DOI: https://doi.org/10.17816/ecogen109142
Review Article

Phylogeny problems of the genus *Vaccinium* L. and ways to solve them

Roman R. Zhidkin, Tatiana V. Matveeva
Saint Petersburg State University, Saint Petersburg, Russia

The genus *Vaccinium* includes almost 500 species, among which there are economically important species of cranberries *V. macrocarpon* Ait. and *V. oxycoccos* L., lingonberries *V. vitis-idaea* L., bilberries *V. myrtillus* L. and blueberries *V. uliginosum* L., *V. angustifolium* Ait., *V. corymbosum* L., *V. virgatum* Ait. Despite the fact that many of these species were actively used by humans in medicine and food, their active selection began in the 20th century, in connection with which a classification of the genus according to morphological characters was developed. Many of these data remain relevant to the present day. The development of the ideas of molecular phylogeny prompted a revision of the old classification, identifying a number of difficulties that do not allow one to unambiguously determine phylogenetic relationships within the genus. Today, the genus includes 33 sections, while the species composition of the sections and the evolutionary relationships between them remain controversial. This review discusses various approaches to the study of the structure of the genus *Vaccinium*: from classical to phylogenomic, the main results of using these approaches and their prospects.

Keywords: *Vaccinium*; phylogeny; DNA barcoding; DNA fingerprinting; phylogenomics.

To cite this article:
Zhidkin RR, Matveeva TV. Phylogeny problems of the genus *Vaccinium* L. and ways to solve them. *Ecological genetics*. 2022;20(2):151–164. DOI: https://doi.org/10.17816/ecogen109142

Received: 01.07.2022 **Accepted:** 16.07.2022 **Published:** 02.09.2022

DOI: https://doi.org/10.17816/ecogen109142
Обзорная статья

Проблемы филогении рода *Vaccinium* L. и пути их решения

Р.Р. Жидкин, Т.В. Матвеева
Санкт-Петербургский государственный университет, Санкт-Петербург, Россия

Род *Vaccinium* L. включает почти 500 видов, среди которых экономически важные виды клюквы *V. macrocarpon* Ait. и *V. oxycoccos* L., брусники *V. vitis-idaea* L., черники *V. myrtillus* L. и голубики *V. uliginosum* L., *V. angustifolium* Ait., *V. corymbosum* L., *V. virgatum* Ait. Несмотря на то что многие из этих видов человек уже использовал в пищевых и медицинских целях, их активная селекция началась только в XX в., соответственно, возникла потребность в филогенетических и таксономических исследованиях рода, которые изначально базировались на анализе морфологических признаков. Многие из этих данных сохранили актуальность до настоящего времени. Развитие идей молекулярной филогении побудило пересмотреть старую классификацию, обозначив ряд сложностей, которые не позволяют однозначно определить филогенетические отношения в пределах рода. Сегодня система рода включает в себя 33 секции, при этом видовой состав секций и эволюционные отношения между ними остаются спорными. В данном обзоре обсуждаются различные подходы к изучению структуры рода *Vaccinium*: от классических до филогеномных, основные результаты использования этих подходов и их перспективы.

Ключевые слова: *Vaccinium*; филогения; ДНК-штрихкодирование; ДНК-фингерпринтинг; филогеномика.

Как цитировать:
Жидкин Р.Р., Матвеева Т.В. Проблемы филогении рода *Vaccinium* L. и пути их решения // Экологическая генетика. 2022. Т. 20. № 2. С. 151–164. DOI: https://doi.org/10.17816/ecogen109142

Рукопись получена: 01.07.2022 **Рукопись одобрена:** 16.07.2022 **Опубликована:** 02.09.2022

BACKGROUND

Vaccinium L. is an economically important genus belonging to the family *Ericaceae* Juss., tribe *Vaccinieae* Rchb. [1]. The tribe *Vaccinieae* is a taxon including a large number (~1000) of woody plant species of the family *Ericaceae*, different in morphological traits, and common in temperate and tropical zones of all continents except Australia and Antarctica [2]. Most of the species occur in the tropics, mainly in the mountain rain forests.

This tribe includes the genera *Agapetes* G.Don, *Anthopteropsis* A.C. Sm., *Anthopterus* Hook., *Calopteryx* Ruiz & Pav., *Cavendishia* Lindl., *Ceratostema* Juss., *Costera* J.J. Sm., *Demosthenesia* A.C. Sm., *Didonica* Luteyn & Wilbur, *Dimorphanthera* (Drude) F. Muell., *Diogenesia* Sleumer, *Disterigma* (Klotzsch) Nied., *Gaylussacia* Kunth, *Gonocalyx* Planch. & Linden, *Lateros-pora* A.C. Smith, *Macleania* Hook., *Mycerinus* A.C. Sm., *Notopora* Hook.f., *Oreanthes* Benth., *Orthaea* Klotzsch, *Paphia* Schltr., *Pellegrinia* Sleumer, *Periclesia* A.C. Sm., *Plutarchia* A.C. Sm., *Polyclita* A.C. Sm., *Psammisia* Klotzsch, *Rusbya* Britton, *Satyria* Klotzsch, *Semiramisia* Klotzsch, *Siphonandra* Klotzsch, *Sphyrospermum* Poepp. & Endl., *Symphysia* (Vahl) Wilbur & Luteyn, *Themistoclesia* Klotzsch, *Thibaudia* Ruiz & Pav., *and Utleya* Wilbur & Luteyn [3].

The genus *Vaccinium* includes approximately 500 species growing on all continents except Australia and Antarctica [4]. Most species occur in the tropics on open mountain slopes and the rest are distributed in subtropical, temperate, and boreal regions of the northern hemisphere [5]. Slightly less than two-thirds of the species are occur in south-east Asia, more than 50 species in America, and the rest are dispersed throughout the world [6].

Many species in the genus *Vaccinium* have colorful leaves, flowers, and fruits, making them valuable ornamental plants [7]. Some species have edible fruits, which are used as medicine in various communities [8]. Cranberries, blueberries, and lingonberries are among the most studied of these species, having been domesticated in the XIX and XX centuries [9, 10]. Currently, 42,746 hectares of land are used for growing cranberries, 126,144 hectares for blueberries, and 29 hectares for lingonberries [11].

Blueberries and a number of other species in the genus *Vaccinium* also have a great potential as new crops. The most economically important *Vaccinium* species belong to the sections *Cyanococcus* A. Gray, *Oxycoccus* (Hill) Koch, *Vitis-Idaea* (Moench) Koch, *Myrtillus* Dumortier, and *Vaccinium* L. [12].

The berries of these crops contain an average content of vitamin C, fiber and basic microelements, four organic acids, namely cinchona, citric, hydroxysuccinic, and benzoic acids [7]. A high content of flavonoids, mainly anthocyanins, imparts the fruits with a bright color [13]. The presence of these compounds accounts for the antioxidant, antimutagenic, and antitumor activity of berries in the geneus *Vaccinium*. As anthocyanins are the main consumed antioxidants in the Western diet, their content is one of the key indicators of the quality of berries and an important selection trait [14, 15].

Currently, there is a growing increase in the demand for berries of domesticated *Vaccinium* species, which necessitates the breeding of new crops [12]. When breeding for new crops, it is important to determine the phylogenetic relationships between representatives of the genus and their closest relatives; however, such studies on the genus *Vaccinium* are retarded by challenges arising from the peculiarities of speciation within this genus.

HISTORY OF THE TAXONOMY OF THE GENUS *VACCINIUM*

The genus *Vaccinium* was first described by Carl Linnaeus in 1753. It included the species *V. frondosum* L., *V. album* L., *V. stamineum* L., *V. uliginosum* L., *V. vitisidaea* L., *V. oxycoccos* L., *V. myrtillus* L., *V. corymbosum* L., *V. arctostaphylos* L., *V. hispidulum* L., *V. ligustrinum* L., *and V. mucronatum* L. [16]. No major systematic analysis of the described new species was performed until the beginning of the XX century when active breeding work for cranberries and blueberries began in the USA [10, 17]. Therefore, the first work in their taxonomy was of an applied nature and mainly concerned species distributed in North America. The main difficulties in such studies became apparent, namely the absence of fertility barriers in morphologically different organisms, which leads to the formation of several hybrids, and the occurrence of both autopolyploidy and allopolyploidy throughout the genus [17]. For example, *V. myrsinites* Lam. is an allopolyploid species resulting from the hybridization of *V. tenellum* Ait. and *V. darrow* Camp species [18].

Camp was among the first to present work on the genus *Vaccinium* in 1945 [18]. He classified the genus according to morphological features. However, this work was confined to species growing in the northern hemisphere, with special attention to North American blueberries. Therefore, the genus was divided into several sections, with 9 diploid, 12 tetraploid, and 3 hexaploid species included in the North American blueberry section *Cyanococcus* [9]. During World War II, field work was limited. The incompleteness of field data, resulted in errors in classification, leading to some organisms being designated as separate species, which later turned out to be hybrids or polyploids [19]. To resolve this problem, several species were combined into one with different levels of ploidy, and in the new classification, Kloet retained the previous division into sections [6],

and the *Cyanococcus* section included 6 diploid, 5 tetraploid, and 1 hexaploid blueberry species [9]. This reduction in the number of species was due to the inclusion of all crown-forming species of North American blueberries into one species, *V. corymbosum*, with three levels of ploidy.

Thus, the differentiation of *Vaccinium* species is complicated by polyploidy, similar morphology, and introgression during hybridization [9]. Therefore, the use of morphological characteristics in phylogenetic studies of this genus does not always enable us to assess unambiguously the evolutionary relationships between the studied species, which necessitates use of modern methods of phylogeny.

MODERN PHYLOGENETIC METHODS

The development of molecular genetics and biochemical studies has brought new approaches to phylogenetic studies. In the mid-to-late XX century, molecular labeling began to develop rapidly, and at the turn of the century, the Barcode of Life project was launched [20]. The main thrust of the Barcode of Life was to combine the efforts of classical and molecular biologists to improve taxonomy and phylogeny. It involves selecting taxonomically significant DNA sequences and entering them into databases together with taxonomic information, which enables creation of a system of molecular identification of organisms, including plants.

Despite progress in the approach, markers for DNA barcoding have certain disadvantages. Based on Matveeva et al. [20], we compiled the characteristics of the main markers used in DNA barcoding of plants (Table 1).

Table 1 shows that traditional markers used for DNA barcoding in plants can be conventionally divided into nuclear and cytoplasmic ones. Cytoplasmic markers are usually maternally inherited. Nuclear markers, such as ITS, are multicopy, but in species of hybrid origin, the proportion of sequences of the ribosomal gene cluster inherited from one of the parents can be reduced to such an extent that ITSs of this parent are not detected using traditional DNA barcoding protocols [21]. The features of these markers can lead to ambiguities in the reconstruction of phylogenetic relationships, which results in trees of the same species with slightly different topologies. To solve this problem, multilocus analysis methods are used, which use information on several marker sequences.

Since the development of these algorithms, sequencing methods have developed significantly. Thus, the Next-Generation Sequencing algorithms developed in the 2000s enabled simplification and reduction of the cost of whole-genome projects, resulting in the generation of unprecedented amounts of data on the sequences of both model and non-model organisms. Open access to these data gave rise to a new approach, phylogenomics, which determines the phylogenetic relationships of species based on the analysis of their genomes [22]. Phylogenomic methods are based on whole-genome sequences or on the traits of the entire genome [23].

Methods based on nucleotide sequence information from genomes require alignment of orthologous genes from which a phylogenetic tree is derived using two alternative approaches, namely the supermatrix approach, which is based on combining all genomic regions into a single matrix that includes all taxa, then such a combined dataset is subjected to phylogenetic inference using the desired phylogenetic method (distance, maximum likelihood, maximum parsimony, Bayesian approach) [24], and the supertrees approach (or a tree of trees), which involves combining trees obtained based on the analysis of individual genes [23].

Methods based on whole-genome traits involve the reconstruction of phylogenetic relationships not by nucleotide sequences, but by the presence of genes (gene repertoire) or by the order of genes [23]. In the first case, the presence, absence, or duplication of genes constitutes the phylogenomic data, whereas in the second case, large-scale karyotypic changes in the genome constitute the phylogenomic data [24]. These methods are associated with rare genomic changes that are less prone to homoplasia and therefore more informative than methods based on the analysis of nucleotide sequences.

These methods include the obligatory stage of assembly and annotation of the genome, as well as the search for orthologous sequences, which is complicated when dealing with non-model organisms. To simplify this analysis, the assembly and alignment-free (AAF) method was developed [25]. This method allows phylogeny to be determined directly from unassembled genome sequence reads, making phylogenomic analysis available when dealing with species without an appropriate reference genome or large sequence coverage.

Apart from DNA marking, chemosystematics, an interdisciplinary field that uses information about the chemical composition of plants to determine interspecific and intraspecific phylogenetic relationships, has begun to develop in recent years [26]. The occurrence of chemical compounds and their structures are often taxonomically specific, so they can be used as markers for distinguishing between taxa [27]. As such, both primary and secondary metabolites can be used in plants. However, the same compounds are often formed during completely different biosynthetic pathways in unrelated plants; therefore, such methods can be useful in determining the boundaries of lower taxonomic ranks [28].

To date, various methods have been developed that allow reconstructing phylogenetic relationships without using morphological traits. Phylogenetic markers have advantages such as presence in a wide range of plant

Table 1. Characterization of the main markers for DNA barcoding of plants

Таблица 1. Характеристика основных маркеров для ДНК-штрихкодирования растений

Marker	General characteristics	Advantages	Disadvantages
matK	Plastid gene encoding maturase K	Rapidly evolving genes pre-served in non-chlorophyllic plants	Primers are not universal enough
rbcL	Plastid gene encoding the large rubisco subunit	Described well in various plant groups, which increases its versatility	Insufficient resolution, therefore it cannot be used independently
rpoB and rpoC1	Plastid genes coding for RNA polymerase subunits	Highly conserved sequences providing primer versatility	Low resolution
psbK-psbI	Intergenic spacer between plastid genes, encoding polypeptides K and I, which are part of photosystem II	Slightly inferior to matK in resolution, versatility, and sequence quality	Insufficient versatility of primers in relation to gymnosperms
trnH-psbA	Intergenic spacer between plastid genes, encoding histidine tRNA and D1 protein of photosystem II	Highly variable, while selected primers provide universality for many plant species	Lack of sequence in non-chlorophyllic plants, poor reading quality, and variability in length in different species
atpF-atpH	Spacer between plastid genes, encoding ATP synthase subunits	Highly variable, universal in angiosperms	Lack of consistency in non-chlorophyllic plants, lack of universality, and variable in length
ITS (Internal Transcribed Spacer)	A nuclear sequence was represented by an internal transcribed spacer in a cluster of ribosomal genes	Present in all living organisms, conservatism of rRNA genes provides universality of primers, high copy number, relative conservatism in length, and biparental inheritance	Present in the genome in the form of many copies, which makes intraspecific or intraorganismal polymorphism possible, has a high level of homoplasia
Fingerprinting (RFLP, AFLP, RAPD, SSR, ISSR etc.)	Markers based on the use of polymerase chain reaction, restriction, or both methods together to obtain a specific pattern of DNA fragments that characterize genetic differences between samples. The resulting patterns can be converted into a binary matrix for the reconstruction of phylogenetic relationships.	They can be used as markers auxiliary to DNA barcodes for a more detailed description of phylogeny, more often for intraspecific polymorphism	

species, low search, and sequencing costs, and disadvantages such as different rates of divergence and ambiguity of interpretation in taxa of hybrid origin. Despite their disadvantages, phylogenetic markers enable determination of phylogenetic relationships between different taxa when used together.

APPLICATION OF MODERN METHODS IN PHYLOGENETIC STUDIES OF THE GENUS *VACCINIUM*

The methods described above, such as DNA barcoding, fingerprinting, phylogenomics, and chemosystematics, began to be used in the study of the genus *Vaccinium*, allowing revision of its taxonomy proposed by Kloet. In the first such work, the matK and ITS markers were used to determine the phylogenetic relationships of various representatives of the entire tribe *Vaccinieae* [2]. Based on the data of K. Kron et al. [2] supplemented with new sequences from NCBI (www.ncbi.nlm.nih.gov), we reconstructed the phylogeny of the genus (Fig. 1). The resulting dendrograms and those of Kron et al. [2] did not confirm the traditional genus boundaries, but several well-supported clades were found on the tree, namely Andean; Mesoamerican/Caribbea, East Malaysian; *Agapetes*, consisting of some Asiatic *Vaccinium* and *Agapetes*; *Bracteata-Oarianthe*, including representatives of the respective sections; *Orthaea/Notopora*, which includes the genera *Orthaea* and *Notopora; Myrtillus* and *Vaccinium*, including some *Vaccinium*. Moreover, most of the recovered clades in their composition-united representatives of various genera, whereas the clades *Vaccinium* and

Myrtillus included species of the genus *Vaccinium*, which had been assigned to different sections in the previous classifications. Based on these results, Kron et al. concluded that it is necessary to reassess the taxonomy of the genus *Vaccinium* as the genus is not monophyletic. Although the work on this reassessment started in 2003 [29], many researchers have reported radical differences from the theoretical genus structure, which could be due to the difficult interpretation of the results of phylogenetic analysis obtained based on the classical markers, such as ITS and matK, in species in which evolution, the processes of hybridization and polyploidization played a significant role [30].

To date, due to the lack of a well-resolved molecular phylogeny of the entire genus, the well-founded phenotypic classification of the genus proposed by Kloet [31] is a priori accepted in the studies. Thus, the modern classification assumes the division of the genus *Vaccinium* into two subgenera and includes 33 sections. Using GRIN data, we described the species mentioned in this review, taking into account their taxonomic position and geographical distribution [3] (Table 2).

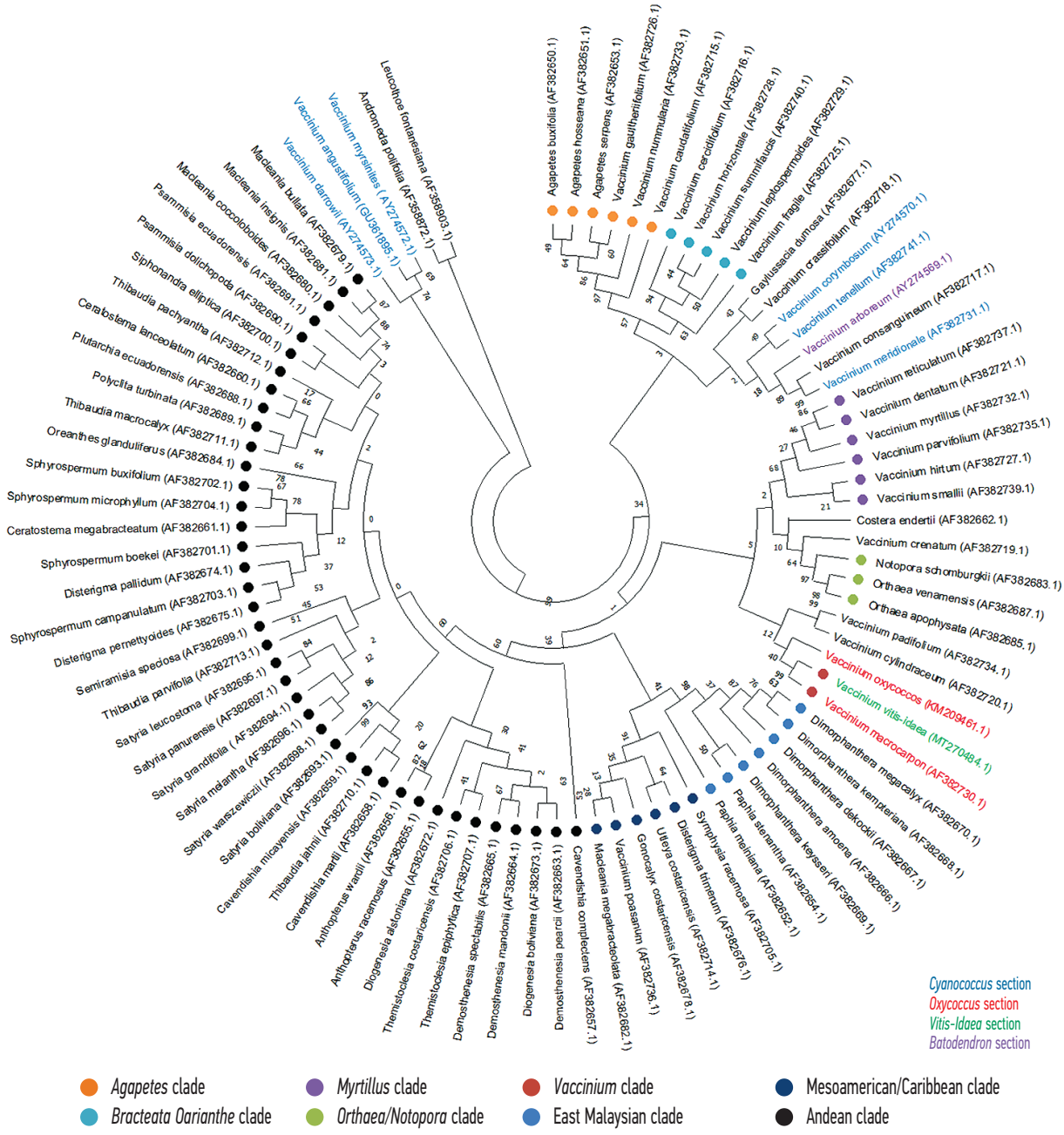

Fig. 1. The phylogenetic tree obtained from the analysis of the matK and ITS sequences of various species of the *Ericaceae* family based on the data of K. Kron et al. [2], supplemented by us

Рис. 1. Филогенетическое дерево, полученное при анализе последовательностей matK и ITS различных видов семейства *Ericaceae* на основе данных K. Kron и соавт. [2], дополненных нами. Эволюционная история была выведена с использованием метода максимального правдоподобия и модели General Time Reversible [33]. Эволюционные анализы проводили в MEGA X [34]

As the use of DNA barcoding does not allow unambiguous reconstruction of the phylogeny of the genus *Vaccinium*, more time-consuming and expensive methods of molecular phylogenetics are used in genetic studies of economically significant species. In particular, the genomic and transcriptome resources of the American cranberry (*V. macrocarpon*) were used in the development of nuclear [31], chloroplast, and mitochondrial SSR markers [32] for the analysis of genetic diversity and genetic mapping within a species. The dendrogram plotted on their basis distributed species into genera and sections within *Vaccinium* in a manner similar to the morphological classification. Figure 2 presents the phylogenetic relationships determined by Schlautman et al. [32] based on cytoplasmic SSR markers between species, which were previously investigated using ITS and matK markers. In fact, the analysis performed became a kind of approximation to multilocus analysis since the markers used were relatively evenly distributed throughout the genome and plasmon.

Phylogenetic analysis using SSR markers identified the genus *Vaccinium* as monophyletic [32], and also showed the monophyly of the sections *Cyanococcus, Oxycoccus, Vitis-idaea*, whereas data based on DNA

Table 2. Brief description of some *Vaccinium* species
Таблица 2. Краткое описание некоторых видов *Vaccinium*

Subgenera	Section	Representative	Habitat
Oxycoccus (Hill) A. Gray	*Oxycoccoides* (Hooker f.) Sleumer	*V. japonicum* Miq.	East Asia
	Oxycoccus (Hill) Koch	*V. macrocarpon* Ait.	North America
		V. microcarpum Schmalh., *V. oxycoccos* L.	Circumboreal zone
Vaccinium L.	*Aethopus* Airy Shaw	*V. paucicrenatum* Sleumer	Southeast Asia
	Baccula-Nigra Kloet.	*V. fragile* Franch.	East Asia
	Barandanum Kloet.	*V. barandanum* S. Vidal	Southeast Asia
	Batodendron (Nuttall) A. Gray	*V. arboreum* Marshall	North America
	Brachyceratium Kloet.	*V. dependens* (G. Don) Sleumer	South America
	Bracteata J.J. Smith	*V. alvarezii* Merr., *V. cercidifolium* J.J. Smith, *V. horizontale* Sleumer, *V. summifaucis* Sleumer	Southeast Asia
	Cinctosandra (Klotzsch) Hook.f.	*V. africanum* Britton	Africa
	Conchophyllum Sleumer	*V. conchophyllum* Rehder, *V. emarginatum* Hayata, *V. nummularia* Hook. f. et Thoms	East Asia
	Cyanococcus A. Gray	*V. angustifolium* Ait., *V. constablaei* A. Gray, *V. corymbosum* L., *V. darrowii* Camp, *V. elliottii* Chapm., *V. fuscatum* Ait, *V. meridionale* Sw., *V. myrsinites* Lam., *V. myrtilloides* Michx., *V. pallidum* Ait., *V. tenellum* Ait., *V. virgatum* Ait.	North America
	Eococcus Sleumer	*V. meridionale* Sw.	North of South America
	Epigynium (Klotzsch) Hooker f.	*V. vacciniaceum* (Roxb.) Sleumer	Southeast Asia
	Euepigynium Kloet.	*V. carneolum* Sleumer	New Guinea
	Galeopetalum J.J. Smith	*V. caudatifolium* Hayata, *V. gaultheriifolium* (Griff.) Hook. f.	East Asia

Table 2 (continued) / Продолжение таблицы 2

Subgenera	Section	Representative	Habitat
Vaccinium L.	*Hemimyrtillus* Sleumer	*V. hirtum* Thunb., *V. smallii* A. Gray	East Asia
		V. arctostaphylos L.	Bulgaria, Iran, Northern Caucasus, South Caucasus, Turkey
		V. cylindraceum Smith	Azores
		V. padifolium J.E. Sm. ex A.Rees	Madeira
	Herpothamnus (Small) Sleumer	*V. crassifolium* Andrews	North America
	Macropelma (Klotzsch) Hook. f.	*V. dentatum* Smith, *V. reticulatum* Smith	Hawaii
	Myrtillus Dumortier	*V. ovalifolium* Sm.	North America and East Asia
		V. myrtillus L.	Circumboreal zone
		V. parvifolium Smith	North America
		V. calycinum Smith	Hawaii
	Neojunghuhnia Koord.	*V. insigne* (Koorders) J.J. Sm.	New Guinea
	Nesococcus Copel.	*V. philippinense* Warb. (Luzon).	Philippines
	Neurodesia (Klotzsch) Hook. f.	*V. crenatum* (Dunal) Sleumer	South America
	Oarianthe Schltr	*V. finisterrae* Schltr., *V. leptospermoides* J.J. Smith	New Guinea
	Oreades Sleumer	*V. poasanum* J.D. Smith	Central America
	Polycodium (Rafinesque) Rehder	*V. stamineum* L.	North America
	Praestantia Nakai.	*V. praestans* Lamb.	East Asia
	Pseudocephalanthos C.Y.Wu & R.C.Fang.	*V. lanigerum* Sleumer	East Asia
	Pyxothamnus Sleumer	*V. consanguineum* Klotzsch, *V. floribundum* Kunth	Central and South America
		V. ovatum Pursh	North America
	Rigiolepis (Hook.f.) Sleumer	*V. acuminatissimum* Miq.	Southeast Asia
	Vaccinium L.	*V. vulcanorum* Kom.	Far East
		V. gaultherioides Bigelow, *V. uliginosum* L.	Circumboreal zone
	Vitis-idaea (Moench) Koch	*V. vitis-idaea* L.	Circumboreal zone
		V. minusculum Sleumer	New Guinea

barcoding revealed polyphyly of the genus, but defined the tribe *Vaccinieae* as monophyletic [2], with members of different genera clustered according to their geographical origin. For example, the Andean clade includes representatives of 17 genera, which diversity is concentrated in the region of the northern Andes, or the Mesoamerican/Caribbean clade includes 6 genera, which representatives are common in Central America and the Caribbean islands. Perhaps such discrepancies are related to the different breadth of species coverage, as information on microsatellite repeats was obtained only for economically important species. Therefore, further more extended analysis will help resolve the remaining taxonomic issues within *Ericaceae* and its many genera. Additionally, it may be practical to use other chloroplast markers presented in Table 1.

SSR markers also allow assessment of genetic diversity in populations of wild relatives of cultivated species. This knowledge helps develop effective conservation strategies and facilitates their use for agricultural purposes.

The natural habitats of *V. macrocarpon* and *V. oxycoccos* overlap in many areas. Thus, in order to understand better the relationship between the two cranberry

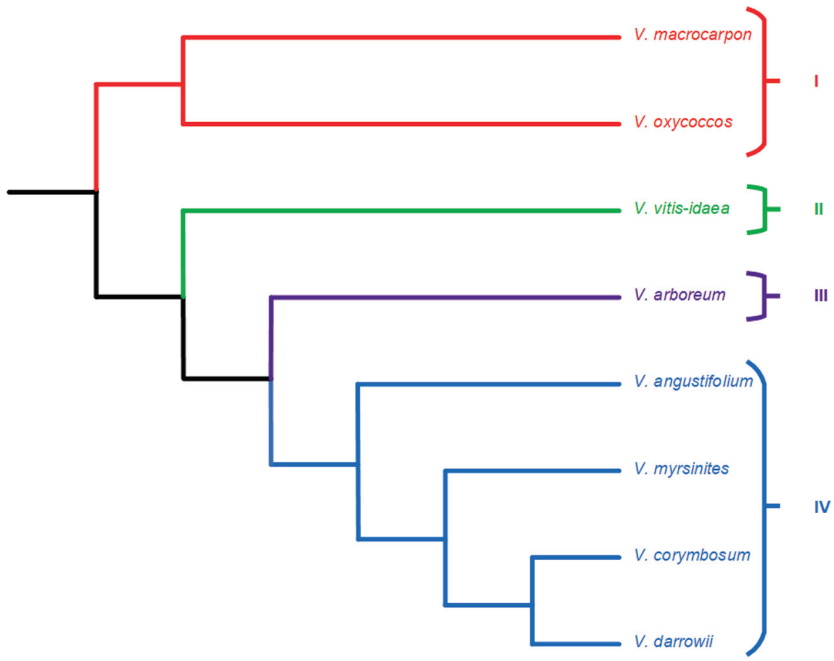

Fig. 2. Phylogenetic tree of economically important species of the genus *Vaccinium*, built on the basis of the SSR loci of mitochondria and chloroplasts [32]. I — Species belonging in the *Oxycoccus* section, II — *Vitis-idaea*, III — *Batodendron*, IV — *Cyanococcus*
Рис. 2. Филогенетическое дерево экономически важных видов рода *Vaccinium*, построенное на основе локусов SSR митохондрий и хлоропластов [32]. I — Вид, входящий в секцию *Oxycoccus*, II — *Vitis-idaea*, III — *Batodendron*, IV — *Cyanococcus*

species, Rodriguez-Bonilla et al. [35] estimated the genetic distance on microsatellite sequences of organisms from wild populations. Consequently, the populations were divided into two main clusters, one of which contained all accessions of *V. oxycoccos*, and the other included all accessions of *V. macrocarpon*. This was also confirmed by principal component analysis, which also revealed geographic clustering within species.

Genetic evaluations of both species showed very high levels of heterozygosity. These results are consistent with the biology of cranberries, which is characterized by cross-pollination and reduced fertility in experimentally obtained inbred lines [36]. These features contribute to the maintenance of a high level of genetic diversity in wild cranberry populations [35].

NGS DATA FOR STUDYING THE SYSTEMATICS AND PHYLOGENY OF THE GENUS *VACCINIUM*

Recent assemblies of the genomes of *V. macrocarpon*, *V. microcarpum, V. oxycoccos*, and *V. corymbosum* facilitated their comparative genomics [15, 37]. Molecular age determination revealed that *V. macrocarpon* diverged from *V. oxycoccos* approximately 2 million years ago, and 4.5 million years ago from *V. microcarpum* the results indicate that divergence of *V. macrocarpon* and *V. corymbosum* occurred between 5 and 10.4 million years ago. Additionally, the analysis showed that the divergence of *Vaccinium* from the more distant relatives, *Rhododendron williamsianum* Rehder & E.H. Wilson (order *Ericales*, family *Ericaceae*) and *Actinidia* Lindl. (order *Ericales*, family *Actinidiaceae*) occurred 22 and 52.1 million years ago, respectively.

Additionally, this analysis revealed two polyploidization events in the evolution of the genus *Vaccinium*, namely an ancient γ-tripplication and a later whole-genome duplication (Vm-α) shared with other members of the *Ericaeae, Theaceae D. Don*, and *Actinidiaceae* Gilg & Werderm families approximately 58 million years ago. This age determination is consistent with the Dl-α duplication of the genome in *Diospyros* L. (order Ericales, family *Ebenaceae* Gürke) and the Ad-α duplication in *Actinidia* (Fig. 3).

Blueberry breeding has a short history and began in the 20th century in the USA. To improve the basic qualities of the crop, breeders used interspecific hybridization of tetraploid and hexaploid blueberry species, which formed naturally through unreduced gametes. This is why cultivated blueberries have several levels of ploidy, namely, tetraploid lowbush *V. angustifolium*, tetraploid highbush *V. corymbosum*, and hexaploid Rabbit-Eye blueberry *V. virgatum*. Additionally, when breeding highbush varieties, species common in the northern states were used, which led to their resistance to the northern climate. These cultivars later came to be known as northern highbush blueberries, which were then crossed with southern blueberries to produce varieties adapted to cultivation in the southern states, southern highbush blueberries.

Since the history of blueberry breeding is well documented, Nishiyama et al. [38] used ddRAD sequencing to

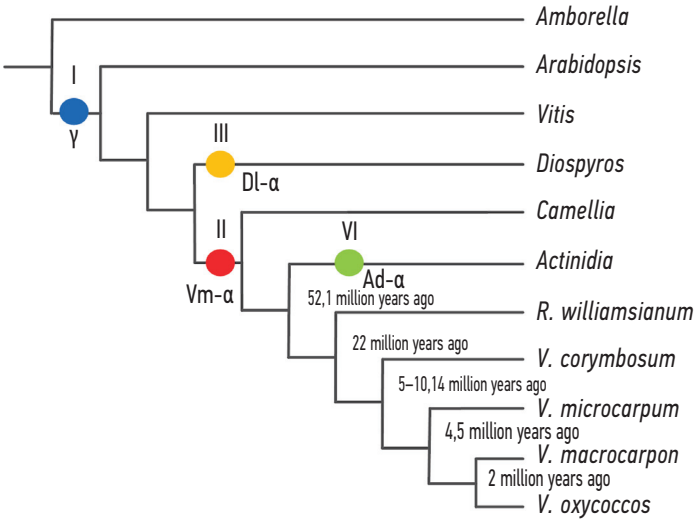

Fig. 3. Whole genome duplications in cranberry evolution based on pooled data [15, 37]. I — represents a γ-triplication, II — represents a Vm-α duplication, both of which formed the modern *Vaccinium* genome; III — Dl-α duplication of the genome characteristic of the genus *Diospyros*; IV — Ad-α duplication of the *Actinidia* genome
Рис. 3. Полногеномные дупликации в эволюции клюквы на основе объединенных данных [15, 37]. I — γ-трипликация, II — Vm-α-дупликация, оба этих события сформировали современный геном *Vaccinium*; III — Dl-α-дупликация генома, характерная для рода *Diospyros*; IV — Ad-α-дупликация генома *Actinidia*

perform its genetic population analysis. This algorithm enabled the sequencing of the genome regions associated with restriction sites, which were selected on the basis of the published blueberry *V. corymbosum* genome. Thus, rapid and economical detection of SNPs and indels in the studied genomes was achieved.

An analysis of the population structure suggests that the blueberry cultivar Rabbit Eye and northern highbush blueberries are relatively homogeneous, but southern highbush blueberries contain a much more mixed genetic background. Taking into account the pedigree of blueberries, the most optimal was the division of the entire data set into nine hypothetical genomes, which correspond to the number of species actively used in the course of breeding (*V. darrowii*, *V. elliottii*, *V. tenellum*, *V. angustifolium*, *V. corymbosum*, *V. constablaei*, *V. virgatum*, *V. myrtilloides, and V. pallidum)*. The trends identified are consistent with the history of blueberry breeding [38].

Thus, this method has shown its adequacy for the genus *Vaccinium* and can be further used for other taxa under study.

In phylogenetic studies, data on biochemical composition can also be useful, given that *Vaccinium* species are producers of important secondary metabolites. One of these metabolites is the iridoid glycoside monotropein, which was found in the fruits of cultivated species of cranberries, lingonberries, bilberries, and bog whortleberry *V. uliginosum*, but does not occur in close relatives, namely North American blueberries *V. corymbosum, V. angustifolium,* and *V. virgatum*. A more detailed analysis, including both cultivated blueberry varieties and wild species, revealed monotropein in five varieties (Bluehaven, Blue Ridge, Ornablue, Ozarkblue, and Summit) and in all 13 wild *Vaccinium* species analyzed (*V. arboreum, V. calycinum, V. consanguineum, V. meridionale, V. cylindraceum, V. elliottii, V. floribundum, V. fuscatum, V. ovatum, V. padifolium, V. reticulatum* Nene*, V. reticulatum* Red Button*, and V. stamineum)*. Ecotypic and pedigree analysis showed that only the Bluehaven variety belonged to the northern highbush ecotype, i.e., blueberry species common in the northern states of the USA were used in its breeding, and the Ornablue variety is a hybrid of the cultivated Concord and wild *V. pallidum*. In the breeding of each of these five varieties, there was hybridization with wild monotropein-positive species. Therefore, we suggest that the presence of monotropein in these varieties is associated with the introgression of wild species into cultivated blueberries [39]. A similar approach can be further used to establish phylogenetic relationships between accessions.

CONCLUSION

In summary, we conclude that currently, the taxonomy of the genus *Vaccinium* is not well established owing to many difficulties faced by researchers. First, the DNA barcoding data clearly showed the polyphyletic nature of the genus *Vaccinium*, as well as the joint clustering of species with similar geographical localization. Second, species that were previously considered to be more phylogenetically distant were included in the same clade, whereas species that were considered close were placed in different clades. One of the reasons for these ambiguous results may be hybridization and polyploidization

during speciation. Due to the existence of these ambiguities, botanists still adhere to the traditional genus system based on morphological characteristics. According to this system, the genus includes 33 sections, but the species composition of the sections and the evolutionary relationships between them remain controversial. Constructions based on the analysis of NGS sequencing results often coincide better with those based on traditional taxonomy than those based on DNA barcoding methods. Although more recent NGS sequencing methods provide new data that expand our knowledge about the origin and evolution of the *Vaccinium* genus and its relatives, they remain more laborious and expensive than DNA barcoding methods. This is why researchers studying the taxonomy, evolution, and domestication of these organisms still use additional sets of molecular markers to conduct large-scale studies of representatives of the genus *Vaccinium* and the tribe *Vaccinieae.*

In some cases, unique DNA sequence fragments recently introduced into genomes as a result of horizontal gene transfer can be regarded as markers. This approach enables combining individual species into clusters and tracking the relationship of species within clusters [20]. Analysis of the published genomes of some representatives of the genus indicates that the genus *Vaccinium* has such sequences. Naturally transgenic organisms were found in the genus [40], containing the sequence of the *rolB/C*-like gene. The presence of this conserved sequence in several species and a common localization site may indicate the transformation of their common ancestor with the subsequent transfer of this DNA fragment to descendants and its gradual divergence. Thus, the *rolB/C*-like gene can be used in the future as a phylogenetic marker for the genus *Vaccinium*.

ADDITIONAL INFORMATION

Author contribution. Thereby, all authors made a substantial contribution to the conception of the work, acquisition, analysis, interpretation of data for the work, drafting and revising the work, final approval of the version to be published and agree to be accountable for all aspects of the work. Contribution of the authors: R.R. Zhidkin — drawing up a plan, literature review, writing the main part of the text; T.V. Matveeva — drawing up a plan, literature review, making final edits.

Competing interests. The authors declare that they have no competing interests.

Funding source. This work was supported by the Ministry of Science and Higher Education of the Russian Federation in accordance with the agreement No. 075-15-2022-322 dated 22.04.2022 on the grant in the form of a subsidy from the federal budget of the Russian Federation. The grant was provided for state support for the creation and development of a world-class Scientific Center "Agrotechnologies of the Future".

REFERENCES

1. Sultana N, Menzel G, Heitkam T, et al. Bioinformatic and Molecular Analysis of Satellite Repeat Diversity in Vaccinium Genomes. *Genes (Basel)*. 2020;11(5):527. DOI: 10.3390/genes11050527

2. Kron K, Powell E, Luteyn J. Phylogenetic relationships within the blueberry tribe (*Vaccinieae*, *Ericaceae*) based on sequence data from MATK and nuclear ribosomal ITS regions, with comments on the placement of *Satyria*. *Am J Bot*. 2002;89(2):327–336. DOI: 10.3732/ajb.89.2.327

3. npgsweb.ars-grin.gov. Genus: *Vaccinium* L. *The Germplasm Resources Information Network* [accessed: 15.05.2022]. Available from: https://npgsweb.ars-grin.gov/gringlobal/taxonomygenus?id=18663

4. Vander Kloet SP, Dickinson TA. A subgeneric classification of the genus *Vaccinium* and the metamorphosis of *V.* section *Bracteata* Nakai: more terrestrial and less epiphytic in habit, more continental and less insular in distribution. *J Plant Res*. 2009;122(3):253–268. DOI: 10.1007/s10265-008-0211-7

5. Luby JJ, Ballington JR, Draper AD, et al. Blueberries and cranberries (*Vaccinium*). *Acta Hortic*. 1991;290:393–458. DOI: 10.17660/actahortic.1991.290.9

6. Vander Kloet SP. *The Genus Vaccinium in North America*. Ottawa: Agriculture Canada, Research Branch, 1988. 218 p.

7. Wang H, Guo X, Hu X, et al. Comparison of phytochemical profiles, antioxidant and cellular antioxidant activities of different varieties of blueberry (*Vaccinium* spp.). *Food Chem*. 2017;217:773–781. DOI: 10.1016/j.foodchem.2016.09.002

8. Celli G, Kovalesk A. Blueberry and Cranberry. *Integrated Processing Technologies for Food and Agricultural By-Products*. 2019: 165–179. DOI: 10.1016/b978-0-12-814138-0.00007-1

9. Hancock JF, Lyrene P, Finn CE, et al. Blueberries and Cranberries. In: J.F. Hancock, editor. *Temperate Fruit Crop Breeding*. Springer Science+Business Media B.V., 2008. P. 115–150. DOI: 10.1007/978-1-4020-6907-9_4

10. Vorsa N, Zalapa J. Domestication, Genetics, and Genomics of the American Cranberry. *Plant Breed Rev*. 2019;43:279–315. DOI: 10.1002/9781119616801.ch8

11. www.fao.org. Crops and livestock products. *FAOSTAT* [accessed: 15.05.2022]. Available from: https://www.fao.org/faostat/en/#data/QCL

12. Song GQ, Hancock JF. Vaccinium. In: C. Kole, editor. *Wild Crop Relatives: Genomic and Breeding Resources*. Springer, Berlin, Heidelberg, 2010. P. 197–221. DOI: 10.1007/978-3-642-16057-8_10

13. Silva S, Costa EM, Veiga M, et al. Health promoting properties of blueberries: a review. *Crit Rev Food Sci Nutr*. 2018;60(2):181–200. DOI: 10.1080/10408398.2018.1518895

14. Abeywickrama G, Debnath SC, Ambigaipalan P, Shahidi F. Phenolics of Selected Cranberry Genotypes (*Vaccinium macrocarpon* Ait.) and Their Antioxidant Efficacy. *J Agric Food Chem*. 2016;64(49): 9342–9351. DOI: 10.1021/acs.jafc.6b04291

15. Diaz-Garcia L, Garcia-Ortega LF, González-Rodríguez M, et al. Chromosome-Level Genome Assembly of the American

Cranberry (*Vaccinium macrocarpon* Ait.) and Its Wild Relative *Vaccinium microcarpum*. *Front Plant Sci*. 2021;12:633310. DOI: 10.3389/fpls.2021.633310

16. naturalhistory2.si.edu. Index Nominum Genericorum. *Smithsonian. National Museum of Natural history* [accessed: 15.05.2022]. Available from: https://naturalhistory2.si.edu/botany/ing/

17. Camp WH. On the Structure of Populations in the Genus *Vaccinium*. *Brittonia*. 1942;4(2):189–204. DOI: 10.2307/2804713

18. Camp WH. The North American blueberries with notes on other groups of Vacciniaceae. *Brittonia*. 1945;5(3):203–275. DOI: 10.2307/2804880

19. Kloet SP. The taxonomy of the highbush blueberry, *Vaccinium corymbosum*. *Canad J Bot*. 1980;58(10):1187–1201. DOI: 10.1139/b80-148

20. Matveeva TV, Pavlova OA, Bogomaz DI, et al. Molecular markers for plant species identification and phylogenetics. *Ecological genetics*. 2011;9(1):32–43. (In Russ.) DOI: 10.17816/ecogen9132-43

21. Rodionov AV, Amosova AV, Belyakov EA, et al. Genetic Consequences of Interspecific Hybridization, Its Role in Speciation and Phenotypic Diversity of Plants. *Russian Journal of Genetics*. 2019;55(3):278–294. DOI: 10.1134/s1022795419030141

22. Young AD, Gillung JP. Phylogenomics — principles, opportunities and pitfalls of big-data phylogenetics. *Syst Entomol*. 2019;45(2): 225–247. DOI: 10.1111/syen.12406

23. Delsuc F, Brinkmann H, Philippe H. Phylogenomics and the reconstruction of the tree of life. *Nat Rev Genet*. 2005;6(5):361–375. DOI: 10.1038/nrg1603

24. Patané JSL, Martins J, Setubal JC. Phylogenomics. In: J. Setubal, J. Stoye, P. Stadler, editors. *Comparative Genomics. Methods in Molecular Biology. Vol. 1704*. New York: Humana Press, 2017. P. 103–187. DOI: 10.1007/978-1-4939-7463-4_5

25. Fan H, Ives AR, Surget-Groba Y, Cannon CH. An assembly and alignment-free method of phylogeny reconstruction from next-generation sequencing data. *BMC Genomics*. 2015;16(1):522. DOI: 10.1186/s12864-015-1647-5

26. Crawford D, Giannasi D. Plant Chemosystematics. *Bioscience*. 1982;32(2):114–124. DOI: 10.2307/1308564

27. Zidorn C. Plant chemophenetics — A new term for plant chemosystematics/plant chemotaxonomy in the macro-molecular era. *Phytochemistry*. 2019;163:147–148. DOI: 10.1016/j.phytochem.2019.02.013

28. Reynolds T. The evolution of chemosystematics. *Phytochemistry*. 2007;68(22–24):2887–2895. DOI: 10.1016/j.phytochem.2007.06.027

29. Powell EA, Kron KA. Molecular Systematics of the Northern Andean Blueberries (Vaccinieae, Vaccinioideae, Ericaceae). *Int J Plant Sci*. 2003;164(6):987–995. DOI: 10.1086/378653

30. Soltis DE, Mavrodiev EV, Doyle JJ, et al. ITS and ETS Sequence Data and Phylogeny Reconstruction in Allopolyploids and Hybrids. *Syst Bot*. 2008;33(1):7–20. DOI: 10.1600/036364408783887401

31. Liu Y-C, Liu S, Liu D-C, et al. Exploiting EST databases for the development and characterization of EST-SSR markers in blueberry (*Vaccinium*) and their cross-species transferability in *Vaccinium* spp. *Sci Hortic*. 2014;176:319–329. DOI: 10.1016/j.scienta.2014.07.026

32. Schlautman B, Covarrubias-Pazaran GC, Fajardo D, et al. Discriminating power of microsatellites in cranberry organelles for taxonomic studies in *Vaccinium* and Ericaceae. *Genet Resour Crop Evol*. 2016;64(3):451–466. DOI: 10.1007/s10722-016-0371-6

33. Thomas RH. Molecular Evolution and Phylogenetics. *Heredity (Edinb)*. 2001;86(3):385. DOI: 10.1046/j.1365-2540.2001.0923a.x

34. Kumar S, Stecher G, Li M, et al. MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. *Mol Biol Evol*. 2018;35(6):1547–1549. DOI: 10.1093/molbev/msy096

35. Rodriguez-Bonilla L, Williams KA, Rodríguez Bonilla F, et al. The Genetic Diversity of Cranberry Crop Wild Relatives, *Vaccinium macrocarpon* Aiton and *V. oxycoccos* L., in the US, with Special Emphasis on National Forests. *Plants*. 2020;9(11):1446. DOI: 10.3390/plants9111446

36. Sarracino JM, Vorsa N. Self and cross fertility in cranberry. *Euphytica*. 1991;58(2):129–136. DOI: 10.1007/bf00022813

37. Kawash J, Colt K, Hartwick NT, et al. Contrasting a reference cranberry genome to a crop wild relative provides insights into adaptation, domestication, and breeding. *PLoS One*. 2022;17(3): e0264966. DOI: 10.1371/journal.pone.0264966

38. Nishiyama S, Fujikawa M, Yamane H, et al. Genomic insight into the developmental history of southern highbush blueberry populations. *Heredity (Edinb)*. 2020;126(1):194–205. DOI: 10.1038/s41437-020-00362-0

39. Leisner CP, Kamileen MO, Conway ME, et al. Differential iridoid production as revealed by a diversity panel of 84 cultivated and wild blueberry species. *PLoS One*. 2017;12(6):e0179417. DOI: 10.1371/journal.pone.0179417

40. Matveeva T. New naturally transgenic plants: 2020 update. *Biological Communications*. 2021;66(1). DOI: 10.21638/spbu03.2021.105

СПИСОК ЛИТЕРАТУРЫ

1. Sultana N., Menzel G., Heitkam T., et al. Bioinformatic and Molecular Analysis of Satellite Repeat Diversity in Vaccinium Genomes // Genes (Basel). 2020. Vol. 11, No. 5. P. 527. DOI: 10.3390/genes11050527

2. Kron K., Powell E., Luteyn J. Phylogenetic relationships within the blueberry tribe (*Vaccinieae*, *Ericaceae*) based on sequence data from MATK and nuclear ribosomal ITS regions, with comments on the placement of *Satyria* // Am J Bot. 2002. Vol. 89, No. 2. P. 327–336. DOI: 10.3732/ajb.89.2.327

3. npgsweb.ars-grin.gov. Genus: *Vaccinium* L. // The Germplasm Resources Information Network [дата обращения: 15.05.2022]. Доступ по ссылке: https://npgsweb.ars-grin.gov/gringlobal/taxonomygenus?id=18663

4. Vander Kloet S.P., Dickinson T.A. A subgeneric classification of the genus *Vaccinium* and the metamorphosis of *V.* section *Bracteata* Nakai: more terrestrial and less epiphytic in habit, more continental and less insular in distribution // J Plant Res. 2009. Vol. 122, No. 3. P. 253–268. DOI: 10.1007/s10265-008-0211-7

5. Luby J.J., Ballington J.R., Draper A.D., et al. Blueberries and cranberries (*Vaccinium*) // Acta Hortic. 1991. Vol. 290. P. 393–458. DOI: 10.17660/actahortic.1991.290.9

6. Vander Kloet S.P. The Genus *Vaccinium* in North America. Ottawa: Agriculture Canada, Research Branch, 1988. 218 p.

7. Wang H., Guo X., Hu X., et al. Comparison of phytochemical profiles, antioxidant and cellular antioxidant activities of different varie-

ties of blueberry (*Vaccinium* spp.) // Food Chem. 2017. Vol. 217. P. 773–781. DOI: 10.1016/j.foodchem.2016.09.002
8. Celli G., Kovalesk A. Blueberry and Cranberry // Integrated Processing Technologies for Food and Agricultural By-Products. 2019. P. 165–179. DOI: 10.1016/b978-0-12-814138-0.00007-1
9. Hancock J.F., Lyrene P., Finn C.E., et al. Blueberries and Cranberries. In: J.F. Hancock, editor. Temperate Fruit Crop Breeding. Springer Science+Business Media B.V., 2008. P. 115–150. DOI: 10.1007/978-1-4020-6907-9_4
10. Vorsa N., Zalapa J. Domestication, Genetics, and Genomics of the American Cranberry // Plant Breed Rev. 2019. Vol. 43. P. 279–315. DOI: 10.1002/9781119616801.ch8
11. www.fao.org. Crops and livestock products // FAOSTAT [дата обращения: 15.05.2022]. Доступ по ссылке: https://www.fao.org/faostat/en/#data/QCL
12. Song G.Q., Hancock J.F. Vaccinium. In: C. Kole, editor. Wild Crop Relatives: Genomic and Breeding Resources. Springer, Berlin, Heidelberg, 2010. P. 197–221. DOI: 10.1007/978-3-642-16057-8_10
13. Silva S., Costa E.M., Veiga M., et al. Health promoting properties of blueberries: a review // Crit Rev Food Sci Nutr. 2018. Vol. 60, No. 2. P. 181–200. DOI: 10.1080/10408398.2018.1518895
14. Abeywickrama G., Debnath S.C., Ambigaipalan P., Shahidi F. Phenolics of Selected Cranberry Genotypes (*Vaccinium macrocarpon* Ait.) and Their Antioxidant Efficacy // J Agric Food Chem. 2016. Vol. 64, No. 49. P. 9342–9351. DOI: 10.1021/acs.jafc.6b04291
15. Diaz-Garcia L., Garcia-Ortega L.F., González-Rodríguez M., et al. Chromosome-Level Genome Assembly of the American Cranberry (*Vaccinium macrocarpon* Ait.) and Its Wild Relative *Vaccinium microcarpum* // Front Plant Sci. 2021. Vol. 12. ID633310. DOI: 10.3389/fpls.2021.633310
16. naturalhistory2.si.edu. Index Nominum Genericorum // Smithsonian. National Museum of Natural history [дата обращения: 15.05.2022]. Доступ по ссылке: https://naturalhistory2.si.edu/botany/ing/
17. Camp W.H. On the Structure of Populations in the Genus *Vaccinium* // Brittonia. 1942. Vol. 4, No. 2. P. 189–204. DOI: 10.2307/2804713
18. Camp W.H. The North American blueberries with notes on other groups of Vacciniaceae // Brittonia. 1945. Vol. 5, No. 3. P. 203–275. DOI: 10.2307/2804880
19. Kloet S.P. The taxonomy of the highbush blueberry, *Vaccinium corymbosum* // Canad J Bot. 1980. Vol. 58, No. 10. P. 1187–1201. DOI: 10.1139/b80-148
20. Матвеева Т.В., Павлова О.А., Богомаз Д.И., и др. Молекулярные маркеры для видоидентификации и филогенетики растений // Экологическая генетика. 2011. Т. 9, № 1. С. 32–43. DOI: 10.17816/ecogen9132-43
21. Rodionov A.V., Amosova A.V., Belyakov E.A., et al. Genetic Consequences of Interspecific Hybridization, Its Role in Speciation and Phenotypic Diversity of Plants // Russian Journal of Genetics. 2019. Vol. 55, No. 3. P. 278–294. DOI: 10.1134/s1022795419030141
22. Young A.D., Gillung J.P. Phylogenomics — principles, opportunities and pitfalls of big-data phylogenetics // Syst Entomol. 2019. Vol. 45, No. 2. P. 225–247. DOI: 10.1111/syen.12406
23. Delsuc F., Brinkmann H., Philippe H. Phylogenomics and the reconstruction of the tree of life // Nat Rev Genet. 2005. Vol. 6, No. 5. P. 361–375. DOI: 10.1038/nrg1603
24. Patané J.S.L., Martins J., Setubal J.C. Phylogenomics. In: J. Setubal, J. Stoye, P. Stadler, editors. Comparative Genomics. Methods in Molecular Biology. Vol. 1704. New York: Humana Press, 2017. P. 103–187. DOI: 10.1007/978-1-4939-7463-4_5
25. Fan H., Ives A.R., Surget-Groba Y., Cannon C.H. An assembly and alignment-free method of phylogeny reconstruction from next-generation sequencing data // BMC Genomics. 2015. Vol. 16, No. 1. ID 522. DOI: 10.1186/s12864-015-1647-5
26. Crawford D., Giannasi D. Plant Chemosystematics // Bioscience. 1982. Vol. 32, No. 2. P. 114–124. DOI: 10.2307/1308564
27. Zidorn C. Plant chemophenetics — A new term for plant chemosystematics/plant chemotaxonomy in the macro-molecular era // Phytochemistry. 2019. Vol. 163. P. 147–148. DOI: 10.1016/j.phytochem.2019.02.013
28. Reynolds T. The evolution of chemosystematics // Phytochemistry. 2007. Vol. 68, No. 22–24. P. 2887–2895. DOI: 10.1016/j.phytochem.2007.06.027
29. Powell E.A., Kron K.A. Molecular Systematics of the Northern Andean Blueberries (Vaccinieae, Vaccinioideae, Ericaceae) // Int J Plant Sci. 2003. Vol. 164, No. 6. P. 987–995. DOI: 10.1086/378653
30. Soltis D.E., Mavrodiev E.V., Doyle J.J., et al. ITS and ETS Sequence Data and Phylogeny Reconstruction in Allopolyploids and Hybrids // Syst Bot. 2008. Vol. 33, No. 1. P. 7–20. DOI: 10.1600/036364408783887401
31. Liu Y.-C., Liu S., Liu D.-C., et al. Exploiting EST databases for the development and characterization of EST-SSR markers in blueberry (*Vaccinium*) and their cross-species transferability in *Vaccinium* spp. // Sci Hortic. 2014. Vol. 176. P. 319–329. DOI: 10.1016/j.scienta.2014.07.026
32. Schlautman B., Covarrubias-Pazaran G.C., Fajardo D., et al. Discriminating power of microsatellites in cranberry organelles for taxonomic studies in *Vaccinium* and Ericaceae // Genet Resour Crop Evol. 2016. Vol. 64, No. 3. P. 451–466. DOI: 10.1007/s10722-016-0371-6
33. Thomas R.H. Molecular Evolution and Phylogenetics // Heredity (Edinb). 2001. Vol. 86, No. 3. P. 385. DOI: 10.1046/j.1365-2540.2001.0923a.x
34. Kumar S., Stecher G., Li M., et al. MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms // Mol Biol Evol. 2018. Vol. 35, No. 6. P. 1547–1549. DOI: 10.1093/molbev/msy096
35. Rodriguez-Bonilla L., Williams K.A., Rodríguez Bonilla F., et al. The Genetic Diversity of Cranberry Crop Wild Relatives, *Vaccinium macrocarpon* Aiton and *V. oxycoccos* L., in the US, with Special Emphasis on National Forests // Plants. 2020. Vol. 9, No. 11. ID 1446. DOI: 10.3390/plants9111446
36. Sarracino J.M., Vorsa N. Self and cross fertility in cranberry // Euphytica. 1991. Vol. 58, No. 2. P. 129–136. DOI: 10.1007/bf00022813
37. Kawash J., Colt K., Hartwick N.T., et al. Contrasting a reference cranberry genome to a crop wild relative provides insights into adaptation, domestication, and breeding // PLoS One. 2022. Vol. 17, No. 3. ID e0264966. DOI: 10.1371/journal.pone.0264966
38. Nishiyama S., Fujikawa M., Yamane H., et al. Genomic insight into the developmental history of southern highbush blueberry populations // Heredity (Edinb). 2020. Vol. 126, No. 1. P. 194–205. DOI: 10.1038/s41437-020-00362-0
39. Leisner C.P., Kamileen M.O., Conway M.E., et al. Differential iridoid production as revealed by a diversity panel of 84 cultivated and wild blueberry species // PLoS One. 2017. Vol. 12, No. 6. ID e0179417. DOI: 10.1371/journal.pone.0179417
40. Matveeva T. New naturally transgenic plants: 2020 update // Biological Communications. 2021. Vol. 66, No. 1. DOI: 10.21638/spbu03.2021.105

AUTHORS' INFO

***Roman R. Zhidkin,** Student; address: 7/9, Universitetskaya em., 199034, Saint Petersburg, Russia; e-mail: zhidkinr@gmail.com

Tatiana V. Matveeva, Dr. Sci. (Biol.), Professor;
ORCID: https://orcid.org/0000-0001-8569-6665;
eLibrary SPIN: 3877-6598; Scopus: 7006494611;
e-mail: radishlet@gmail.com

* Corresponding author / Автор, ответственный за переписку

ОБ АВТОРАХ

***Роман Романович Жидкин,** студент; адрес: Россия, 199034, Санкт-Петербург, Университетская наб., д. 7/9; e-mail: zhidkinr@gmail.com

Татьяна Валерьевна Матвеева, д-р биол. наук, профессор; ORCID: https://orcid.org/0000-0001-8569-6665; eLibrary SPIN: 3877-6598; Scopus: 7006494611; e-mail: radishlet@gmail.com