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INTERSPECIES HYBRIDS OF *JUGLANS REGIA* L.

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Abstract*. Persian walnut (Juglans regia L.) is an important tree primarily for its nutritious nuts and high-quality wood. Based on the analysis of literature sources, it was found that hybridization played a significant role in the evolution of the genus Juglans. Persian walnut can interbreed with many walnut species with the formation of fertile hybrids. There are two-species, three-species, and four-species hybrids in different combinations of crossings. They are used in forestry as a source of wood, in horticulture as rootstocks, and in breeding for more durable resistance against pathogens and tolerance against abiotic stresses. Some interspecific hybrids have validly published scientific names, but many of the proposed names do not meet the rules of the International Code of Nomenclature for algae, fungi, and plants.*

Keywords: *remote hybridization, species, Persian walnut, Juglans*

Introduction. Walnut (*Juglans regia* L.) is the most important nut crop in Ukraine with significant export potential. Ukraine is one of the five most powerful walnut-producing countries in the world and ranks second among walnut exporters after the USA. In Ukraine walnut growing entered the stage of a wide varietal industrial culture, which causes the expansion of breeding work.

Aim. The purpose of the work is to find out the state and possibilities of applying the species potential of the genus *Juglans* in the walnut breeding.

Materials and methods. Domestic and foreign literature of XIX–XXI centuries about interspecific hybrids of *Juglans* were analyzed.

Results. Hybridization played a significant role in the evolution of the genus *Juglans*. The ancient hybrid origin of *J. regia* and *J. cinerea* is proven [68]. The natural Chinese taxon *J. hopeiensis* is the consequence of interspecific hybridization [61]. Currently, gene flow is between species of sections *Cardiocaryon* and *Rhysocaryon* and between species in these sections [5; 66; 70]. The walnut species quite easily hybridize under domestication [11; 12, 13; 28; 29; 50; 56]. The numerous artificial interspecific hybrids were also obtained (Fig. 1).

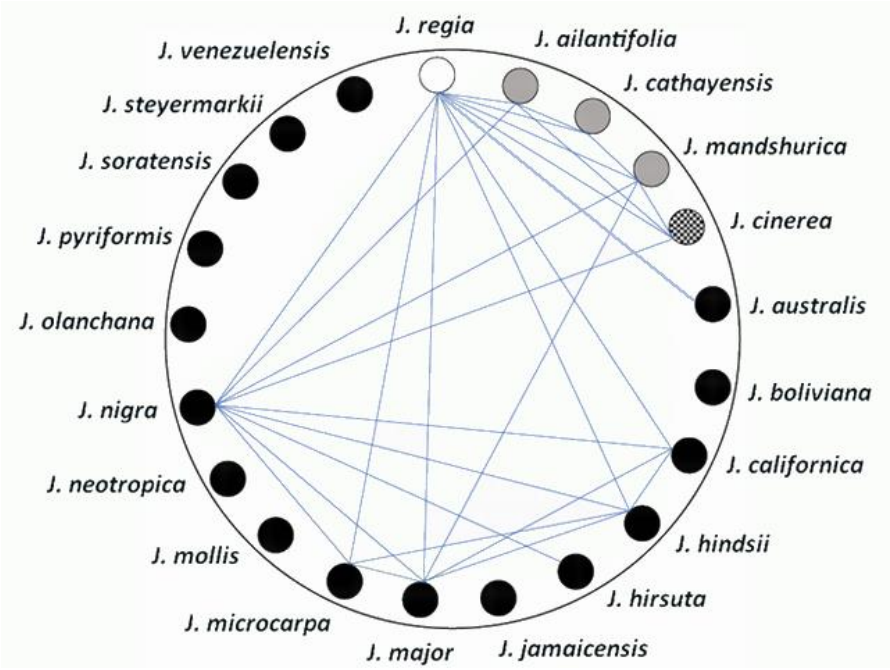

Fig. 1. Interspecific hybrids in *Juglans* genus [40, modified]

***J. nigra* L. × *J. regia* = *J.* ×*intermedia* Jacques.** The first interspecific hybrid of the newest time arose as a result of spontaneous hybridization between Persian walnut and black walnut introduced in Europe, two *Juglans* species that have the greatest economic values. The heterosis hybrid raised from black walnut seeds sown in 1820. It was described by French gardener Henri Antoine Jacques [22]. Later, Élie Abel Carrière [12] described two hybrids between Persian walnut and black walnut, one of which is known to come from seeds sown in 1815 [59]. The latter plant is probably the first recorded spontaneous *J. nigra* × *J. regia* hybrid. In the future, seedlings were obtained from their seeds in many institutions of several countries. Today, numerous offspring of subsequent generations and from new artificial crosses, including backcrosses, grow in France, Italy, Spain, and other Western European countries [14; 20; 23; 39]. *J.* ×*intermedia* is also developed and cultivated in the USA [9; 10; 16; 19]. In Ukraine, artificial and spontaneous *J. nigra* × *J. regia* hybrids were repeatedly developed [1; 2; 4; 27; 31; 34; 52; 54; 53; 65; 72]. Some hybrids were given names: *J.* ×*timirjazewii* Krotkewitsh, *J.* ×*weselowskii* Krotkewitsh [28; 29]. The name *J.* ×*rubra* Schepotiev was given hybrids with the reddish color of shoots [52; 54]. The hybrids backcrossed with Persian walnut were also obtained [2; 30]. *J.* ×*intermedia* was also developed artificially in Kyrgyzstan [43; 55; 67], Moldova [25; 26], Russia [41; 42; 43], and Uzbekistan [24; 49; 51].

***J. cinerea* L. × *J. regia* = *J.* ×*quadrangulata* (Carrière) Rehder.** In 1858, Élie Abel Carrière raised seedlings of Persian walnut pollinated by butternut in the Paris Museum of Natural History

Garden [12]. Alfred Rehder [46] established a species rank for these hybrids. *J. cinerea* × *J. regia* hybrids were discovered and artificially developed in the USA [8; 16], Russia [32; 56; 57], Ukraine [28; 29; 54; 52; 53], Kyrgyzstan [43; 55], Moldova [25; 26], Uzbekistan [24; 20; 51], and France [20]. The names *J.* ×*kondratiewii* Krotkewitsh, *J.* ×*kononjukii* Krotkewitsh, *J.* ×*wysockii* Krotkewitsh [28; 29], *J. silvosteposa* N. Vechov [57], and *J.*×*viridis* Schepotiev [54] have been proposed for these hybrids. Fedir Shchepotiev uses the latter name to hybrids of Persian walnut with both butternut and Manchurian walnut.

***J. ailantifolia* Carrière × *J. regia* = *J.* ×*notha* Rehder**. In 1878, the first hybrid between these species was raised from seeds sent by Pierre Alphonse Lavallée, founder of the Segrez Arboretum (Saint-Sulpice-de-Fevières, Ile-de-France, France), in Arnold Arboretum. In 1919, Willard Bixby discovered a hybrid tree in the garden of R. Bates (Jackson, South Carolina, USA) [47]. The artificial and spontaneous hybrids between Japanese walnut and Persian walnut there are in USA [11; 16], Kyrgyzstan [43; 67], Russia [41; 42; 43], Uzbekistan [20; 24; 50], Moldova [25; 26], Ukraine [2; 31; 35], and Georgia [15].

***J. ailantifolia* var. *cordiformis* (Makino) Rehder × *J. regia* = *J.* × *notha* var. *batesii* Rehder.** The hybrid was discovered by Willard Bixby in the garden of R. Bates in South Carolina (USA) in 1919 [47]. The artificial hybridization between these taxa was made in Ukraine [1; 35], Kyrgyzstan [43], Russia [43], Moldova [25; 26], and Uzbekistan [20; 24]. Such hybrids occur in Belarus too [18].

***J. hindsii* (Jeps.) R. E. Sm. × *J. regia* = 'Paradox'** [*J.* × *paradox* Burbank]. A hybrid between walnut and the California walnut species was developed by Luther Burbank in 1878 [11]. Later an aboriginal California black walnut was divided into two separate species: *J. californica* S. Watson (Southern California black walnut) and *J. hindsii* (Northern California black walnut). The latter species is a component of crossbreeding with Persian walnut, carried out by Burbank [45]. Spontaneous hybrids between these species also occur in California [16]. 'Paradox' seedlings were used as rootstocks, and subsequently, the name "paradox hybrids" passed to all American black walnut hybrids in the section *Rhysocaryon*. 'Paradox' seedlings grow in different areas along with other North American walnuts and have the ability to be pollinated by ones. Molecular studies have established an additional gene flow from *J. nigra* and *J. major* (Torr.) A. Heller at least to some paradox-hybrids [45]. In the American breeding program, paradox hybrids of various origins are tested, including backcrosses with both Persian walnut and interspecific hybrids with a different pedigree than 'Paradox' [9]. The crossing of Persian walnut with Northern

California black walnut was also carried out in Uzbekistan [51].

***J. californica* × *J. regia*.** The crossing of Southern California black walnut with Persian walnut was carried out in Ukraine [4] and in the USA [9]. In the first case, gynogenetic plants were obtained [3], and in the second case, hybridity was confirmed by molecular methods [7; 9].

***J. mandshurica* Maxim.× *J. regia* = *J.* ×*hopeiensis* Hu.** This natural hybrid is described by Hu Hsen Hsu [21]. Its hybridogenous origin is proved by the analysis of molecular data [60; 61]. Likely, the taxonomic status of the taxon does not exceed the level of a horticultural variety, due to the origin with the participation of two species *J. cathayensis* Dode and *J. mandshurica*, which spontaneously hybridized with Persian walnut [70]. The many artificial and spontaneous hybrids between Manchurian walnut and Persian walnut were developed in Russia [6; 41; 42; 58; 63; 65], Ukraine [2; 4; 31; 34; 27; 52; 53; 54], Uzbekistan [20; 24; 50; 51], and Moldova [25; 26], as well as backcrosses with Persian walnut [2]. Pavlo Krotkevych [28; 29] proposed for these hybrids the names *J.* ×*aleksejewii* Krotkewitsh, *J.* ×*mitshurinii* Krotkewitsh, and *J. morosowii* Krotkewitsh. Fedir Shchepotiev [52; 54] name *J.* ×*viridis* also spread to Persian walnut hybrids with butternut, because they were distinguished by the green bark of the trunk and emerald green leaves and shoots. Alfred Rehder [48] suggested hybrid origin from crossing between *J. mandshurica* and *J. regia* for *J.* ×*sinensis* (C. DC.) Dode.

***J. cathayensis* Dode × *J. regia*.** The Persian walnut can hybridize with a *J. cathayensis* under conditions of artificial crossing [62]. The spontaneous hybrids between these species were found in Hebei Province (China) [17; 70].

***J. major* (Torr.) A. Heller × *J. regia*.** In France, interspecies hybrids were obtained from crossing Arizona black walnut with Persian walnut [20; 36]. The crossing Persian walnut with Arizona black walnut was carried out in Uzbekistan [51]. The plants obtained in Ukraine in this combination of crosses [4] have no signs of the parent species-pollinator [3].

J. microcarpa* Berland. × *J. regia. True hybrids from the crossing of Texas black walnut with Persian walnut were obtained in the USA [9; 71]. The crossing of these species was also carried out in Uzbekistan [51] and Ukraine, but the resulting plants were gynogenetic type [3].

J. australis* Griseb. × *J. regia. The Brazilian walnut hybridizes with Persian walnut [38]. The same authors point to the prospect of involvement *J. neotropica* Diels and *J. olanchana* Standl. & L. O. Williams to hybridization with Persian walnut.

It was reported that three-species hybrids were developed, in particular, **(*J. ailantifolia* × *J. mandshurica* Maxim.) × *J. regia*** [64]; **(*J. ailantifolia***

× ***J. cinerea*****)** × ***J. regia*** [64; 69]; **(*J. californica* × *J. nigra*)** × ***J. regia*** [9]; ***(J. mandshurica* × *J. nigra)* × *J. regia***, and **(*J. nigra* × *J. regia)* × *J. mandshurica.*** The backcrossing of both *J. mandshurica* × *J. regia* and *J. nigra* × *J. regia* hybrids with Persian walnut were carried out in Russia [64]. The spontaneous hybrid between *J.* ×*intermedia* and Manchurian walnut was found in Germany [39]. A four-species hybrid **[(*J. major* × *J. hindsii*)** × ***J. nigra*]** × ***J. regia*** was developed in the USA [10].

***J. regia* × *J. sigillata* Dode = Sichuan walnut.** The Persian walnut and iron walnut have sympatric habitats and interbreed spontaneously with each other [17]. Now, *J. sigillata* is considered only a subspecies of *J. regia* [37; 70]. There are no genetic barriers between these taxa and the gene flow goes mainly from *J. regia* to *J. sigillata*.

A significant barrier that prevents Persian walnut from crossing with other walnut species is a disjunction in flowering time. But, under favorable pollination conditions, prezygotic barriers, such as differences in floral size and conspecific pollen, significantly affect the effectiveness of interspecific hybridization [44]. The species differences lead to disturbances at the stage of zygote formation and embryo development and the resulting hybrids can be low-fertile or sterile. However, *J. regia* hybridized with all *Juglans* species with which it came into contact in nature, and in the absence of natural contacts, it successfully crossed due to artificial pollination. There are hybrids of Persian walnut with *J. ailantifolia, J. australis, J. californica, J. cathayensis, J. cinerea, J. hindsii, J. major, J. mandshurica, J. microcarpa, J. nigra.* This list does not include only tropical species from Central and South America, which are not cultivated outside the natural areas. Three-species and four-species hybrids with the participation of Persian walnut were also developed. The interspecies hybrids are used in forestry, rootstock breeding, and breeding for winter hardiness and resistance against pathogens.

The Persian walnut hybrids with *J. ailantifolia*, *J. cinerea*, *J. mandshurica*, and *J. nigra* have nothospecies names, respectively, *J.* ×*notha*, *J.* ×*quadrangulata*, *J.*×*hopeiensis*, and *J.* ×*intermedia.* Many later names, such as *J.* ×*aleksejewii*, *J.* ×*kondratiewii, J.* ×*kononjukii, J.* ×*mitshurinii, J.* ×*morosowii, J.* ×*rubra, J.* ×*silvosteposa, J.* ×*timirjazewii, J.* ×*viridis, J.* ×*weselowskii,* and *J.* ×*wysockii,* which applied to these nothotaxa, are effective, but not validly published, because they were not accompanied by a Latin description or diagnosis, according to the International Code of Nomenclature for algae, fungi, and plants. Also, the authors of these names, for the same combination of crosses gave several different names or used the same name for the results of different combinations of crosses. These

names are *nomen nudum*, but can use as the names of cultivars, selected from interspecific hybrids.

Conclusions. The Persian walnut can interbreed with other *Juglans* species, despite the barriers preventing remote hybridization. There are also three-species and four-species hybrids with the participation of Persian walnut. The interspecific hybrids of Persian walnut are used in forestry as a source of wood, in horticulture as rootstocks, and in the breeding on resistance against abiotic and biotic stressors. Synonymous names of interspecific hybrids, which are not validly published, can be used as cultivar names.

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МІЖВИДОВІ ГІБРИДИ JUGLANS REGIA L.

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Анотація. Волоський горіх (*Juglans regia* L.) має значення насамперед як *джерело поживних горіхів та високоякісної деревини. На підставі аналізу літературних джерел встановлено, що гібридизація зіграла значну роль в еволюції роду Juglans. Волоський горіх здатний схрещуватися з багатьма*

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видами горіха з утворенням плодовитих гібридів. Відомі дво-, три- та чотиривидові гібриди, що отримані в прямих і зворотних комбінаціях схрещувань. Вони використовуються в лісовому господарстві як джерело деревини, у садівництві як підщепи та в селекції на стійкість проти патогенів та абіотичних чинників довкілля. Деякі міжвидові гібридів мають дійсно оприлюднені наукові назви, проте багато із запропонованих назв не відповідають правилам Міжнародного кодексу номенклатури для водоростей, грибів та рослин.

***Ключові слова**: віддалена гібридизація, види, волоський горіх, Juglans*

МІЖВИДОВІ ГІБРИДИ *JUGLANS REGIA* L.

В. Н. Меженский

Аннотация. Грецкий орех (*Juglans regia* L.) имеет значение прежде всего как источник питательных орехов и высококачественной древесины. На основании анализа литературных источников установлено, что гибридизация сыграла значительную роль в эволюции рода *Juglans*. Грецкий орех способен скрещиваться со многими видами ореха с образованием плодовитых гибридов. Известны двух-, трех- и четырехвидовые гибриды, полученные в прямых и обратных комбинациях скрещиваний. Они используются в лесном хозяйстве как источник древесины, в садоводстве в качестве подвоя и в селекции грецкого ореха на устойчивость против патогенов и абиотических факторов среды. Некоторые межвидовые гибридов имеют действительно обнародованные научные названия, однако многие из предложенных названий не соответствуют требованиям Международного кодекса номенклатуры водорослей, грибов и растений.

***Ключевые слова*:** отдаленная гибридизация, виды, грецкий орех, *Juglans*