

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).

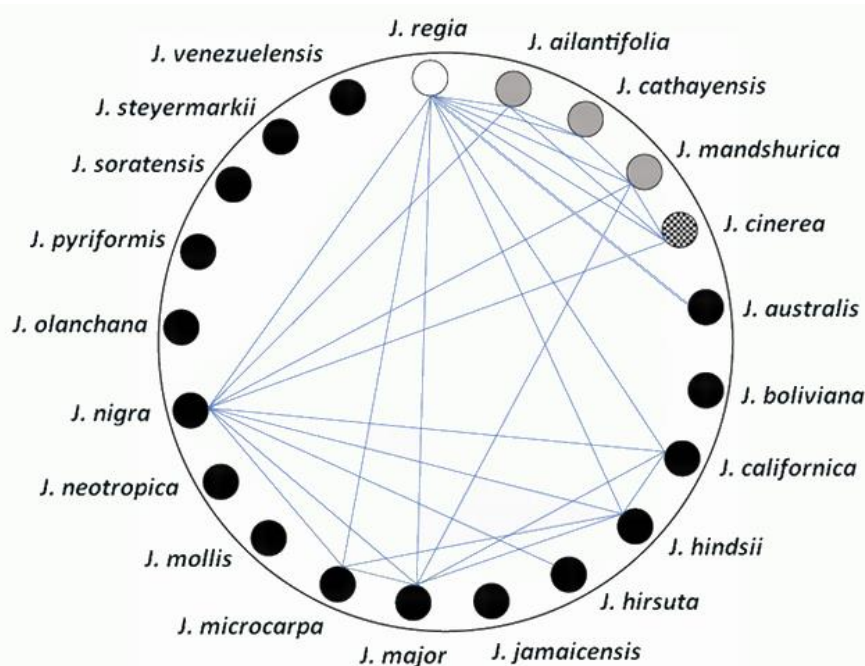


Fig. 1. Interspecific hybrids in *Juglans* genus [40, modified]

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

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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. silvestrosa* 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

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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***

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× *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

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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.

References

1. Badalov, P. P. (1983). The use of hybridization and apomixis methods to obtain promising walnut forms. *Lesnoe Khozyaystvo* [Forestry], 12, 24–25. (in Russian)
2. Badalov, P. P. (1987). Biologicheskie osnovy kultury orekhov roda *Juglans* v stepnoy chasti Ukrainy [Biological bases of the culture of walnut of the genus *Juglans* in the steppe part of Ukraine] (Extended Abstract of Doct. Agric. Sci. Diss.). Ukrainian Agr. Acad. Kyiv. (in Russian)
3. Badalov, P. P., & Badalov, K. P. (2010). The use of apomixis in the genera *Quercus* L. and *Juglans* L. to obtain genetically improved homozygous seed material. *Lisivnytstvo i Ahrolisomeliorsiya* [Forestry and Agroforestry], 117, 206–212. (in Russian)
4. Badalov, P. P., & Malytskyi, I. V. (1999). Some results of breeding of interspecific hybrids of *Juglans* L. on growth rate and fruit quality. *Lisivnytstvo i Ahrolisomeliorsiya* [Forestry and Agroforestry], 96, 63–65. (in Ukrainian)
5. Bai, W.-N., Wang, W.-T., & Zhang, D.-Y. (2016). Phylogeographic breaks within Asian butternuts indicate the existence of a phytogeographic divide in East Asia. *New Phytologist*, 209(4), 1757–1772. <https://doi.org/10.1111/nph.13711>
6. Balashov, P. K. (1982). Growth of hybrids between Persian walnut and Manchurian walnut. *Lesnoe Khozyaystvo* [Forestry], 3, 39–40. (in Russian)
7. Baumgartner, K., Fujiyoshi, P.T., Browne, G. T., Leslie, C., & Kluepfel, D. A. (2013). Evaluating paradox walnut rootstocks for resistance to *Armillaria* root disease. *HortScience*, 48(1), 68–72. <https://doi.org/10.21273/HORTSCI.48.1.68>
8. Bisset, P. (1914). The James River walnut. *Journal Heredity*, 5(3), 98–101.
9. Browne, G. T., Leslie, C. A., Grant, J. A., Bhat, R. G., Schmidt, L. S., Hackett, W. P. ... McGranahan, G. H. (2015). Resistance to species of phytophthora identified among clones of *Juglans microcarpa* × *J. regia*. *HortScience*, 50(8), 1136–1142. <https://doi.org/10.21273/HORTSCI.50.8.1136>
10. Browne, G., Schmidt, L., Hackett, W., Beede, B., Krueger, B., Prichard, T. ... Westerdahl B. (2007). Biology and management of phytophthora crown and root rot of walnut. *Walnut Research Reports*. California Walnut Board, 219–227.
11. Burbank, L. (1915). *His methods and discoveries and their practical application*. (Vol. 2). New York; London: Luther Burbank Press.
12. Carrière, E. A. (1865). *Juglans intermedia alata*. *Revue Horticole*, 37, 446–447.
13. Carrière, E.-A. (1870–71). *Juglans intermedia quadrangulata*. *Revue Horticole*, 42–43, 493–495.
14. Chevalier, A. (1941). Variabilité et hybridité chez les Noyers. Notes sur des *Juglans* peu connus, sur *l'Annamocarya* et un *Carya* d'Indochine. *Revue de botanique appliquée et d'agriculture coloniale*, 21(241–242), 477–509. DOI: 10.3406/jatba.1941.1646
15. Chodrishvili, I. I. (1976). *Gretskiy orekh v Gruzii* [Walnut in Georgia]. Tbilisi: Sabchota Sakartvelo. (in Russian)
16. Crane, H. L., Reed, C. A., & Wood, M. N. (1937). Nut breeding. *Yearbook of Agriculture*. USDA (pp. 827–883).
17. Dang, M., Yue, M., Zhang, M., Zhao, G., & Zhao, P. (2019). Gene introgression among closely related species in sympatric

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populations: a case study of three walnut (*Juglans*) species. *Forests*. 10(11), 965. doi:10.3390/f10110965

18. Fedoruk, A. T. (1990). Intraspecific variability of *Juglans* L. species cultivated in Belarus. *Rastitel'nye Resursy* [Plant Resources], 26(2), 151–160. (in Russian)

19. Forde, H. I. (1975). Walnuts. In J. Janick, J. N. Moore (Eds.) *Advances in Fruit Breeding*. (pp. 439–455). West Lafayette (IN): Purdue Univ. Press.

20. Germain, E. (Ed.). (2004). *Inventory of walnut research, germplasm and references*. ESCORENA. Rome. FAO Tech. Ser. 66. <http://www.fao.org/3/y5704e/y5704e00.htm>

21. Hu, H. H. (1932). Notulae systematicae ad Florem Sinensium. *Bulletin of the Fan Memorial Institute of Biology* 3, 162–173.

22. Jacques, [H. A.] (1833–34). *Juglans*. *Annales de Flore et de Pomone*, 2, 213–216.

23. Jay-Allemand, C., Dufour, J., & Germain, E. (1990). Screening of interspecific hybrid walnuts (*Juglans nigra* × *Juglans regia*) by means of morphological criteria. *Revue Horticole*, 311, P. 39–42.

24. Kalmykov, S. S. (1960). The method of distant hybridization in the breeding of nut crops. In *Otdalennaya hybridizatsiya rasteniy i zhivotnykh* [Distant hybridization of plants and animals] (pp. 127–139). Moscow: Izdatel'stvo AN SSSR. (in Russian)

25. Komanich, I. G. (1980). *Biologiya, kul'tura, selektsiya gretskogo orekha* [Biology, growing, and breeding of walnut]. Kishinev: Shtiintsa. (in Russian)

26. Komanich, I. G. (1989). *Otdalennaya gibridizatsiya vidov orekha (Juglans L.)*. [Distant hybridization of walnut species (*Juglans* L.)] Kishinev: Shtiintsa. (in Russian)

27. Kondratenko, E. N. (1957). Fast growing and winter hardy hybrid (*Juglans mandshurica* × *J. regia*). *Zap. Kharkov. Selskokhoz. Instituta* [Bulletin of Kharkiv Agricultural Institute], 16, 223–227. (in Russian)

28. Krotkevich, P. G. (1954). Fruiting natural hybrids of walnuts. *Lesnoe Khozyaystvo* [Forestry], 11, 66–68. (in Russian)

29. Krotkevich, P. H. (1950). Natural hybrids of walnuts. *Dopovidi AN URSS*

[Reports of the Academy of Sciences of the Ukrainian SSR], 6, 473–482. (in Ukrainian)

30. Kryvobokova, N. Ya. (2001). *Selektsiia a vykorystannia horikha voloskoho v Pivdennomu stepu Ukrainy* [Breeding and use of walnut in the Southern steppe of Ukraine] (Extended Abstract of Cand. Agric. Sci. Diss.). Ukrainian Research Institute of Forestry and Forest Melioration named after G. M. Vysotsky. Kharkiv. (in Ukrainian)

31. Kushnir, A. I. (1987). *Biologo-ekologicheskie svoystva otdalennykh gibridov orekhov* [Biological and ecological properties of distant walnut hybrids] (Extended Abstract of Cand. Biol. Sci. Diss.). Central Republic Botanical Garden. Kyiv (in Russian)

32. Lebedev, G. I. (1953). *Akklimatizatsiya drevesnykh i kustarnikovykh porod* [Acclimatization of tree and shrub species]. Moscow: Izdatel'stvo Ministerstva kommunalnogo khozyaystva RSFSR. (in Russian)

33. Luo, X., & Chen, J. (2020). Distinguishing Sichuan Walnut cultivars and examining their relationships with *Juglans regia* and *J. sigillata* by FISH, early-fruited gene analysis, and SSR analysis. *Frontiers in Plant Science*, 11, 27. doi: 10.3389/fpls.2020.00027

34. Makhmet, B. M. (1975). Inheritance of the properties and traits of distant nut hybrids by their offspring. *Lesovodstvo i Agrolesomeliatsiya* [Forestry and Agroforestry], 42, 95–100. (in Russian)

35. Makhmet, B. M. (1982). The results of hybridization of walnuts in the arboretum of the Ukrainian Agricultural Academy. *Lesnoy Zhurnal* [Forest Journal], 4, 124–126. (in Russian)

36. Malvolti, M. E., Spada, M., Beritognolo, I., & Cannata, F. (1997). Differentiation of walnut hybrids (*Juglans nigra* L. × *Juglans regia* L.) through RAPD markers. *Acta Horticulturae*, 442, 43–52.

37. Marrano, A., Britton, M., Zaini, P. A., Zimin, A. V., Workman, R. E., Puiu, D. ... Neale, D. B. (2020). High-quality chromosome-scale assembly of the walnut (*Juglans regia* L.) reference genome. *GigaScience*, 9, 1–16. doi: 10.1093/gigascience/giaa050

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38. McGranahan G., & Leslie C. (2012). Walnuts. In M. L. Badenes, & D. H. Byrne (Eds.). *Fruit Breeding*. New York: Springer Science + Business Media.
39. Mettendorf, B. von. (2008). Anbau von *Juglans*-Hybriden. *AFZ-Der Wald*, 16, 858–861.
40. Mezhenskyj, V. M. (2020). *Voloskyi horikh (Juglans regia L.)* [Walnut (*Juglans regia* L.)]. Kyiv: Lira-K. (in Ukrainian)
41. Michurin, I. V. (1948). *Sochinenia* [Works]. (Vol. 4.). Moscow: OGIZ; Gosselkhozizdat. (in Russian)
42. Nilolaev, E. A., & Slavskiy V. A. (2010). Interspecific hybridization as a method for breeding walnuts of the genus *Juglans* in the Central Black Earth Region. *Vest. Voronezh. Gos. Univer. Ser. Geograf. Geoekol.* [Annals Voronezh State University. Ser. Geography. Geoecology], 2, 132–134. (in Russian)
43. Ozol, A. M., & Khorkov, E. I. (1958). *Gretskiy orekh* [Walnut]. Riga: Izdatel'stvo AN LatSSR (in Russian)
44. Pollegioni, P., Olimpieri, I., Woeste, K. E., De Simoni, G., Gras, M., & Malvolti, M. E. (2012). Barriers to interspecific hybridization between *Juglans nigra* L. and *J. regia* L. species. *Tree Genetics & Genomes*, 9, 291–305. DOI 10.1007/s11295-012-0555-y
45. Potter, D., Gao, F. Y., Baggett, S., McKenna, J. R., & McGranahan, G. H. (2002). Defining the sources of Paradox: DNA sequence markers for North American (*Juglans* L.) species and hybrids. *Scientia Horticulturae*, 94, 157–170. [https://doi.org/10.1016/S0304-4238\(01\)00358-2](https://doi.org/10.1016/S0304-4238(01)00358-2)
46. Rehder, A. (1900). *Juglans*. In Bailey, L. H. *Cyclopedia of American horticulture*. (Vol. 2, pp. 845–847). London: MacMillan & Co.
47. Rehder, A. (1924). New species, varieties and combinations from herbarium and the collections of the Arnold Arboretum. *Journal Arnold Arboretum*, 5(4), 235–242.
48. Rehder, A. (1940). *Manual of cultivated trees and shrubs hardy in North America*. New York: Macmillan.
49. Rovskiy, V. M. (1951). Breeding of forest species in Uzbekistan. *Tr. Inst. lesa AN SSR* [Scientific papers of the Forest Institute of the Academy of Sciences of the USSR], 8, 132–151. (in Russian)
50. Rusanov, F. N. (1973). Species of the genus *Juglans* L., introduced by the Botanical Garden of the Academy of Sciences of the Uzbek SSR in Tashkent. *Dendrologia Uzbekistana. Klenovye, orekhovye, ivivye, berezovye* [Dendrology of Uzbekistan. Maple family, walnut family, willow family, and birch family] (Vol. 5, pp. 158–178). Tashkent: Fan (in Russian)
51. Shamsiev, K. S. Walnut hybridization for frost resistance and fruit quality. In G. P. Ozolin (Ed.) *Orekhoplodnye v Uzbekistane* [Nuts in Uzbekistan] (pp. 33–41). Tashkent: Mekhnat. (in Russian)
52. Shchepotiev, F. L. (1960) Distant hybridization between *Juglans* species in Ukraine. In *Otdalennaya hybridizatsiya rasteniy i zhivotnykh* [Distant hybridization of plants and animals] (pp. 140–154). Moscow: Izdatel'stvo AN SSSR. (in Russian)
53. Shchepotiev, F. L. (1964). Breeding walnuts for winter hardiness and high quality of fruits in Ukraine. In *Selektsiya, introduktsiya i semenovodstvo drevesnykh lesnykh porod* [Breeding, Introduction, and Seed Production of Woody Forest Species] (pp. 24–34). Kyiv: Urozhai (in Russian)
54. Shchepotiev, F. L. (1985). Walnut. In Shchepotiev, F. L., Rikhter, A. A., Pavlenko, F. A., Molotkov, P. I., Kravtchenko, V. I., & Iroshnikov, A. I. *Orekhoplodovye i sadovye kultury* [Forest and Horticultural Nut Crops] (pp. 4–82). Moscow: Lesnaya promyshlennost'. (in Russian)
55. Shevchenko, V. S. (1966). Walnut breeding. *Tr. Yuzhno-Kirgiz. lesoplod. opyt. st.* [Scientific papers of South-Kyrgyz Forrest and Fruit Experimental Station], 1, 51–54. (in Russian)
56. Vekhov, N. K. (1934). On the biology of species of the genus *Juglans*. In *Orekh: biologiya, kul'tura i khozyaystvo* [Walnuts: biology, growing, and economy], 3, 5–152. (in Russian)
57. Vekhov, N. K. (1953). *Derev'ya i kustarniki Lesostepnoy selektsionnoy opytной stantsii* [Trees and shrubs of Forest-steppe breeding experimental station]. Moscow: Izdatel'stvo Ministerstva kommunalnogo khozyaystva RSFSR. (in Russian)
58. Veresin, M. M., & Ulyukina, M. K. (1970). Walnut breeding for winter resistance

Меженський В. М.

by selection and hybridization. In *Lesnaya Genetika, Seleksiya i Semenovodstvo* [Forest Genetic, Breeding, and Seed Production] (pp. 365–369). Petrozavodsk. (in Russian)

59. Vilmorin, M. L. de. (1891). *Juglans Vilmoriniana*. *Garden and Forest*, 4(154), 51–52.

60. Wang, H., Zhao, S., Zhang, Z., Gao, Y., Zhao, Y., Fang, J., & He, F. (2010). Genetic relationship and diversity of eight *Juglans* species in China estimated through AFLP analysis. *Acta Horticulturae*, 861, 143–150. <https://doi.org/10.17660/ActaHortic.2010.861.18>

61. Wu, Y., Pei, D., Xi, S., & Li, R. (2000). Study on the genetic relationships among species of walnut by using RAPD. *Acta Phytotaxonomica Sinica*, 27, 17–22.

62. Xu, Y., Zhang, M.Y., & Gao, L. (2007). The research of interspecific hybridization in genus *Juglans*. *Deciduous Fruits*, 32, 6–8.

63. Yablokov, A. S. (1936). Breeding walnuts for fast growth and winter hardiness. *Tr. Moskov. NII lesn. khozyaystva* [Scientific papers of Moscow Research Institute of Forestry], 2, 7–42. (in Russian)

64. Yablokov, A. S. (1953). *Akklimatizatsiya derev`ev i kustarnikov metodom otdalennoy polovoy gybridizatsii* [Acclimatization of trees and shrubs by the method of distant sexual hybridization]. Moscow: Znanie (in Russian)

65. Yermolenko, A. P. (1936). Hybridization in the genus *Juglans* L. *Zb. robıt po seleksii i fiziologii derevnykh porid. Ukr NDILHA* [Collection of Works on Breeding and Physiology of Wood Species. Ukrainian Research Institute of Forestry and Forest Melioration], 17, 47–57. (in Ukrainian)

66. Yuan, X.-Y., Sun, Y.-W., Bai, X.-R., Dang, M., Feng, X.-J., Zulfiqar, S., & Zhao, P.

(2018). Population structure, genetic diversity, and gene introgression of two closely related walnuts (*Juglans regia* and *J. sigillata*) in Southwestern China revealed by EST-SSR markers. *Forests*, 9(10), 646. DOI: 10.3390/f9100646

67. Zarubin, A. F. (1951). About breeding of late flowering walnut. *Tr. Inst. lesa AN SSSR* [Scientific papers of the Forest Institute of the Academy of Sciences of the USSR], 8, 125–127. (in Russian)

68. Zhang, B.-W., Xu, L.-L., Nan, L., Yan, P.-C., Jiang, X.-H., Woeste, K. E. ... Bai, W.-N. (2019). Phylogenomics reveals an ancient hybrid origin of the Persian walnut. *Molecular Biology and Evolution*, 36(11), 2451–2461. doi:10.1093/molbev/msz112

69. Zhao, P., & Woeste, K. E. (2010). DNA markers identify hybrids between butternut (*Juglans cinerea* L.), and Japanese walnut (*Juglans ailantifolia* Carr.). *Tree Genetics & Genomes*, 7(3), 511–533. DOI: 10.1007/s11295-010-0352-4

70. Zhao, P., Zhou, H. J., Potter, D., Hu, Y. H., Feng, X. J., Dang, M., Feng, L. ... Woeste, K. (2018). Population genetics, phylogenomics and hybrid speciation of *Juglans* in China determined from whole chloroplast genomes, transcriptomes, and genotyping-by-sequencing (GBS). *Molecular Phylogenetics and Evolution*, 126, 250–265. <https://doi.org/10.1016/j.ympev.2018.04.014>

71. Zhu, T., Wang, L., You, F. M., Rodriguez, J. C., Deal, K. R., Chen, L. ... Luo, M.-C. (2019). Sequencing a *Juglans regia* × *J. microcarpa* hybrid yields high-quality genome assemblies of parental species. *Horticulture Research*, 6, 55. <https://doi.org/10.1038/s41438-019-0139-1>

72. Zhuravskaya, E. I. (1958). Hybrid walnut in Dubliany village. *Lesnoe Khozyaystvo* [Forestry], 9, 75–76. (in Russian)

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.

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Анотація. Грецький 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 плодовых 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 обнаруженные 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*