ISSN 2079-0864, Biology Bulletin Reviews, 2022, Vol. 12, No. 5, pp. 516–526. © Pleiades Publishing, Ltd., 2022.
Russian Text © The Author(s), 2022, published in Zhurnal Obshchei Biologii, 2022, Vol. 83, No. 1, pp. 38–50.

Characteristics of *Varroa underwoodi* mites (Acari: Varroidae) in the population of *Apis cerana ussuriensis* (Hymenoptera: Apidae) in the Primorsky Krai of Russia

R. A. Ilyasov[a, b, c, *], J. I. Takahashi[d, **], M. L. Lee[b], M. Y. Proshchalykin[e], A. S. Lelej[e, *], H. W. Kwon[b, ****], V. N. Danilenko[a, *****], and A. G. Nikolenko[c, ******]**

[a] *Vavilov Institute of General Genetics, Russian Academy of Sciences, Moscow, 119991 Russia*
[b] *Incheon National University, Division of Life Sciences, Major of Biological Sciences, and Convergence Center for Insect Vectors, Incheon, 22012 Korea*
[c] *Institute of Biochemistry and Genetics, Ufa Federal Research Centre of the Russian Academy of Sciences, Ufa, 450054 Russia*
[d] *Faculty of Life Sciences Kamigamo Motoyama, Kyoto Sangyo University, Kyoto, 603-8555 Japan*
[e] *Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far East Branch of Russian Academy of Sciences, Vladivostok, 690022 Russia*
**e-mail: apismell@hotmail.com*
***e-mail: jit@cc.kyoto-su.ac.jp*
****e-mail: lelej@biosoil.ru*
*****e-mail: hwkwon@inu.ac.kr*
******e-mail: valerid@vigg.ru*
*******e-mail: a-nikolenko@yandex.ru*

Received August 30, 2021; revised October 5, 2021; accepted October 19, 2021

Abstract—Species of the genus *Varroa* are ectoparasitic mites of the *Apis* honey bees. Unlike the well-known species of mites *V. destructor* and *V. jacobsoni*, *V. underwoodi* is still poorly studied. According to foreign publications, the currently recognized distribution of *V. underwoodi* in the *A. cerana* population includes Nepal, South Korea, Japan, Malaysia, India, Indonesia, Papua New Guinea, Vietnam, and China. Recently it has been detected in Russia (Primorsky krai) on *A. cerana ussuriensis* honey bees. Since *V. destructor* and *V. jacobsoni* have the ability to easily switch to other bee species, there is a possibility that later *V. underwoodi* may also extensively switch from the Asian honey bees *A. cerana* to the European honey bees *A. mellifera*. The first case of *V. underwoodi* parasitizing in *A. mellifera* colonies was recorded in Papua New Guinea. The parasitic mite *V. underwoodi* requires careful study, since it is a new potential parasite of the honey bees *A. mellifera*, which can also bring new species and strains of viruses and bacteria, change the composition of the gut microbiome, and disrupt the protective and adaptive mechanisms of the bees. This article presents the data of morphometry and polymorphism of the *COX1* gene mtDNA. *Varroa underwoodi* was compared with the other mite species *V. destructor* and *V. jacobsoni*. The mean genetic divergence and p-distance between *V. underwoodi* and other *Varroa* species were 9% and 0.09, respectively, which is consistent with the level of species differences in insects. The nucleotide sequences of the *COX1* gene mtDNA of *V. underwoodi* from Primorsky krai of Russia LC532104 and from the Jilin province of China MH205176 turned out to be identical and were assigned to the *China 1 MH205176* haplotype. It is assumed that there is continuous migration between the *A. cerana* populations of Russia and China, which led to the spread of *V. underwoodi* in the natural population of *A. cerana ussuriensis* in the Primorsky krai of Russia, and the mite is currently distributed up to 45.06° N. Thus, the northern border of the *V. underwoodi* range is located on the territory of the Russian Far East and, probably, coincides with the range of *A. cerana ussuriensis*. It is likely that the selection of *A. mellifera* bee colonies for hygienic behavior against the *V. destructor* mite may also be effective against *V. underwoodi* and will prevent the possible transition of *V. underwoodi* from Asian *A. cerana* to European *A. mellifera*.

DOI: 10.1134/S2079086422050048

INTRODUCTION

Parasitic mites of the genus *Varroa* Oudemans, 1904, belong to the family Varroidae of the infraorder Gamasina of the order Mesostigmata of the superorder Parasitiformes. Mites g. *Varroa* are ectoparasites of the bees g. *Apis* and are represented by four species (Anderson and Trueman, 2000; Rosenkranz et al., 2010): (1) *V. jacobsoni*, described in *A. cerana* (Java Island, Indonesia) (Oudemans, 1904), later found on

A. nigrocincta in Indonesia (Hadisoesilo and Otis, 1998; Anderson and Trueman, 2000) and *A. mellifera* in Papua New Guinea (Roberts et al., 2015); (2) *V. destructor* (initially erroneously identified as *V. jacobsoni*) described in *A. cerana* (China, Japan, South Korea, Thailand), later found on *A. mellifera* in Japan (Anderson, 2000; Anderson and Trueman, 2000); (3) *V. rindereri* in *A. koschevnikovi* (Sabah, Malaysia) (Guzman and Delfinado-Baker, 1996), and not yet found in other bee species; and (4) *V. underwoodi*, described in *A. cerana* (Nepal) (Delfinado-Baker and Aggarwal, 1987), later found in *A. nigrocincta* in Indonesia (Anderson et al., 1997; Kuznetsov, 2005).

The *A. mellifera* honey bee is predominantly affected worldwide by *V. destructor* (Traynor et al., 2020), and in Papua New Guinea by *V. jacobsoni* (Roberts et al., 2015). Several mitochondrial haplotypes of *V. destructor* have been described, of which two, *K* (Korean) and *J* (Japanese), are able to reproduce and parasitize in *A. mellifera* families (Anderson, 2000; Anderson and Trueman, 2000; Muñoz et al., 2008). The mites *V. rindereri* and *V. underwoodi* are least studied (Oudemans, 1904; Delfinado-Baker and Aggarwal, 1987; Guzman and Delfinado-Baker, 1996; Anderson et al., 1997; Rath, 1999; Anderson and Trueman, 2000; Wang et al., 2019a).

Another species of honey bee, *A. cerana*, is mainly affected by the mite *V. destructor* and, to a lesser extent, *V. underwoodi*; the latter occurs in smaller numbers (Wang et al., 2019a, 2019b; Lin et al., 2021). Relatively recently, *V. underwoodi* was also detected in Russia (Primorsky krai), and the morphometry and polymorphism of the *COX1* gene mtDNA in the natural population of *A. cerana* were described (Kuznetsov, 2005; Kuznetsov and Lelej, 2005; Ilyasov et al., 2021). These works are devoted to the first detection of *V. underwoodi* in the natural population of *A. cerana* in Russia; therefore, they discuss the features of the evolution and genetic structure of the *V. underwoodi* population superficially and in insufficient detail, without providing a detailed analysis of the polymorphism of the nucleotide sequence of the mtDNA *COX1* gene of different populations of *Varroa underwoodi* and also do not characterize *V. underwoodi* as a carrier of new pathogens of bees—viruses and bacteria. There is a need to systematize all the available knowledge about the *V. underwoodi* mite, to assess the possible threats of *V. underwoodi* to other bee species of the genus *Apis*, on the basis of which measures can be developed for preventing the expansion of the range of this mite species in Asia and Russia.

Along with the expansion of the range of *V. underwoodi*, its number of host species is growing: *A. cerana* in Nepal (Delfinado-Baker and Aggarwal, 1987), *A. nuluensis* in Malaysia (Delfinado-Baker and Aggarwal, 1987; Guzman et al., 1996; Anderson et al., 1997), *A. nigrocincta* in Indonesia (Anderson et al., 1997; Hadisoesilo, 1997), and *A. mellifera* in Papua New Guinea (Lee, 1995; Anderson et al., 1997; Guzman and Rinderer, 1999). *V. underwoodi* mites reproduce successfully in colonies of *A. cerana* bees, but its detection in colonies of other honey bee species suggests that these mites are capable of interspecific host change. It can be especially dangerous for *A. mellifera* colonies kept close to *A. cerana* colonies, as is common in most Asian countries (Zheng et al., 2011, 2018; Chantawannakul et al., 2016; Wang et al., 2019a, 2019b; Roberts et al., 2020).

Since different haplotypes of *Varroa* mites have differing ability to parasitize different types of bees of the genus *Apis* (Anderson, 2000; Anderson and Trueman, 2000; Muñoz et al., 2008) (haplotypes *K* and *J* of six *V. destructor* mite haplotypes are able to parasitize on *A. mellifera* bees), there is a high probability that some *V. underwoodi* can parasitize *A. mellifera* bees and then, similar to *V. destructor*, spread throughout the world. *Varroa underwoodi* is characterized by a high level of genetic diversity (Navajas et al., 2010; Roberts et al., 2015; Wang et al., 2019a). The high level of genetic diversity of this species allows the rapid formation of *V. underwoodi* haplotypes capable of parasitizing on *A. mellifera*. This is also confirmed by the law of homological series of N.I. Vavilov (1920), according to which closely related forms may develop parallel traits and, thus, the ability of *V. destructor* and *V. jacobsoni* to parasitize *A. mellifera* may also manifest itself in *V. underwoodi*. Therefore, *A. mellifera* is a potential host for *V. underwoodi* during its further evolution (Anderson, 2000; Anderson and Trueman, 2000; Muñoz et al., 2008; Wang et al., 2019a, 2019b; Ilyasov et al., 2021).

The transition of *V. underwoodi* to a new host, *A. mellifera*, may be accompanied by the transmission of new species and strains of viruses and bacteria, provoking new diseases leading to microbiome disruption, reduced survival and reduced immunity (Sandionigi et al., 2015; Hubert et al., 2017; Raymann et al., 2017; Diaz et al., 2019; Marche et al., 2019; Wang et al., 2019a, 2019b; Bleau et al., 2020; Chen et al., 2021). The study of the features of *V. underwoodi* will make it possible to develop methods for combating the new parasite in advance (Guzman and Rinderer, 1999; Kolar and Lodge, 2001; Woolhouse et al., 2005). One such method is the selection of *A. mellifera* bee colonies based on hygienic behavior against the *V. destructor* mite, which will probably also work against the *V. underwoodi* mite (Mondragón et al., 2005; Allsopp, 2006; Locke and Fries, 2011; Çakmak and Fuchs, 2013; Locke, 2016; Conlon et al., 2018; McMullan, 2018; Alphen and Fernhout, 2020). In the present work, a detailed characterization of *V. underwoodi* mites in the population of *Apis cerana ussuriensis* in Primorsky Krai is given based on the analysis of morphometry and polymorphism of the *COX1* gene mtDNA; all available knowledge about the *V. underwoodi* mite is systematized, and possible threats of *V. underwoodi* to other g. *Apis* bee species, in particular

A. mellifera, are evaluated with preventive measures proposed to prevent the expansion of the range of this mite species in Asia and Russia.

MATERIALS AND METHODS

Imagoes of *Varroa underwoodi* mites were collected in the summer of 2004 from brood cells of two families, no. 2 and no. 5 of *Apis cerana ussuriensis* in an apiary in the village of Romashka, Khasansky district, Primorsky krai, Russia (43.5° N, 131.3° E). All collected samples of *V. underwoodi* mites were placed in 70% ethanol and stored at –20°C.

V. underwoodi mites were found only in colonies of *A. cerana ussuriensis*, where the infection rate of colonies was 50%.

For preliminary confirmation of the species, the morphometric characteristics and size of adult female *V. underwoodi* mites ($n = 10$) were compared with the literature data (Delfinado-Baker and Aggarwal, 1987; Woo, 1992; Anderson et al., 1997; Huang, 2004; Wang et al., 2019a). Before assessing morphometry, selected samples of *V. underwoodi* mites were dried at room temperature for 1 min. In *V. underwoodi* mites, a dorsal shield with lateral setae was used for morphometry (Delfinado-Baker and Aggarwal, 1987; Woo, 1992; Anderson et al., 1997; Huang, 2004; Wang et al., 2019a). The measurement was carried out using an EOS Kiss X7 digital microscope (Canon, Japan) with an MP-E 65mm f/2.8 1-5x Macro Photo lens (Canon, Japan) at ×150 magnification.

Total DNA was extracted from three mites per *A. cerana ussuriensis* family using the Qiagen DNEasy animal tissue kit with DNA binding columns (Qiagen, Valencia, California). The *COX1* gene mtDNA sequence was used to identify the mite species and determine the mtDNA haplotype. PCR amplification of the *V. underwoodi* mtDNA of the *COX1* gene was carried out according to the method of Wang et al. (Wang et al., 2019a) using pair of primers (*COX1*_821_F: 5'-GGAGTAGGTACAGGTTGAACGG-3' and *COX1*_821_R: 5'-ACAACCCCAGCAATAATAGCAA-3') with a product of 821 bp (Wang et al., 2019a).

All PCR products were purified using the QIAquick PCR Purification Kit (250) (QIAGEN, Hilden, Germany) according to the manufacturer's instructions. The nucleotide sequences of the *COX1* gene mtDNA of *V. underwoodi* samples were determined by two-way sequencing of PCR products using the Sanger sequencing method (Sanger et al., 1977) and a pair of primers (F-V51: 5'-GTAATTTGTATACAAAGAGGG-3' and R-V1400: 5'-CAATATCAATAGAAGAATTAGC-3') (Warrit et al., 2004) on an ABI 3730xl capillary sequencer (Applied Biosystems, Foster City, CA, United States) using the ABI PRISM BigDye Terminator v3.1 Cycle Sequencing Kit according to the manufacturer's instructions. The nucleotide sequence of the *COX1* gene mtDNA of *V. underwoodi*, 458 bp in size was uploaded to the GenBank DDBJ/GenBank database under registration number LC532104.

mtDNA of the *COX1* gene sequences of *V. underwoodi* (MH205173 (Hangzhou, China), MH205174 (Jinhua, China), MH205175 (Nanchang, China), MH205176 (Jilin, China), MH205177 (Maoming, China)), *V. destructor* (KJ403739, KJ507740, KJ403742, KJ403744 (Riyadh, Saudi Arabia)) and *V. jacobsoni* (MF462134 (Port Moresby, Papua New Guinea), AF010479 (Canberra, Australia)) from Genbank were used for comparative analysis with *V. underwoodi* from Primorsky krai. Mite samples of the species *V. destructor* and *V. jacobsoni* were also used for comparative analysis as outgroups.

The level of genetic divergence and the p-distance between the mite species *V. underwoodi*, *V. destructor*, and *V. jacobsoni* was estimated based on the *COX1* gene mtDNA sequences using the CLUSTALW alignment method in MEGA 10.0.5 (Kumar et al., 2018). A nearest neighbor phylogenetic relationship dendrogram based on p-distance of the mtDNA of the *COX1* gene sequences was constructed with 2000 bootstrap replications in CLC Genomics Workbench 21 (Qiagen Inc., Mississauga, ON, Canada). Statistical analysis and analysis of molecular variance (AMOVA) were performed using ARLEQUIN 3.5.2 (Excoffier, Lischer, 2010), STATISTICA 8.0 (StatSoft, OK, United States), and EXCEL 2010 (Microsoft, CA, United States).

RESULTS

The taxonomic affiliation of *V. underwoodi* mite samples was determined using morphometric data and polymorphism of the mtDNA of the *COX1* gene. The ellipsoidal body of *V. underwoodi* females is chestnut brown. The surface of the dorsal shield slightly furrowed and reticulate, with dense oblique setae of approximately equal length and small spines. The lateral setae gradually elongate posteriorly and the last three setae shorten. The body length of an adult female *V. underwoodi* is 767.50 ± 20.5 μm (mean value ± standard deviation), width 1300.50 ± 20.5 μm ($n = 10$). For comparison, the body length and width of adult *V. underwoodi* females in *A. cerana* colonies are 700–752 μm × 1089–1157 μm ($n = 15$); in *A. mellifera* families, 700–735 μm × 1090–1120 μm ($n = 6$); in *A. cerana* families (West Papua Province, Indonesia), 690–730 μm × 1050–1130 μm ($n = 5$); in *A. cerana* families (Sulawesi, Java, Indonesia), 720–780 μm × 1050–1080 μm ($n = 2$); in families of *A. nigrocincta* (Sulawesi), 740–760 μm × 1120–1220 μm ($n = 5$) (Anderson et al., 1997); in *A. cerana* families (Nepal), 741–780 μm × 1151–1168 μm ($n = 2$) (Delfinado-Baker and Aggarwal, 1987); in *A. cerana* families (South Korea), 703–784 μm × 1135–1324 μm ($n = 2$) (Woo, 1992). The morphological parameters of our

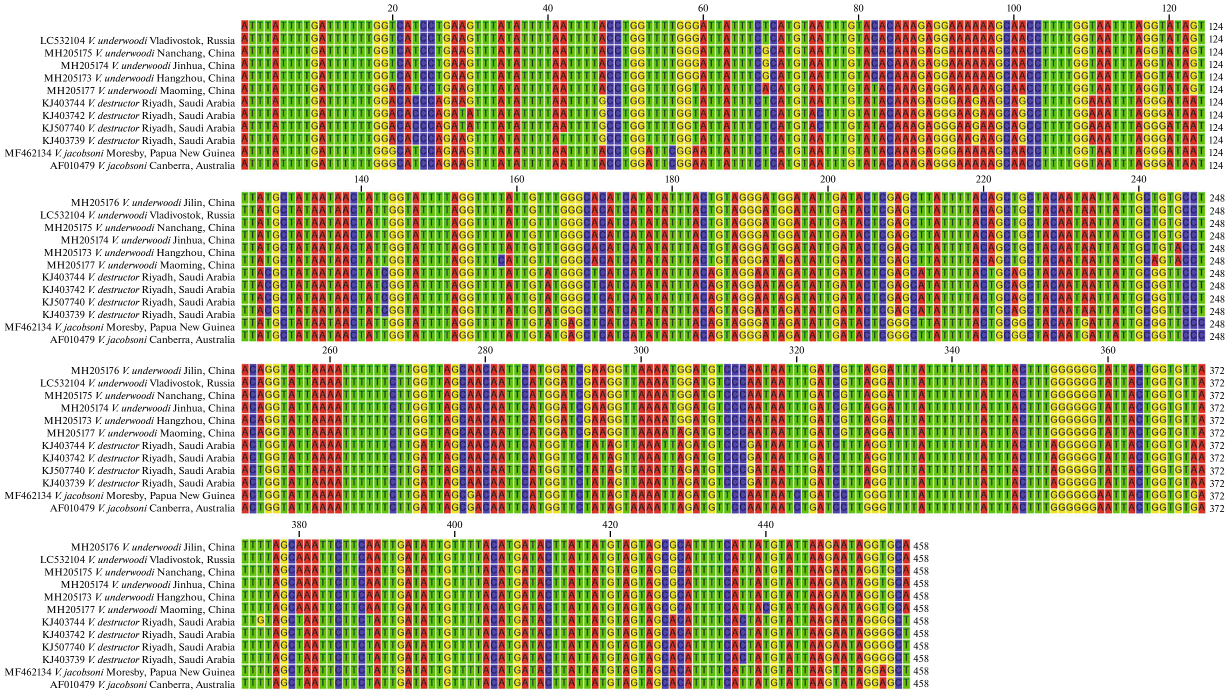

Fig. 1. Comparative analysis of the nucleotide sequence of the mtDNA of the *COX1* gene of ticks *Varroa underwoodi*, *V. destructor*, and *V. jacobsoni*.

specimens correspond to previously published data on *V. underwoodi* (Delfinado-Baker and Aggarwal, 1987; Anderson et al., 1997; Huang, 2004; Wang et al., 2019a).

A comparative analysis of the mtDNA of the *COX1* gene nucleotide sequence was carried out for the mite species *V. underwoodi*, *V. destructor*, and *V. jacobsoni*. Aligned nucleotide sequences of the mtDNA of the *COX1* gene make it possible to calculate the differences in nucleotides in the corresponding positions in different mite samples (Fig. 1).

All differences between *V. underwoodi*, *V. destructor*, and *V. jacobsoni* were calculated based on *COX1* gene mtDNA sequence polymorphism. Table 1 shows the averaged pairwise estimates of the number of nucleotide and amino acid substitutions, p-distance, and the percentage of genetic divergence based on the *COX1* gene mtDNA sequences of *V. underwoodi* mites (LC532104 (Primorsky krai, Russia), MH205173 (Hangzhou, China), MH205174 (Jinhua, China), MH205175 (Nanchang, China), MH205176 (Jilin, China), MH205177 (Maoming, China)), *V. destructor* (KJ403739, KJ507740, KJ403742, KJ403744 (Riyadh, Saudi Arabia)), and *V. jacobsoni* (MF462134 (Port Moresby, Papua New Guinea), AF010479 (Canberra, Australia)). The nucleotide sequences of the *COX1* gene mtDNA of *V. underwoodi* LC532104 samples from Primorsky krai (Russia) were found to be identical to MH205176 from Jilin Province (China) (Wang et al., 2019a).

The mtDNA of the *COX1* gene sequences of *V. underwoodi*, *V. destructor*, and *V. jacobsoni* differ at a statistically significant level ($p \leq 0.05$). The nucleotide sequence of the mtDNA *COX1* gene makes it possible,

Table 1. Estimation of mean values of p-distance and genetic divergence (below the diagonal) and nucleotide and amino acid substitutions (above the diagonal) between *Varroa* mite species based on the mtDNA *COX1* gene sequence.

Varroa species		*V. underwoodi*	*V. destructor*	*V. jacobsoni*
		$n = 6$	$n = 4$	$n = 2$
		number of nucleotide substitutions/number of amino acid substitutions		
V. underwoodi	p-distance/genetic divergence, %		45/36	44/34
V. destructor		* 0.099/10		33/26
V. jacobsoni		* 0.097/10	* 0.072/7	

* Statistically significant differences ($p \leq 0.05$).

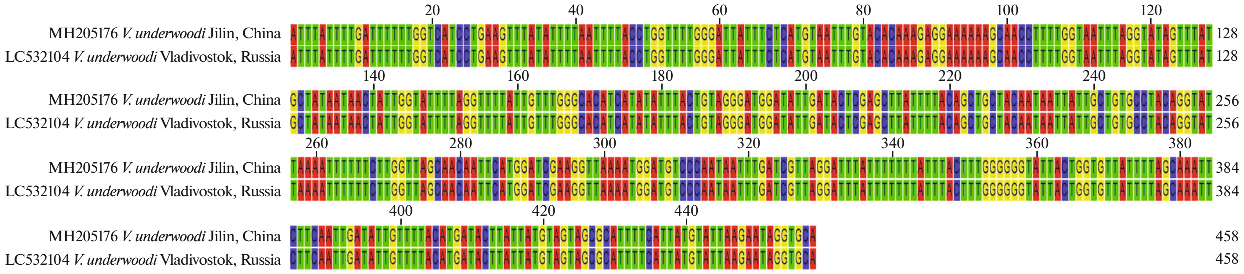

Fig. 2. Comparative analysis of the nucleotide sequence of the mtDNA of the *COX1* gene of *Varroa underwoodi* from China (Jilin) and Russia (Primorsky Territory)—haplotype *China 1 MH205176*.

with a 95% probability, to distinguish between mite species g. *Varroa*. Of the three mite species, *V. destructor* and *V. jacobsoni* are closest to each other with a genetic divergence of 7%. *Varroa underwoodi* is equidistant from *V. destructor* and *V. jacobsoni* and differs from them in the genetic divergence value of 10%.

Table 2 shows pairwise genetic distances, genetic divergence, and the number of nucleotide and amino acid substitutions between each sample of *V. underwoodi* ($n = 6$), *V. destructor* ($n = 4$) and *V. jacobsoni* ($n = 2$), calculated based on the comparison of mtDNA *COX1* gene sequences.

Between samples of the *V. underwoodi* mtDNA *COX1* gene, the values of genetic divergence varied from 0 to 2%, p-distance from 0.000 to 0.022, the number of nucleotide substitutions from 0 to 10 and amino acid substitutions from 0 to 8. No genetic differences were observed between the samples MH205176, *V. underwoodi* (Jilin, China) and LC532104, *V. underwoodi* (Primorsky krai, Russia), as well as MH205175, *V. underwoodi*, (Nanchang, China) and MH205174, *V. underwoodi* (Jinhua, China).

The smallest genetic differences were observed between samples MH205176, *V. underwoodi* (Jilin, China) and MH205175, *V. underwoodi* (Nanchang, China); LC532104, *V. underwoodi* (Primorsky krai, Russia) and MH205175, *V. underwoodi* (Nanchang, China); MH205176, *V. underwoodi* (Jilin, China) and MH205174, *V. underwoodi* (Jinhua, China); and LC532104, *V. underwoodi* (Primorsky krai, Russia) and MH205174, *V. underwoodi* (Jinhua, China). The greatest genetic differences were observed between MH205177 (Maoming, China) and the rest of the *V. underwoodi* specimens. Alignment of the nucleotide sequences of the mtDNA *COX1* gene MH205176 (Jilin, China) and LC532104 (Primorsky krai, Russia) shows the absence of nucleotide substitutions between them. These sequences of the mtDNA *COX1* gene are designated as the *China 1 MH205176* haplotype (Fig. 2) (Ilyasov et al., 2021).

Between *V. destructor* samples, genetic divergence varied from 0 to 1%, p-distance from 0.000 to 0.022, the number of nucleotide substitutions from 0 to 4, and the number of amino acid substitutions from 0 to 1. The smallest genetic differences were observed between *V. destructor* KJ403744 and KJ403739 from Saudi Arabia (Riyadh). No genetic differences were found between specimens *V. destructor* KJ403742 and KJ403740 from Saudi Arabia (Riyadh), nor between specimens *V. jacobsoni* MF462134 from Papua New Guinea (Port Moresby) and AF010479 from Australia (Canberra).

We constructed a dendrogram of phylogenetic relationships using the nearest neighbor method with 2000 bootstrap replications based on p-distances between mtDNA *COX1* gene sequences of three species of mites *V. underwoodi*, *V. destructor*, and *V. jacobsoni*. The *COX1* gene mtDNA sequence LC532104 of *V. underwoodi* from Russia (Primorsky krai) (*China 1* haplotype *MH205176*) is combined into one cluster with all sequences of *V. underwoodi* representatives MH205173, MH205174, MH205176, MH205177 from China. The *COX1* mtDNA sequences of representatives of *V. destructor* KJ403739, *KJ403742*, *KJ403742*, *KJ403742* (Riyadh, Saudi Arabia) and representatives of *V. jacobsoni* MF462134 (Port Moresby, Papua New Guinea), AF010479 (Canberra, Australia) are affiliated to separate clusters (Fig. 3).

On the dendrogram of phylogenetic relationships in the *V. underwoodi* cluster, specimen LC532104 (Primorsky krai, Russia) is located closest to the northernmost specimen MH205176 (Jilin, China), located at a distance of 450 km, and furthest from the southernmost specimen MH205177 (Maoming, China), located at a distance of 3000 km. The *V. underwoodi* cluster is genetically closer to the *V. destructor* cluster than to the *V. jacobsoni* cluster. The southern specimen MH205177 *V. underwoodi* (Maoming, China) is the most distant from the other *V. underwoodi* specimens and is closer to the *V. destructor* cluster (Fig. 3).

DISCUSSION

The *Varroa underwoodi* mite probably originated in the southern regions of Asia and later spread north as a result of co-migration with *Apis cerana* bees. Previous studies based on the study of mtDNA morphology and the *COX1* gene showed parasitism of the *V. underwoodi* mite in *A. cerana* bee colonies in Nepal (Delfi-

Table 2. Pairwise differences and genetic divergence between *Varroa* species calculated from *COX1* gene sequence polymorphisms

Species *Varroa*		1. MH205176, *V. underwoodi*	2. LC532104, *V. underwoodi*	3. MH205175, *V. underwoodi*	4. MH205174, *V. underwoodi*	5. MH205173, *V. underwoodi*	6. MH205177, *V. underwoodi*	7. KJ403744, *V. destructor*	8. KJ403742, *V. destructor*	9. KJ507740, *V. destructor*	10. KJ403739, *V. destructor*	11. MF462134, *V. jacobsoni*	12. AF010479, *V. jacobsoni*
		number of nucleotide substitutions/number of amino acid substitutions											
1. MH205176, *V. underwoodi*, Jilin, China	p-distance/genetic divergence, %		0/0	1/1	1/1	2/2	10/8	44/36	46/36	46/36	44/35	44/34	4 /34
2. LC532104, *V. underwoodi*, Primorsky krai, Russia		0.000/0		1/1	1/1	2/2	10/8	44/36	46/36	46/36	44/35	44/34	44/34
3. MH205175, *V. underwoodi*, Nanchang, China		0.002/0	0.002/0		0/0	1/1	10/8	45/37	47/37	47/37	45/36	45/35	45/35
4. MH205174, *V. underwoodi*, Jinhua, China		0.002/0	0.002/0	0.000/0		1/1	10/8	45/37	47/37	47/37	45/6	45/35	45/35
5. MH205173, *V. underwoodi*, Hangzhou, China		0.004/0	0.004/0	0.002/0	0.002/0		9/7	45/37	47/37	47/37	45/36	45/35	45/35
6. MH205177, *V. underwoodi*, Maoming, China		0.022/2	0.022/2	0.022/2	0.022/2	0.020/2		42/36	44/36	44/36	42/35	44/36	44/36
7. KJ403744, *V. destructor*, Saudi Arabia		0.096/10	0.096/10	0.098/10	0.098/10	0.098/10	0.092/9		4/2	4/2	2/1	32/27	32/27
8. KJ403742, *V. destructor*, Saudi Arabia		0.100/10	0.100/10	0.103/10	0.103/10	0.103/10	0.096/10	0.009/1		0/0	4/1	34/27	34/27
9. KJ507740, *V. destructor*, Saudi Arabia		0.100/10	0.100/10	0.103/ 0	0.103/10	0.103/10	0.096/10	0.009/1	0.000/0		4/1	34/27	34/27
10. KJ403739, *V. destructor*, Saudi Arabia		0.096/10	0.096/10	0.098/10	0.098/10	0.098/10	0.092/9	0.004/1	0.009/1	0.009/1		32/26	32/26
11. MF462134, *V. jacobsoni*, Papua New Guinea		0.096/10	0.096/10	0.098/10	0.098/10	0.098/10	0.096/10	0.070/7	0.074/7	0.074/7	0.070/7		0/0
12. AF010479, *V. jacobsoni*, Australia		0.096/10	0.096/10	0.098/10	0.098/10	0.098/10	0.096/10	0.070/7	0.074/7	0.074/7	0.070/7	0.000/0	

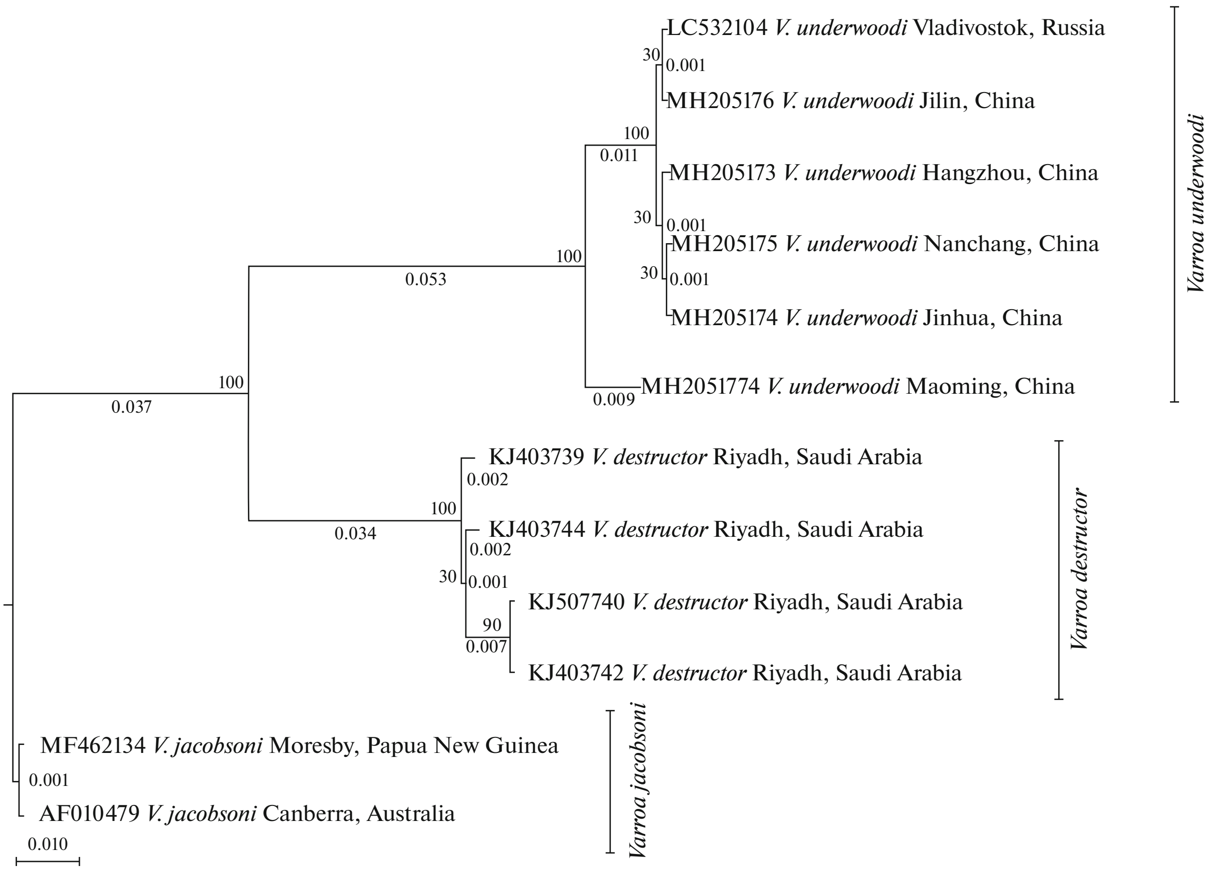

Fig. 3. Dendrogram of phylogenetic relationships by nearest neighbor method with 2000 bootstrap replications based on p-distances between mtDNA *COX1* gene sequences of three *Varroa* species. The numbers on each branch indicate genetic distances.

nado-Baker and Aggarwal, 1987), South Korea (Woo, 1992; Kuznetsov, 2005; Chantawannakul et al., 2016), Indonesia (Anderson et al., 1997; Chantawannakul et al., 2016), Papua New Guinea (Lee, 1995; Anderson et al., 1997; Chantawannakul et al., 2016), China (Huang, 2004; Wang et al., 2019a), as well as Vietnam and Japan (Guzman and Rinderer, 1999; Chantawannakul et al., 2016). Relatively recently, *V. underwoodi* was also detected in Russia (Primorsky krai) (Kuznetsov, 2005; Kuznetsov and Lelej, 2005; Ilyasov et al., 2021). We have shown the distribution of *V. underwoodi* in the Russian Far East in colonies of *A. cerana ussuriensis* bees using the methods of morphometry and sequencing of the mtDNA of the *COX1* mitochondrial gene (Figs. 1, 2) (Ilyasov et al., 2021). The site of discovery of *V. underwoodi* in Primorye is located at a distance of 450 km from the site of discovery of this species in northern China (Ilyasov et al., 2021). According to the results of a comparative analysis of the mtDNA of the *COX1* gene (Fig. 3), all specimens of *V. underwoodi* are combined into one cluster, except for the MH205177 sample (Maoming, China), which is grouped separately (Fig. 3). This specimen should probably be attributed to a new *V. underwoodi* subspecies or even a new species within genus *Varroa*, which may be elucidated additional special research.

V. underwoodi mites have probably always been found in small numbers in the natural population of *A. cerana* wild bees living in tree cavities in Primorsky krai in Russia. In the hives of *A. cerana*, the conditions for the reproduction of *V. underwoodi* turned out to be more favorable than in hollow trees, which led to an increase in the number of mites in apiaries. According to V.N. Kuznetsov (2005), in 2002, in the drone brood of *A. cerana* in the apiary, *V. underwoodi* mites were found only once, but in 2004, mass reproduction of *V. underwoodi* was observed. In 2004, the drone brood in the apiary was infected with *V. underwoodi* mites at 2.8% in June, 35% in July, and 58% in August, while worker bees were only 1% infected. It should be noted that individual drone cells of *A. cerana* contained up to 5–6 adults and 2–3 *V. underwoodi* nymphs. Adults and nymphs of *V. underwoodi* were found on the pupae of *A. cerana* drones and were rarely observed in the brood of worker bees. *V. underwoodi* females were mostly found on young drones and very rarely on young *A. cerana* worker bees. In the summer of 2004, up to 16% of young drones were infected with *V. underwoodi* mites, but adult bees were free of mites in autumn. It is possible that a large number of mites on the brood of bees contributed to the active swarming of *A. cerana* families to clean the bee colony from mites. In 2004, frequent swarming of *A. cerana* colonies was observed in an apiary heavily infected with *V. underwoodi* mites (Kuznetsov, 2005). Presently in Russia, *A. cerana* bees are not bred in special hives in apiaries to obtain honey. This species of honey bee has survived in the Far East of Russia in the wild and lives in forests in hollows of trees.

The level of infection of bees with *V. underwoodi* mites is significantly higher in the northern provinces of China than in the southern provinces (Wang et al., 2019a). This is because that mass reproduction of mites occurs in colonies of bees that grow a brood during the winter flightless period. Higher levels of *V. underwoodi* infestation in North Asia are affected by drone brood rearing time, which is slightly shorter in colder climates (Wang et al., 2019a). The identity of the mtDNA of the *COX1* gene sequences of *V. underwoodi* from Primorsky krai (Russia) LC532104 and Jilin Province (China) MH205176 suggests that the *China 1 MH205176 V. underwoodi* haplotype is adapted to parasitize *A. cerana* bees living in the cold climate of North Asia. It is possible that the Far East region is inhabited by a single population of *V. underwoodi* haplotype *China 1 MH205176*, distributed over the vast territory of North Asia as a result of migration of *A. cerana* families (Traynor et al., 2020; Ilyasov et al., 2021).

Varroa mites collected in Primorsky krai (Russia) are identified as *V. underwoodi* based on their morphometry, which is in the range of previously described populations of this species (Delfinado-Baker and Aggarwal, 1987; Anderson et al., 1997; Huang, 2004; Wang et al., 2019a), as well as the *COX1* gene sequence mtDNA, which was identical to the MH205176 sample from Jilin Province (China) (Table 2, Fig. 2) (Wang et al., 2019a; Ilyasov et al., 2021). The length and width of the body of adult females of *V. underwoodi* from Primorsky krai is slightly greater than that of representatives of this species from southern populations, which can be explained by its northern distribution. The rate of molecular evolution in mite species g. *Varroa* is very low and their genomes are more conserved than those of their host bee species g. *Apis* (Ilyasov et al., 2021). These genetic features of *V. underwoodi* representatives from the remote regions of the Russian Far East and Northern China can be explained by the parasitic mode of life within *A. cerana* families. Similarly, the absence of differences between *V. destructor* specimens from remote regions of Saudi Arabia, on the one hand, and Papua New Guinea and Australia, on the other hand, can be explained.

The average level of genetic divergence between *V. destructor* and *V. jacobsoni* in this work (7%) is very close to that (6%) between *V. destructor* from seven countries (South Korea, France, Vietnam, China, Japan, Nepal, and Sri Lanka) and *V. jacobsoni* from four countries (Indonesia, Malaysia, Laos, and Papua New Guinea) (Table 1) (Techer et al., 2019). The average genetic divergence between the three mite species *V. underwoodi*, *V. destructor*, and *V. jacobsoni* in the nucleotide sequence of the mtDNA *COX1* gene varies from 7 to 10%, and the p-distance ranges from 0.072 to 0.099. This is consistent with the range of genetic differences between insect species (8–17% and 0.100–0.200, respectively) (Tan et al., 2007; Han et al., 2016; Eimanifar et al., 2017; Ilyasov et al., 2018, 2019).

The presence of *V. underwoodi* mites in closed cells of the worker brood in one family of *A. mellifera* in Papua New Guinea (Roberts et al., 2015) indicates that interspecific host change and *V. underwoodi* transition from *A. cerana* to *A. mellifera* can occur. At present, *V. underwoodi* is not found on a large scale in apiaries in the families of *A. mellifera* in the Russian Far East. However, the migration of *A. cerana* between Russia and China may lead to the emergence of new *V. underwoodi* haplotypes from China in the Russian Far East, which are capable of parasitizing *A. mellifera* families. The *V. underwoodi* mite is genetically close to *V. destructor*, which is a common parasite of both *A. mellifera* and *A. cerana*, so the transition of *V. underwoodi* to *A. mellifera* is highly probable (Roberts et al., 2020). One must be prepared for the emergence of a new parasite *V. underwoodi* in *A. mellifera* bees with devastating effects on the population (Anderson, 2000; Anderson and Trueman, 2000; Muñoz et al., 2008; Rosenkranz et al., 2010; Roberts et al., 2015; Wang et al., 2019a; Ilyasov et al., 2021).

Destructive effects to *A. mellifera* bees can be caused not so much by the mites themselves, but by the transmission of new pathogens that are not characteristic of this species—viruses and bacteria. The parasitic mites *V. destructor* and *V. underwoodi* have a different species composition of the gut microbiome and can carry different types of viruses (eight RNA viruses and one DNA virus) (Sandionigi et al., 2015; Wang et al., 2019b; Sacca and Lodesani, 2020; Chen et al., 2021). In the *A. cerana* population, *V. destructor* mites carry *DWV, IAPV, BQCV, KBV, CBPV, SBV*, and *AmFV* viruses, while *V. underwoodi* carries *DWV, CBPV, AmFV, BQCV, IAPV*, and *KBV* viruses (Wang et al., 2019b; Chen et al., 2021). In addition, the same virus has a different effect on different types of bees. Thus, the Korean Sacbrood Virus (*kSBV*) destroyed 95% of the *A. cerana* population and was not virulent for the *A. mellifera* population (Choi et al., 2010; Koetz, 2013; Vung et al., 2017; Wang et al. , 2019b). In colonies of *A. mellifera* bees infected with the parasitic mite *V. destructor*, there was an increased number of *Snodgrassella alvi* bacteria and a decrease in the number of bacteria of the Lactobacillaceae family in the intestines of worker bees (Hubert et al., 2017; Marche et al., 2019; Bleau et al., 2020). The microbiome of mite-infested larvae becomes similar to that of *V. destructor*, indicating an exchange of the gut microbiome between the bee and the ectoparasitic mite (Sandionigi et al., 2015). Artificial infection of bees with the pathogenic microsporidia *Nosema ceranae* also changes the composition of the intestinal microbiome and provokes an increase in the abundance of the bacterium *Gilliamella apicola* (Rubanov et al., 2019). Infection with the parasitic mite *V. destructor* is a more important factor in the disruption and changes in the composition of the intestinal microbiome of adult *A. mellifera* bees than infection with microsporidia *Nosema ceranae*, *N. apis*, and trypanosome *Lotmaria passim* (Hubert et al., 2017). To combat these parasites, beekeepers often use chemicals such as fumagillin (against *Nosema* spp.) and oxalic acid (against *V. destructor*), which in turn reduce the diversity and abundance of *A. mellifera* gut microbiome bacteria (Raymann et al., 2017; Diaz et al., 2019). Such changes in the gut microbiome of bees can negatively affect physiology, immunity, survival, and adaptation to environmental conditions (Bleau et al., 2020; Sacca and Lodesani, 2020; Ilyasov et al., 2021).

To combat the spread of *V. destructor* and prevent the potential transition of *V. underwoodi*, it is possible to use selection of bees for hygienic behavior resistant to parasitism by *Varroa* spp. mites. There are currently nine *V. destructor* mite-resistant *A. mellifera* honey bee populations in the world, which have been developed through targeted breeding: (1) the North County Dublin honey bee population in Ireland; (2) the population of the honey bee subspecies *A. m. scutellata* in Brazil and South Africa; (3) the population of honey bees in Toulouse in France; (4) the population of honey bees on the island of Fernando de Noronha in Brazil; (5) the coastal population of honey bees in the Primorsky krai of Russia; (6) the population of honey bees in Gotland, Sweden; (7) the honey bee population of Avignon in France; (8) Arnot Forest Ithaca honey bee population in New York State, USA; and (9) the honey bee population on Marmara Island in Turkey (Mondragón et al., 2005; Allsopp, 2006; Locke and Fries, 2011; Çakmak and Fuchs, 2013; Locke, 2016; Conlon et al., 2018; McMullan, 2018; Alphen and Fernhout, 2020). Selection of honey bee colonies based on hygienic behavior for resistance to the *V. destructor* mite will make it possible to use less acaricides and prevent disturbances in the intestinal microbiome, which provides the protective function of the body and plays an important role in the immunity and adaptation of bees to environmental conditions (Çakmak and Fuchs, 2013). Selection of bee colonies for hygienic behavior against the *V. destructor* mite may also be effective against the *V. underwoodi* mite.

CONCLUSIONS

Until recently, the known range of *Varroa underwoodi* mites covered almost all countries where the honey bee *Apis cerana* is found, including the Russian Far East. The identity of the *COX1* gene sequences in *V. underwoodi* specimens from Northern China and Primorsky Krai of Russia, separated by 450 km from each other, indicates the possible free migration of *A. cerana* and the dispersal of the parasite, as well as the low rate of molecular evolution of the *V. underwoodi* genome as a result of parasitic lifestyle. Although the northern boundaries of the range of *V. underwoodi* have not yet been studied, in 2020 samples of *A. cerana ussuriensis* were collected in the area of the village of Terney, Primorsky krai (45.06° N, 136.61° E), the northern border of the range of this bee species. Thus, it is possible that the northern boundary of the range of the mite *V. underwoodi* will coincide with the northern boundary of the range of *A. cerana*. In the future, characterization of the *V. underwoodi* population is planned using additional *COX3, ATP6*, and *CYTB* markers, which will make it possible to find genetic differences between Russian and Chinese specimens of *V. underwoodi* and identify its biogeographic relationships. The honey bee *A. mellifera* may become a new host for the parasitic mite *V. underwoodi*, as it is widely found in *A. cerana* colonies adjacent to *A. mellifera* colonies. The possible transition of the *V. underwoodi* mite to a new host, *A. mellifera*, may be accompanied by the transmission of new species and strains of viruses and bacteria, changes in the gut microbiome, immune suppression, and adaptation to changing climatic conditions. Selection of honey bee colonies based on hygienic behavior for resistance to the *V. destructor* mite can be an effective defense against the transition of the closely related mite *V. underwoodi* from *A. cerana* to *A. mellifera*.

ACKNOWLEGEMENTS

The authors are grateful to T.F. Domatskaya and V.E. Gokhman for the review and revision of the article.

FUNDING

This work was supported by the state assignment (registration number AAAA-A21-121011990120-7)—I.R., grants from the Russian Foundation for Basic Research (RFBR) (grant no. 19-54-70002 e-Asia_t)—N.A. and Postdoctoral Research Program at Incheon National University (2017–2019)—I.R.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare no conflict of interest.

This article does not contain the results of any studies using warm-blooded animals as subjects.

REFERENCES

Allsopp M.H., Analysis of *Varroa destructor* infestation of Southern African honeybee populations, *MSc (Nat.*

and Agric. Sci.) Dissertation, Pretoria: Univ. Pretoria, 2006.

Anderson, D.L., Variation in the parasitic bee mite *Varroa jacobsoni* Oud., *Apidologie,* 2000, vol. 31, no. 2, pp. 281–292.

Anderson, D.L. and Trueman, J.W., *Varroa jacobsoni* (Acari: Varroidae) is more than one species, *Exp. Appl. Acarol.,* 2000, vol. 24, no. 3, pp. 165–189.

Anderson, D.L., Halliday, R.B., and Otis, G.W., The occurrence of *Varroa underwoodi* (Acarina: Varroidae) in Papua New Guinea and Indonesia, *Apidologie,* 1997, vol. 28, nos. 3–4, pp. 143–147.

Bleau, N., Bouslama, S., Giovenazzo, P., and Derome, N., Dynamics of the honeybee (*Apis mellifera*) gut microbiota throughout the overwintering period in Canada, *Microorganisms,* 2020, vol. 8, no. 8. https://doi.org/10.3390/microorganisms8081146

Çakmak, I. and Fuchs, S., Exploring a treatment strategy for long-term increase of *Varroa* tolerance on Marmara Island, Turkey, *J. Apic. Res,* 2013, vol. 52, no. 5, pp. 242–250.

Chantawannakul, P., Guzman, L.I., Li, J., and Williams, G.R., Parasites, pathogens, and pests of honeybees in Asia, *Apidologie,* 2016, vol. 47, pp. 301–324.

Chen, G., Wang, S., Jia, S., Feng, Y., Hu, F., et al., A new strain of virus discovered in China specific to the parasitic mite *Varroa destructor* poses a potential threat to honey bees, *Viruses,* 2021, vol. 13. https://doi.org/10.3390/v13040679

Choi, Y.S., Lee, M.Y., Hong, I.P., Kim, N.S., Kim, H.K., et al., Occurrence of sacbrood virus in Korean apiaries from *Apis cerana* (Hymenoptera: Apidae), *J. Apic.,* 2010, vol. 25, pp. 187–191.

Conlon, B.H., Frey, E., Rosenkranz, P., Locke, B., Moritz, R.F.A., and Routtu, J., The role of epistatic interactions underpinning resistance to parasitic *Varroa* mites in haploid honey bee (*Apis mellifera*) drones, *J. Evol. Biol,* 2018, vol. 31, no. 6, pp. 801–809.

De Guzman, L.I. and Delfinado-Baker M., A new species of *Varroa* (Acari: Varroidae) associated with *Apis koschevnikovi* (Apidae: Hymenoptera) in Borneo, *Int. J. Acarology,* 1996, vol. 22, no. 1, pp. 23–27.

De Guzman, L.I. and Rinderer, T.E., Identification and comparison of *Varroa* species infesting honey bees, *Apidologie,* 1999, vol. 30, nos. 2–3, pp. 85–95.

De Guzman, L.I., Rinderer, T.E., Delatte G.T., and Macchiavelli R.E., *Varroa jacobsoni* Oudemans tolerance in selected stocks of *Apis mellifera* L., *Apidologie,* 1996, vol. 27, no. 4, pp. 193–210.

Delfinado-Baker, M. and Aggarwal, K., A new *Varroa* (Acari: Varroidae) from the nest of *Apis cerana* (Apidae), *Int. J. Acarology,* 1987, vol. 13, no. 4, pp. 233–237.

Diaz, T., Del-Val, E., Ayala, R., and Larsen, J., Alterations in honey bee gut microorganisms caused by *Nosema* spp. and pest control methods, *Pest Manage. Sci.*, 2019, vol. 75, no. 3, pp. 835–843.

Eimanifar, A., Kimball, R.T., Braun, E.L., Moustafa, D.M., Haddad, N., et al., The complete mitochondrial genome of the Egyptian honey bee, *Apis mellifera lamarckii* (Insecta: Hymenoptera: Apidae), *Mitochondrial DNA B Resour.,* 2017, vol. 2, no. 1, pp. 270–272.

Excoffier, L. and Lischer, H.E., Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows, *Mol. Ecol. Resour.,* 2010, vol. 10, no. 3, pp. 564–567.

Hadisoesilo, S., A comparative study of two species of cavity-nesting honey bees of Sulawesi, Indonesia, *PhD Thesis,* Guelph: The Univ. Guelph, 1997.

Hadisoesilo, S. and Otis, G.W., Differences in drone cappings of *Apis cerana* and *Apis nigrocincta, J. Apic. Res,* 1998, vol. 37, no. 1, pp. 11–15.

Han, T., Lee, W., Lee, S., Park, I.G., and Park, H., Reassessment of species diversity of the subfamily Denticollinae (Coleoptera: Elateridae) through DNA barcoding, *PLOS One,* 2016, vol. 11, no. 2. https://doi.org/10.1371/journal.pone.0148602

Huang, S., The main kinds of honeybee ectoparasitic mites and the first found of *Varroa underwoodi* in China, *Apic. China,* 2004, vol. 55, p. 6. (In Chinese)

Hubert, J., Bicianova, M., Ledvinka, O., Kamler, M., Lester, P.J., et al., Changes in the bacteriome of honey bees associated with the parasite *Varroa destructor,* and pathogens *Nosema* and *Lotmaria passim, Microb. Ecol.,* 2017, vol. 73, no. 3, pp. 685–698.

Ilyasov, R.A., Park, J., Takahashi, J., and Kwon, H.W., Phylogenetic uniqueness of honeybee *Apis cerana* from the Korean peninsula inferred from the mitochondrial, nuclear, and morphological data, *J. Apic. Sci.,* 2018, vol. 62, no. 2, pp. 189–214.

Ilyasov, R.A., Han, G.Y., Lee, M.-L., Kim, K.W., Proshchalykin, M.Y., et al., Phylogenetic relationships of Russian Far-East *Apis cerana* with other North Asian populations, *J. Apic. Sci.,* 2019, vol. 63, no. 2, pp. 289–314.

Ilyasov, R.A., Marsova M.V., Kovtun A.S., Vatlin A.A., Yunes R.A., et al., Role of the gut microbiome of the honey bee, *Pchelovodstvo,* 2021a, no. 7, pp. 18–20.

Ilyasov, R.A., Takahashi, J.I., Proshchalykin, M.Y., Lelej, A.S., Lee, M.L., et al., First evidence of presence of *Varroa underwoodi* mites on native *Apis cerana* colonies in Primorsky Territory of Russia based on COX1 gene, *J. Apic. Sci.,* 2021b, vol. 65, no. 1, pp. 177–186.

Koetz, A.H., Ecology, behaviour and control of *Apis cerana* with a focus on relevance to the Australian incursion, *Insects*, 2013, vol. 4, pp. 558–592.

Kolar, C.S. and Lodge, D.M., Predicting invaders: response from Kolar and Lodge, *Trends Ecol. Evol.,* 2001, vol. 16, no. 10, p. 546.

Kumar, S., Stecher, G., Li, M., Knyaz, C., and Tamura, K., MEGA X: molecular evolutionary genetics analysis across computing platforms, *Mol. Biol. Evol.,* 2018, vol. 35, no. 6, pp. 1547–1549.

Kuznetsov, V.N., *Kitaiskaya voskovaya pchela Apis cerana cerana F. (Hymenoptera, Apidae) na Dal'nem Vostoke Rossii* (Chinese Wax Bee *Apis cerana cerana* F. (Hymenoptera, Apidae) in the Russian Far East), Moscow: KMK, 2005.

Kuznetsov, V.N. and Lelej, A.S., On the parasitism of mites *Varroa* Oudemans, 1904 (Acari: Varroidae) on the Chinese wax bee *Apis cerana cerana* Fabricius, 1793 (Hymenoptera: Apidae) in Primorsky krai, *Chteniya pamyati A.I. Kurentsova,* 2005, no. 16, pp. 39–46.

Lee, B., Mites, bees, and plagues that are and might be, *Partners in Research for Development,* 1995, no. 8, pp. 2–9.

Lin, Z., Wang, S., Neumann, P., Chen, G., Page, P., et al., Population genetics and host specificity of *Varroa de-*

structor mites infesting eastern and western honeybees, *J. Pest Sci.,* 2021, vol. 94, no. 4, pp. 1487–1504.

Locke, B., Natural *Varroa* mite-surviving *Apis mellifera* honeybee populations, *Apidologie,* 2016, vol. 47, no. 3, pp. 467–482.

Locke, B. and Fries, I., Characteristics of honey bee colonies (*Apis mellifera*) in Sweden surviving *Varroa destructor* infestation, *Apidologie,* 2011, vol. 42, no. 4, pp. 533–542.

Marche, M.G., Satta, A., Floris, I., Pusceddu, M., Buffa, F., and Ruiu, L., Quantitative variation in the core bacterial community associated with honey bees from *Varroa*-infested colonies, *J. Apic. Res,* 2019, vol. 58, no. 3, pp. 444–454.

McMullan, J., Adaptation in honey bee (*Apis mellifera*) colonies exhibiting tolerance to *Varroa destructor* in Ireland, *Bee World,* 2018, vol. 95, no. 2, pp. 39–43.

Mondragón, L., Spivak, M., and Vandame, R., A multifactorial study of the resistance of honeybees *Apis mellifera* to the mite *Varroa destructor* over one year in Mexico, *Apidologie,* 2005, vol. 36, no. 3, pp. 345–358.

Muñoz, I., Dall'Olio, R., Lodesani, M., and De La Rúa, P., Sequence variation in the mitochondrial tRNAleu-COX2 intergenic region of African and African-derived honey bee populations, *EurBee. 3rd European Conference of Apidology,* Belfast: Queens Univ. P., 2008, p. 73.

Navajas, M., Anderson, D.L., Guzman, L.I., Huang, Z.Y., Clement, J., et al., New Asian types of *Varroa destructor*: a potential new threat for world apiculture, *Apidologie,* 2010, vol. 41, pp. 181–193.

Oudemans, A.C., On a new genus and species of parasitic Acari, *Notes from the Leyden Museum,* 1904, vol. 24, pp. 216–222.

Rath, W., Co-adaptation of *Apis cerana* Fabr. and *Varroa jacobsoni* Oud., *Apidologie,* 1999, vol. 30, nos. 2–3, pp. 97–110.

Raymann, K., Shaffer, Z., and Moran, N.A., Antibiotic exposure perturbs the gut microbiota and elevates mortality in honeybees, *PLoS Biol.,* 2017, vol. 15, no. 3. https://doi.org/10.1371/journal.pbio.2001861

Roberts, J.M., Anderson, D.L., and Tay, W.T., Multiple host shifts by the emerging honeybee parasite, *Varroa jacobsoni, Mol. Ecol.,* 2015, vol. 24, no. 10, pp. 2379–2391.

Roberts, J.M.K., Schouten, C.N., Sengere, R.W., Jave, J., and Lloyd, D., Effectiveness of control strategies for *Varroa jacobsoni* and *Tropilaelaps mercedesae* in Papua New Guinea, *Exp. Appl. Acarol.,* 2020, vol. 80, no. 3, pp. 399–407.

Rosenkranz, P., Aumeier, P., and Ziegelmann, B., Biology and control of *Varroa destructor, J. Invertebr. Pathol.,* 2010, vol. 103, suppl. 1, pp. 96–119.

Rubanov, A., Russell, K.A., Rothman, J.A., Nieh, J.C., and McFrederick, Q.S., Intensity of *Nosema ceranae* infection is associated with specific honey bee gut bacteria and weakly associated with gut microbiome structure, *Sci. Rep.,* 2019, vol. 9. https://doi.org/10.1038/s41598-019-40347-6

Sacca, M.L. and Lodesani, M., Isolation of bacterial microbiota associated to honey bees and evaluation of potential biocontrol agents of *Varroa destructor, Benefic. Microbes,* 2020, vol. 11, no. 7, pp. 641–654.

Sandionigi, A., Vicario, S., Prosdocimi, E.M., Galimberti, A., Ferri, E., et al., Towards a better understanding of *Apis mellifera* and *Varroa destructor* microbiomes: introducing 'phyloh' as a novel phylogenetic diversity analysis tool, *Mol. Ecol. Resour.,* 2015, vol. 15, no. 4, pp. 697–710.

Sanger, F., Nicklen, S., and Coulson, A.R., DNA sequencing with chain-terminating inhibitors, *Proc. Natl. Acad. Sci. USA,* 1977, vol. 74, no. 12, pp. 5463–5467.

Tan, K., Warrit, N., and Smith, D.R., Mitochondrial DNA diversity of Chinese *Apis cerana, Apidologie,* 2007, vol. 38, pp. 238–246.

Techer, M.A., Rane, R.V., Grau, M.L., Roberts, J.M.K., Sullivan, S.T., et al., Divergent evolutionary trajectories following speciation in two ectoparasitic honey bee mites, *Commun. Biol.,* 2019, vol. 2. https://doi.org/10.1038/s42003-019-0606-0

Traynor, K.S., Mondet, F., Miranda, J.R., Techer, M., Kowallik, V., et al., *Varroa destructor*: a complex parasite, crippling honey bees worldwide, *Trends Parasitol.,* 2020, vol. 36, no. 7, pp. 592–606.

Van Alphen, J.J.M. and Fernhout B.J., Natural selection, selective breeding, and the evolution of resistance of *honeybees* (*Apis mellifera*) against *Varro*a, *Zoological Letters,* 2020, vol. 6. https://doi.org/10.1186/s40851-020-00158-4

Vavilov, N.I., The law of homologous series in hereditary variability, in *Tr. 3-go Vseross. s"ezda po selektsii i semenovodstvu* (Proc. 3rd All-Russian Congress on Selection and Seed Production), Saratov: Gubpoligrafotdel, 3-e Otdelenie, 1920, pp. 41–56.

Vung, N.N., Lee, M.-L., Lee, M.-Y., Kim, H.K., Kang, E.J., et al., Breeding and selection for resistance to Sacbrood Virus for *Apis cerana, J. Apic.,* 2017, vol. 32, no. 4, pp. 345–352.

Wang, S., Chen, G., Lin, Z., Wu, Y., Hu, F., et al., Occurrence of multiple honeybee viruses in the ectoparasitic mites *Varroa* spp. in *Apis cerana* colonies, *J. Invertebr. Pathol.,* 2019a, vol. 166. https://doi.org/10.1016/j.jip.2019.107225

Wang, S., Lin, Z., Dietemann, V., Neumann, P., Wu, Y., et al., Ectoparasitic mites *Varroa underwoodi* (Acarina: Varroidae) in eastern honeybees, but not in western honeybees, *J. Econ. Entomol.,* 2019b, vol. 112, no. 1, pp. 25–32.

Warrit, N., Hagen, T.A.R., Smith, D.R., and Çakmak, I., A survey of *Varroa destructor* strains on *Apis mellifera* in Turkey, *J. Apic. Res.,* 2004, vol. 43, no. 4, pp. 190–191.

Woo, K.S., New honeybee mite *Varroa underwoodi* on *Apis cerana* in South Korea, *Honeybee Sci.,* 1992, vol. 13, pp. 173–174 (in Japanese).

Woolhouse, M.E., Haydon, D.T., and Antia, R., Emerging pathogens: the epidemiology and evolution of species jumps, *Trends Ecol. Evol.,* 2005, vol. 20, no. 5, pp. 238–244.

Zheng, H.-Q., Wei, W.-T., and Hu, F.-L., Beekeeping industry in China, *Bee World,* 2011, vol. 88, pp. 41–44.

Zheng, H., Cao, L., Huang, S., Neumann, P., and Hu, F., Current status of the beekeeping industry in China, in *Asian Beekeeping in the 21st Century*, Heidelberg: Springer, 2018, pp. 125–158.

Translated by A. Deryabina