromosomes of apples are combined from the fragments of the fifth and

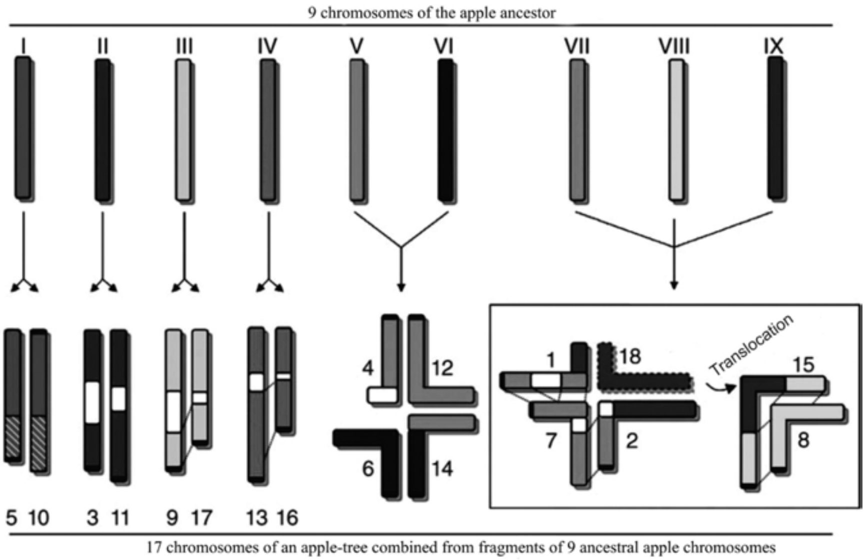

FIGURE 11.2 The scheme of forming 17-chromosome karyotype of *Malus domestica* Borkh. (the scheme could be extended to other apples, including the genus *Amelanchier*): the virtual chromosome 18 is shown as a source of genetic material for 1, 2 and 15 apple chromosomes; white areas indicate that sequences localized at them have no ancestral prototypes (according to R. Velasco et al., 2010 [33] as amended [51]).

sixth ones. The first and the second chromosomes are developed from the fragments of the seventh and ninth ancestors of the apples and from the seventh chromosome – seventh one respectively. The origin of 8 and 15 chromosomes of apples is a little more complicated. If the eighth chromosome of apples contains sequences of the eighth apple ancestor chromosome, then 15 consists of fragments of the eighth and ninth ones. But there is a reason to believe that the translocation of genetic material of the ninth chromosome took place before the above-mentioned nullisomy (loss of the18th pair of chromosomes) [33].

It is assumed an existence (currently unidentified) of the gene regulator of conjugation of homologous chromosomes apple with functions similar to the display of the gene *Ph1*, which governs the on-goings of wheat chromosomes during meiosis, preventing from multivalent conjugation of partially homologous chromosomes poliploids. It provided mainly bivalent conjugation (pairs) and the formation of functional diploids from the ancestral autotetraploid.

11.3.4 THE AREAL OF THE GENUS AMELANCHIER

The genus *Amelanchier* representatives grow mainly in the forested areas of the moderate zone in the Northern Hemisphere mostly in light woodland slopes, light forests to an altitude of 1900 m above the sea level, and grow well on a variety of soils [21].

The areal of the genus *Amelanchier* is quite wide, it occupies the extratropical Northern Hemisphere and covers almost all of North America and Europe, partially extratropical North Africa and extratropical Asia. Some species can be found in the subtropics and occasionally in the tropical latitudes (Figure 11.3), but mainly in the mountains, where conditions are similar to moderate or subtropical climate [21, 22, 30].

The analysis of the genus *Amelanchier* existence is defined by Armen Takhtajan (1978) biogeographic regions confirms the predominant settlement in the moderate latitudes of the Northern Hemisphere. Types of *Amelanchier* occur in all regions of the Boreal subkingdom, namely in Circumboreal, East Asian, Atlantic and North-American regions and the region of the Rocky Mountains; in Mediterranean and Irano-Turanian regions of the Ancient Mediterranean Subkingdom and in Madrean area of the Madrean (Sonoran) Subkingdom in Holarctic Kingdom (Figure 11.4) [22, 66].

However, the vast majority of species of the genus grows within the original areal in the North America territory, from 18 to 26 [41, 50, 65].

FIGURE 11.3 The distribution of the genus *Amelanchier* in the world (based on site EOL (Encyclopedia of Life) [65]).

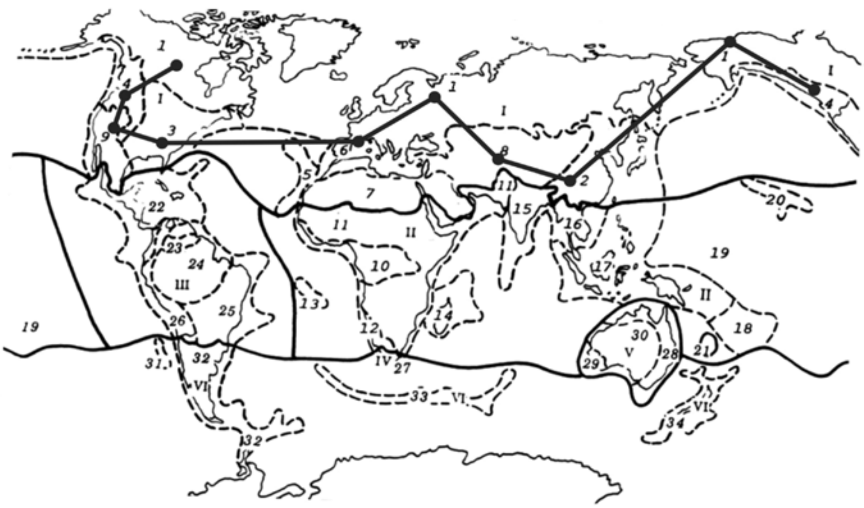

FIGURE 11.4 The distribution of the genus *Amelanchier* in floristic regions defined by Armen Takhtajan (1978) [66]. The firm line defines the conventional boundaries of floristic kingdoms, dashed – areas; point (conditional core of the floristic region) at the figures shows the distribution of the genus within the regions: 1 – Circumboreal 2 – East Asian, 3 – Atlantic, North American, 4 – Rocky Mountain region, 6 – Mediterranean, 8 – Irano-Turanian, 9 – Madrean.

One species is typical for Europe, Africa, and Turkey (*A. ovalis*) [21, 30, 67]. Another one occurs in Greece, on the island of Crete (*A. cretica*), the other – European natural hybrid of *A. lamarckii*, and 2 species grow in Turkey (*A. integrifolia; A. parviflora*) [30]. Two species grow in China, Korea, and Japan (*A. sinica; A. asiatica*) [30, 68].

11.3.5 THE INVASIVENESS PROBLEMS OF THE GENUS AMELANCHIER INDIVIDUAL REPRESENTATIVES

The genus *Amelanchier* representatives actively spread and are able to naturalize in natural phytocenoses of the second range. Thus, the distribution of some of them in the territory of some European countries and the European part of Russia can apply the character of phytoinvasion (Table 11.3).

The data in Table 11.3 show that *A. spicata* is characterized as the most aggressive in the European countries among presented species.

TABLE 11.3 The Invasion Degree of the Genus *Amelanchier* Individual Representatives in Northern and Central Europe counTries and the European Part of Russia, According to the Materials of the Website NOBANIS [69]

Species	Country								
	Belgium	**Denmark**	**Estonia**	**The European part of Russia**	**Latvia**	**Lithuania**	**Norway**	**Finland**	**Sweden**
A. alnifolia	–	n/i	–	–	–	–	i	p/i	i
the growth place: mixed coniferous and deciduous forests, open areas, damaged areas, urban areas									
A. canadensis	–	–	–	n/i	–	–	–	–	–
the growth place: mixed coniferous and deciduous forests, urban areas									
A. laevis	–	–	–	–	–	–	–	p/i	n/i
the growth place: mixed coniferous and deciduous forests, open areas, damaged areas, wetlands									
A. lamarcki	p/i	p/i	–	–	–	–	i	p/i	i
the growth place: mixed coniferous and deciduous forests, open areas, damaged areas, wetlands									

TABLE 11.3 Continued

Species	Country								
	Belgium	**Denmark**	**Estonia**	**The European part of Russia**	**Latvia**	**Lithuania**	**Norway**	**Finland**	**Sweden**
A. ovalis	–	–	–	n/i	–	–	n/i	–	–
the growth place: mixed coniferous and deciduous forests, urban areas									
A. spicata	–	i	i	n/i	i	i	i	i	i
the growth place: mixed coniferous and deciduous forests, open areas, damaged areas, agricultural areas, urban areas									

Note: n/i – non-invasive; p/i – potentially invasive; i – invasive; dash – no information available.

The invasiveness of the rest of the presented species of the genus *Amelanchier* has a non-systemic character. You can accept the opinion of A.S. Mosyakin [70] that the invasive processes are controlled by multidirectional biotic and abiotic factors, the interaction of which depends on the invasive possibility of a certain type. In particular, this invasive possibility is not some fixed trait, proper to species, it is found only in specific environmental conditions.

11.3.6 THE REPRESENTATIVES OF THE GENUS AMELANCHIER IN THE FLORA OF UKRAINE

In the flora of Ukraine, a number of the genus *Amelanchier* species is limited to two or three [3, 52, 70, 71]. These are: *A. ovalis*, *A. canadensis* and *A. spicata*. Herewith, *A. ovalis* is defined as an indigenous species, and *A. canadensis* and *A. spicata* are defined as introduced and naturalized in the secondary habitat. *A. rotundifolia*, *A. integrifolia*, *A. oligocarpa*, *A. laevis*, *A. alnifolia*, *A. florida*, *A. utahensis*, *A. asiatica*, which are unsystematically cultivated, mainly as ornamental, in private collections, botanical gardens and arboreta are referred to as a promising species for introduction, apart from *A. canadensis* and *A. spicata*.

Until recently, in the collection of the National Dendrological Park (NDP) "Sofiyivka," the genus *Amelanchier* was represented only by two species *A. ovalis* and *A. canadensis* [72].

Among the supplies of the last decade, there are representatives of the species: *A. alnifolia*, *A. asiatica*, *A. canadensis*, *A. florida*, *A. laevis*, *A. ovalis*, *A. spicata*, *A. stolonifera*, *A. utahensis* and *A. pumila*. Among them, there were plants that were delivered to "Sofiyivka" in 50–60 years of the last century, but identified only in 2004–2014, as well as new supplies from various botanical institutions. In some cases, the re-introduction of species contributed to the species specification of existing plants. Now 14 species names can be counted in the collection of the NDP "Sofiyivka." Table 11.4 introduced the species names of the genus *Amelanchier* specimens growing in the NDP "Sofiyivka," the plants of which were identified and also 28 species names, accepted in the database of Royal Botanical Gardens Kew [56]. During the time that has passed since our previous report [52], the collection of NDP "Sofiyivka" was enlarged to 14 species.

TABLE 11.4 The Genus *Amelanchier* Collection List of the NDP "Sofiyivka" of NAS of Ukraine Compared to the Catalogue of Life: 2014 Annual Checklist

Catalogue of Life., 2014 [56]	**Collection list of the NDP "Sofiyivka," 2014**
A. alnifolia (Nutt.) Nutt. ex M. Roem.	*A. alnifolia* (Nutt.) Nutt. ex M. Roem.
A. arborea (F. Michx.) Fernald	absent
A. asiatica (Siebold & Zucc.) Endl. ex Walp.	*A. asiatica* (Siebold & Zucc.) Endl. ex Walp.
A. australis Standl.	absent
A. bakeri Greene	absent
A. bartramiana (Tausch) M. Roem.	absent
A. canadensis (L.) Medik.	*A. canadensis* (L.) Medik.
A. covillei Standl.	absent
A. cretica (Willd.) DC.	absent
A. cusickii Fernald	absent
Provisionally accepted name	*A. florida* Wiegand
A. grandiflora Rehder	*A. grandiflora* (Wiegand) Wiegand
A. interior E.L. Nielsen	absent
A. intermedia Spach	absent
A. laevis Wiegand	*A. laevis* Wiegand
Absent	*A. lamarckii* F.G. Schroed.
A. neglecta Eggl. ex G.N. Jones	absent
A. obovalis (Michx.) Ashe	absent
A. ovalis Medik.	*A. ovalis* Medik.
A. pallida Greene	absent
A. parviflora Boiss.	absent
A. pumila (Nutt. ex Torr. & A. Gray) M. Roem.	*A. pumila* (Nutt. ex Torr. & A. Gray) M. Roem.
A. quinti-martii Louis-Marie	absent
Provisionally accepted name	*A. rotundifolia* (Lam.) K. Koch
A. sanguinea (Pursh) DC.	*A. sanguinea* (Pursh) DC.
A. sinica (C.K. Schneid.) Chun	absent
A. spicata (Lam.) K. Koch	*A. spicata* (Lam.) K. Koch
A. stolonifera Wiegand	*A. stolonifera* Wiegand
A. turkestanica Litv.	absent
A. utahensis Koehne	*A. utahensis* Koehne

*Catalogue by Royal Botanical Gardens Kew.

Besides, cited databases [48, 56] in recent years became very close to the list of species names, which gave a reason to limit them to comparing the species names of the collection NDP "Sofiyivka" from the Annual checklist of Catalogue by Royal Botanical Gardens Kew.

The species *A. alnifolia* was imported from the Krivoy Rog Botanical Garden of NAS of Ukraine. This species name was considered synonymous with *A. sanguinea* var. *alnifolia* (Nutt.) P. Landry in the past in the working list of known plant species The Plant List Royal Botanic Gardens, Kew and Missouri Botanical Garden, but now it is recognized as a separate species name in the above mentioned catalog The Plant List [48], as well as in the Catalogue of Life, 2014 [56].

The species *A. asiatica* were delivered to the NDP "Sofiyivka" collection from O.V. Fomin Botanical Garden, Taras Shevchenko Kyiv National University research institutions in 2009. This species name is accepted in all catalogs known to us.

A. canadensis plants were first imported from Minsk Botanical Garden (now the Central Botanical Garden of NAS of Belarus) in 1959, but certainty about their species belonging was questioned after transferring plants from the domestic park arboretum to the active research and commercial arboretum, that prompted to the re-introduction of this species in 2010 from the Krivoy Rog botanical Garden. The species name is now accepted in both above mentioned databases [48, 56].

The similar story of the repeated (in 2010) introduction from the Krivoy Rog Botanical Garden of *A. florida* plants, representatives of which were first imported in 1959 from Leningrad Botanical Garden (now V.L. Komarov Botanical Garden of the Botanical Institute of RAS). In the Plant List [48], the name of *A. florida* Wiegand is considered unresolved, and *A. florida* Lindl. is synonymous with *A. alnifolia var. semi-integrifolia* (Hook.) CLHitchc., and in the Catalogue of Life [56] *A. florida* Wiegand name is given as a provisionally accepted name without the name *A. florida* Lindl.

The species *A. grandiflora,* in the NDP "Sofiyivka" collection, is represented by two cultivars: 'Autumn Brilliance' and 'Forest Prince.' Its species name – *Amelanchier grandiflora* (Wiegand) Wiegand is now accepted in The Plant List [48] a synonym of *Amelanchier sanguinea* var. *grandiflora* (Wiegand) Rehder., but in the same catalog the accepted name

Amelanchier×grandiflora Rehder is given. Instead, in the Catalogue of Life [56] the accepted name *A. grandiflora* Rehder is given, whereas *A. grandiflora* Wieg. is considered a synonym for *A. sanguinea* (Pursh) DC.

A. laevis plants were first delivered in 1958 from the Botanical Garden of Uzbekistan (now the Botanical Garden of the Uzbekistan AS) and re-imported in 2010 from the Krivoy Rog Botanical Garden, which contributed to specifying the plant species. This species name is now accepted as a separate species in both above mentioned databases [48, 56].

In the NDP "Sofiyivka" collection, the species *A. lamarckii* FG Schroed. is presented as a cultivar 'Prince William.' This species name is an accepted name in the database of The Plant List [48]. But in the Catalogue of Life: 2014 Annual Checklist [56] this species name (*A. lamarckii*) is removed, although in the Catalogue of Life: 2010 Annual Checklist it was given as an accepted name.

A. ovalis Wieg. plants are classified as representatives of the long and widely spread species (in all parts of "Sofiyivka") by the NDP "Sofiyivka" catalog in 2000 [72]. This name is accepted by both the above mentioned catalogs [48, 56].

The species name *A. pumila* (Nutt. ex Torr. & A.Gray) M.Roem. is now accepted in both above mentioned databases [48, 56].

The species name *A. rotundifolia* (Lam.) K. Koch, plants of which were imported from Kaunas Botanical Garden (now the Vytautas the Great University Botanical Garden) in 1958, is included in The Plant List [48] as an unresolved name, and in the Catalogue of Life [56] is considered as a synonym for *A. ovalis subsp. ovalis* Medik.

Re-introduction (in 2010) from the Krivoy Rog Botanical Garden of *A. sanguinea* (Pursh) DC. plants, representatives of which were first imported from Leningrad Botanical Garden (now V.L. Komarov Botanical Garden of the Botanical Institute of RAS) in 1958, will contribute to specifying species belonging of existing plants. The species name is accepted by both the above-mentioned catalogs, which gives grounds for certainty in its status [48, 56].

A. spicata (Lam.) K. Koch, as well as *A. ovalis* are classified by NDP "Sofiyivka" Catalogue of 2000 as a long spread species in all parts of the park [72]. However, the features of vegetative and generative organs variation, that is referred to this species plants, prompts for further more grounded analysis. Therefore, *A. spicata* representatives delivered from the Krivoy Rog Botanical Garden in 2010 were planted in the NDP "Sofiyivka" collection to compare and specify the status of the existing plants under this plant name. In the Plant List [48] *A. spicata* is accepted as a species name. But in the Catalogue of Life [56] *A. spicata* is considered as a synonym for *A. canadensis* (L.) Medik.

The plants *A. stolonifera* Wiegand and *A. utahensis* Koehne, imported from the Krivoy Rog Botanical Garden in 2010, belong to new supplies of the genus *Amelanchier* specimens. Thus, in the Plant List … [48] and in the Catalogue of Life … [56] are both accepted species names.

The similar divergences in approaches to systematize species names and specify the composition the genus are observed when comparing the names of other *Amelanchier* species, so far absent in NDP "Sofiyivka" of NAS of Ukraine collection, but available in other catalogs [48, 56]. The desired consensus can be achieved by combining the results of the species identification by classical (morphological) and molecular genetic criteria. Today, collecting new genotypes of the genus *Amelanchier* continues, and exploring new supplies has already started.

In addition to the above-mentioned species of *Amelanchier* in the NDP "Sofiyivka" collection, a number of cultivars are researched, seedlings of which are grown from in vitro propagated plants: 'Autumn Brilliance,' 'Forest Prince,' 'Krasnojarskaja,' 'Pembina,' 'Prince William,' 'Slate,' 'Snowcloud,' 'Smoky,' including old cultivars: 'Pembina,' 'Smoky.'

The analysis of differences in species names and common names of the genus *Amelanchier* specimens in some well-known websites [48, 56], demonstrates the need for their further arranging. However, as a great advantage of these [48, 56] and other similar electronic databases of plant species names, one should accept their general availability, ease of use and, what is very important, is a constant dynamism, the ability to collect and analyze new information and arrange it.

11.4 CONCLUSION

Thus, in Ukraine, the representatives of the genus *Amelanchier* are still unconventional plants for the culture, but interest in them is constantly growing, due to their fruit ornamental value, nectareous, medicinal phytomeliorative abilities.

The results of the phylogenetic and molecular genetic studies performed by scientists from different countries give an opportunity to specify the systematic position of the representatives of the genus *Amelanchier* of the family Rosaceae Juss. grown in Ukraine, and temporarily place them in a large subfamily Amygdaloideae Arn., which unites the former subfamilies Amygdaloideae, Spiraeoideae and Maloideae, tribe – Maleae Small, subtribe – Malinae Rev.

The divergences in species and interspecies classification of the genus *Amelanchier* representatives found in various publications indicate incompleteness of the genus system and necessity for further studies by classical and molecular genetic methods.

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KEYWORDS

- **areal**
- **biodiversity**
- **chromosome number**
- **DNA sequence**
- **family**
- **floristic region**
- **Juneberry**
- **phytomeliorative**
- **taxonomy**
- **tribe**

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