



***VAIRIMORPHA APIS* VERSUS *VAIRIMORPHA CERANAE*, REPLACEMENT OR DYNAMIC PREVALENCE?**

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ABSTRACT

Nosematosis is currently a frequently discussed disease of bees caused by two species of microsporidia: *Vairimorpha apis*, and *Vairimorpha ceranae*. *Vairimorpha apis* represents the original species of *Apis mellifera* parasite, and *Vairimorpha ceranae*, is a species introduced from Asia. In the last two decades, epidemiological data on the growth of the prevalence of *V. ceranae* infection have increased, which has led to its dominant position at the expense of its congener *V. apis*, practically all over the world. This process is assumed to be the result of asymmetric competition within the host, where *V. ceranae*, showed a better ability to adapt to higher temperatures, which was first manifested by its spread in warmer climate zones. However, several results of studies from recent years somewhat unexpectedly showed that it is premature to talk about the complete replacement of *V. apis* by *V. ceranae*. They pointed to a greater influence of seasonality and average temperatures in winter and summer in a given year on the result of the current prevalence of infection and co-infection of *Vairimorpha* spp., regardless of the climatic zone in which the colonies were located. Considering the different clinical and subclinical manifestations of

infection caused by *V. apis*, and *V. ceranae*, and its impact on the defense, survival and productivity of bee colonies, the aim of our work was to analyze the factors affecting the distribution and prevalence of *Vairimorpha* spp.

Key words: nosematosis; prevalence of infection; *Vairimorpha apis*; *Vairimorpha ceranae*

INTRODUCTION

Honey bees (*Apis mellifera*) are one of the most important animal species for human nutrition, as they pollinate up to 78 % of flowering plants on Earth and approximately 70 % of the main agricultural crops. Unlike other pollinators, honey bees do not specialize in certain types of plants, they fly to a distance of approx. 4.5 km from the hive, so one bee colony is able to pollinate an area of up to 6360 ha [64]. Honey bees (*Apis mellifera*) pollinate 9.5 % of agricultural crops intended for human consumption [48], and their economic importance also lies in the production of honey and other bee products, and the contribution of bees to the preservation of biodiversity is also significant. In the last 50 years, the volume of cultivation of crops dependent

on bee pollination has tripled, which places demands on the number of honey bee colonies [48, 26].

According to FAO estimates, there were 22.5 million bee colonies in Europe in 1990. By the turn of the millennium, their number had fallen. Although populations are recovering, in 2021 there were approximately 25.1 million bee colonies. Beekeeping and apiculture have also increased significantly worldwide in the recent two decades. The FAO estimated that the number of bee colonies worldwide to be around 101.6 million in 2021. Compared to 1990, this corresponded to an increase of 47 %. Most bee colonies in 2021 were in Asia (45.3 million). Despite the global increase in the number of bee colonies, fluctuations were recorded in certain periods or regions, such as Eastern Europe, where there was a decrease of 24.9 % in the given period [17].

COLOSS (Prevention of Bee COLony LOSSes) monitors honey bee colony losses on an annual basis, and the last published data from the winter of 2016/2017 showed a total loss of honey bee colonies in 30 countries of the world at 20.9 %, which was an alarming figure [10].

The causes of colony losses can be divided into biotic and abiotic [4]. Important abiotic factors include: uncontrolled or excessive use of pesticides, global climate change, loss of food habitats and deficiency of food for bees [1, 2, 28]. Biotic factors include various types of bacteria, viruses, arthropoda and protozoa [18, 20], Fig. 1 [50]. Collapses rarely have only one cause, they are usually a combination of biotic and abiotic factors, and often a synergistic effect is also observed [52].

The parasitic microsporidia *Vairimorpha apis* (formerly *Nosema apis*) [76] and *Vairimorpha ceranae* (formerly *Nosema ceranae*) [32] responsible for nosemosis in *Apis* spp. represent the second most widespread biotic factor related to the decline of bees [52, 72].

Microsporidia, as is a group of highly divergent fungi, that includes obligate, intracellular, spore-forming parasites, are unable thus posing a threat to generate ATP by oxidative phosphorylation, as instead of mitochondria, they have a simplified form – a mitosome. In the reason for course of evolution, their strong genomes, and proteomes, have been reduced, resulting in metabolic dependence on the hosts, which is also the key to their pathogenicity [8, 69].

From the point of view of taxonomy, *Vairimorpha* spp. among the lower eukaryotes within the kingdom fungi [8, 49], and recently, based on their molecular characteristics,

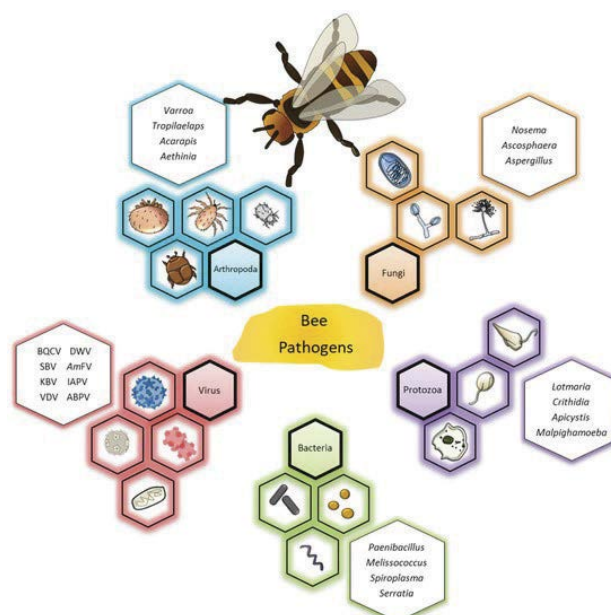


Fig. 1. Main bee pathogens. Schematic representation of the main pathogens affecting *Apis mellifera*, belonging to the arthropoda, fungi, protozoa, bacteria, and virus taxonomic groups [50]. Taxonomy of *Vairimorpha* spp.

their reclassification into *Vairimorpha* spp. was proposed [72]. Historically, microsporidia have had a taxonomy based on unique morphological characters, typical intracellular life cycles, host range, and tissue tropism. These features remain important, but molecular and genomic methods provide much new evidence for revision of microsporidia systematics, species identification, and broader phylogenetic placement [8].

The NCBI taxonomy database currently shows the following lineage for *Vairimorpha apis* and *Vairimorpha ceranae* species: superkingdom: eukaryote; clade: opisthokonta; kingdom: fungi (*fungi incertae sedis*); phylum: microsporidia; suborder: apansporoblastina; family: Nosematidae; genus: *Vairimorpha* (formerly *Nosema*).

Molecular phylogenies based on a single small subunit (SSU) ribosomal RNA gene are not always able to resolve deeper relationships with microsporidia, so it is suggested that future taxonomic definitions of this phylum include additional markers (LSU, ITS) [72].

Distribution and characteristic *Vairimorpha* spp.

Vairimorpha apis has long been known as a pathogen of honey bees (*Apis mellifera*) [29, 47] and was first officially described in 1909 [76], while its congener *V. ceranae* was known as a microsporidian parasite of the honey bee *Apis ceranae* [32], native to South and Southeast Asia.

Vairimorpha neumannii is a newly discovered species of parasite of honey bees (*A. mellifera*), based on molecular characteristics it is close to *V. apis* (97 % similarity) and was first detected in 2016 in Uganda and later it was also discovered in Japan [12].

Vairimorpha ceranae was officially identified as a pathogen in Eastern Europe in 1996 in a diagnosed honey bee [32], and in the early 2000s the pathogen was also found in Western European honey bees (*Apis mellifera*) [41, 44].

After the introduction of the molecular differentiation method [32], working groups around the world, initially focused on the detection of *V. ceranae* in *Apis ceranae*, proved the presence of *V. ceranae* in *Apis mellifera* as well [14, 74]. Retrospective works using the PCR method indicate the existence of *V. ceranae* in the honey bee even before its official discovery of *A. mellifera* infection with this pathogen [27, 60].

The primary factor in the global spread of the pathogen is the globalization of trade in honey bees and bee products [38].

Regardless of the cause of distribution, *V. ceranae* is one of the most common pathogens detected in honey bees [39] and is globally recognized as one of the most common pathogens of intestinal infections in adult honey bees [19, 32]. The huge incidence of *V. ceranae* recorded especially in the USA, while the reason why it became the dominant parasite in the USA remains controversial [14].

It has become a dominant species in Europe as well, and its occurrence in southern countries such as Spain, Italy and Greece is currently even described as the displacement of *V. apis* by *V. ceranae* [30, 53, 57].

This evolution has been interpreted, as a north-south gradient, due to the observed spread of the pathogen in Europe [32], so that this representation does not appear in countries with milder climates [35].

This is also why the influence of climate on the infectious process and prevalence of the pathogen is discussed, especially because experimental results show that *V. ceranae*, is sensitive to cold, compared to *V. apis*, and at the same time reproduces better at higher temperatures [35, 54].

The assumption of clear differences between these two pathogens is also supported by reports from Spain, after which, instead of the seasonality known for the occurrence of *V. apis* infections, a high incidence of spring *V. ceranae* infection could persist from late summer to the following

summer [41, 55]. Therefore, the lack of “seasonality” is defined as one of the main characteristics of *V. ceranae* which is more pronounced for countries in warm climate zones.

Epidemiology and life cycle *Vairimorpha* spp.

In the case of nosemosis, the infectious stage and at the same time the only stage that can survive outside the host are spores. Spores contain sporoplasm and an infectious apparatus that injects the sporoplasm into the host cell of the intestinal. Further, several intracellular cycles of asexual reproduction take place inside the host cell, leading to the formation of primarily autoinfectious and secondarily environmental spores, which are released into the intestinal lumen, where enterocyte lysis and cell degeneration occur [32, 36, 40, 50].

The first (primary) spore attacks other intestinal cells of the intestine, while these (secondary environmental spore) are released into the environment together with feces and spread the infection. Ingestion of food contaminated with spores, trophallaxis and grooming represent the most common ways of transmission of spores [35]. A sexual route of infection was also described, as spores were found in the sperm of drones [62]. It was also proven that SHB (Small Hive Beetle/*Aethina tumida*) can be a biological vector [16].

The intracellular life cycle lasts an average of 72 hours [35]. The developmental course of *V. apis* and *V. ceranae* is generally considered to be similar [15, 32, 40], Fig. 2 [56].

The result of damage to the intestinal epithelium is an immune response in the form of an inflammatory reaction [11].

This, combined with environmental stress and the presence of other pathogens, can weaken bees and, in the long run, the entire hive [38].

A. mellifera infection by *V. apis* is characterized by diarrhea and high winter mortality, while *V. ceranae* infections may progress in a subclinical form. The absence of clinical manifestations prevents early diagnosis and is often associated with high mortality, usually in autumn and spring [33].

Type A nosemosis caused by *V. apis* is opportunistic and often affects already weakened colonies. This disease is often associated with prolonged adverse weather during which bees cannot fly and defecate outside the hive, and

also hibernation and practices that lead to closing the hive [6].

Type C nosemosis caused by *V. ceranae* can be asymptomatic or cause severe damage to bees leading to depopulation [42, 55], often showing a seasonal pattern directly related to increased temperature [37, 43]. *V. ceranae* mainly infects worker bees, can cause high mortality in older bees, which induces early maturation of young bees and consequently causes imbalance in the hive [37, 42, 43].

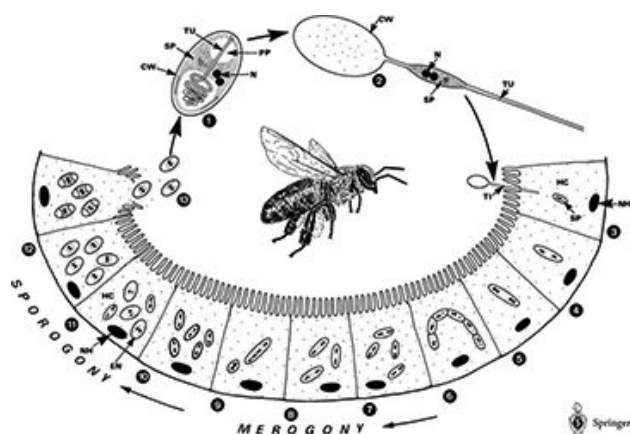


Fig. 2. Life cycle of *Nosema apis*

1 – Infectious spore with a typically binucleate sporoplasm; Bees become infected by ingesting the spores. 2–3 – With the germination of the spore in the intestinal lumen, the infectious apparatus is everted to then close the host cell perforate; the sporoplasm (SP) is injected through the tubule into the epithelial cell. 4–12 – Sporoplasm initially divides asexually in the host cell through four-nucleated stages (merogony); this is followed by final division and encystation (sporogony). 13 – release of *Nosema apis* mature spore from lysed host cells into the intestinal lumen. CW – spore wall; EN – encystation; HC – host cell; N – nucleus; NH – host cell nucleus (intestinal epithelial cell); PP – polar plastic; SP – sporoplasm; TI – tubule (injected); TU – tubule Springer Life Sciences [56].

Infection with *Vairimorpha* spp.

V. ceranae usually has an asymptomatic course, whereas *N. apis* in its typical form causes dysentery and its presence is visibly manifested by burnt frames, combs, and the outer walls of the hive [33].

The course of the infection depends on the infection load and the treatment threshold is considered to be 10^6 per bee, which is usually associated with serious infections and leads to a significant decrease in the health of the bee colony [24]. *In vitro* it could be determined that a dose of about 10^2 or 10^4 viable *Vairimorpha* spp. spores is necessary, to infect 50 % or 100 % of the honey bee workers in an infection test infect [29].

Spore quantification can be facilitated by a portable device that works on the principle of fluorescence, detects

chitin-containing spores, which can detect heavy infections ($> 0.5 \times 10^6$ spores per bee) caused by *Vairimorpha* spp. in a bee colony [66].

Honey bee colony infected with *V. ceranae* go through a long so-called incubation phase, when there are no clinical symptoms in the colony, as the queen produces eggs, which can compensate for the loss of workers. Colony collapse occurs when more than 80 % of bees are infected with more than 10^6 spores per bee [42].

When comparing species, the decrease in the number of spores produced appears to be generally higher in *V. ceranae* infection than in *V. apis* infection [60, 75], which is reflected in for *V. ceranae* compared to *V. apis* higher, the so-called “biotic potential” (maximum ability of pathogen reproduction under optimal environmental conditions) [54].

However, this aforementioned compensatory mechanism shortens the total lifespan of adult honey bees [63] the time during which they are effective as foragers and also shortens the time each honey bee devotes to colony growth and brood care, as younger bees start foraging earlier in the effort to replace the loss of older bees [3].

This leads to a modification of the entire work profile of the colony [73] and when the colony reaches a point where it cannot maintain brood production to compensate for the loss of adult bees, the rate of colony decline accelerates, leading to depopulation [46], which represents the only clear sign of infection described for *V. ceranae* [9, 42].

Changes at the level of endocrine regulatory mechanisms were also observed in colonies infected with *Vairimorpha* spp. An increased level of juvenile hormone has been observed, resulting in accelerated development of honey bees [7, 43], inhibition of gene expression responsible for the production of vitellogenin participating in the immunity of bees [5] and also an increased level of the pheromone ethyl oleate, which delays the maturation of young bees [22].

Changes at the level of endocrinology in infected insects have previously been described as an adaptive mechanism that serves to increase the reproductive capacity of the parasite in an attempt to maximize spore yield [21].

These factors are involved in immunity, the regulation of the division of labor between honey bees, the process of maturation and the transition between the nurse and the feeder, which significantly disrupts homeostasis in the bee

colony and causes significant changes in their biology at the cellular, tissue, organismal, or colony levels [65].

Quantitative and qualitative investigation methods

Recommended laboratory investigation methods for the quantitative and qualitative analysis of Nosematosis are summarized in the Terrestrial Manual of the OIE, 2018 [70].

Methods designed for spore quantification provide an approximate idea of the severity of *Vairimorpha* spp. infection, which helps in deciding the need for treatment. However, these microscopic methods cannot reliably distinguish between the species, as the spores of *V. apis* and *V. ceranae* are minimally different from each other in size and shape [70].

Molecular methods are more sensitive and species specific and can have a high detection sensitivity in the range of 10 to 100 spores per bee for simple PCR and around 1 spore per bee for qPCR or LAMP [25, 51]. Molecular detection of *Vairimorpha* spp. is based on simplex and multiplex PCR, qPCR, RFLP PCR and LAMP, with duplex formats being preferred over uniplex PCR or qPCR protocols. Duplex PCR methods are preferred in cases where a mixed infection is assumed or where it is necessary to distinguish between *V. ceranae* and *V. apis* [34].

Seasonality and prevalence factors

The seasonal course of *V. apis* infection in *A. mellifera* is relatively persistent and is characterized by a low infection rate during the warm summer months, short fluctuations in infection in the autumn, observations show a steady increase in the infection rate during the winter months, with a peak in the spring [31]. In the *V. ceranae* species, the seasonality is not as pronounced as in *V. apis*, the problem is often the absence of symptoms of infection, with the exception of increased mortality during the winter. Severe symptoms have been reported mainly in the south, rarely in temperate climates [53].

However, from the amount of available data, it is clear that the prevalence of *V. apis* infections in different countries is rapidly decreasing in favor of its congener *N. ceranae* [24, 47, 60] and that it even becomes a dominant species in many regions [13, 14, 74]. Based on the amount of epidemiological data, it could appear that *V. ceranae* replaces *N. apis* in honey bee populations worldwide.

This process has been suggested to be caused by asymmetric intra-host competition between *V. apis* and *V. cer-*

anae, which favors the spread of *V. ceranae* [58, 75], but not all studies have supported this claim [29, 57] and we will try in the next part, based on the available data, to analyze the possible reasons why it happened. Temperature appears to be a key factor influencing the geographic distribution of *Vairimorpha* spp. in different climate zones and the seasonal prevalence of infection.

It was reported that in countries located in warmer climate zones, such as southern European countries (Italy, Spain, Greece), *V. ceranae* practically replaced *V. apis*, while in northern Europe (Ireland, Sweden, Norway and Germany) this was not observed [47], which pointed to climatic conditions as a key factor influencing the establishment, spread and prevalence of *V. apis* and *V. ceranae*. However, the issue will probably be more complicated and it is necessary to approach it more comprehensively, and when trying to objectively evaluate the situation, take into account several factors, such as, for example, average winter and summer temperatures, the frequency of collecting samples, the method of their examination, etc.

The results of experimental studies and also the results of long-term, multi-year monitoring of *Vairimorpha* spp. infection in honey bee colonies within larger territorial units can be the most helpful in understanding the rules affecting the geographical distribution and seasonal prevalence of *Vairimorpha* spp. infection. In our work, we tried to summarize and select the knowledge that we consider the most important from the point of view of the distribution and prevalence of *Vairimorpha* spp., with the aim of creating some space for discussion and further research in this area.

Experimental infection of adult bees showed that the proliferation of *V. ceranae*, unlike *V. apis*, is not affected by temperatures above 33°C [54]. G i s d e r et al. [37] also conducted cell culture experiments that demonstrated that *V. ceranae* has a higher ability to multiply than *V. apis* at 27 °C and 33 °C, which potentially explains the increase in prevalence of *V. ceranae* during summer. These data provide clear evidence of a competitive advantage of *V. ceranae* over *V. apis* in warmer climate zones.

Other experiments have shown that *V. ceranae* spores, but not *V. apis* spores, almost lose their ability to germinate and thus their infectivity when exposed to temperatures near or below freezing [30, 35]. Nevertheless, there is evidence of the spread of *V. ceranae* in the region of Western Siberia with average January temperatures of -18

°C [71], where the dominance of the infection prevalence of *V. ceranae* over *V. apis* was even found in the Tyumen region. Similar results were found in Canada with comparable average January temperatures [23]. In a recent study in Switzerland, it was demonstrated that low ambient temperatures favor microsporidia infection of honey bees [61].

Experiments focused on co-infection of bees in a cage with simultaneous feeding of *V. apis* and *V. ceranae* spores did not provide evidence of intraspecific competition between these two species within the host [29, 57].

In contrast, sequential spore feeding of both species led to competition within the host, the former *Vairimorpha* spp. inhibited the growth of the latter regardless of which species' spores were used to infect first. This should prevent the spread of *V. ceranae* as *V. apis* was present in the bee population before the arrival of *V. ceranae*. However, this effect was shown to be asymmetric and *V. ceranae* showed a stronger inhibitory effect on *V. apis* than *V. apis* on *V. ceranae* [39, 58].

Interesting results were obtained by G i s d e r et al. [37], who followed 230 honey bee colonies from 23 apiaries over 12 years in a longitudinal cohort study on the prevalence of *V. apis* and *V. ceranae* in northeastern Germany between 2005 and 2016.

Samples were collected twice a year (spring and fall), resulting in a total of 5,600 bee samples that were subjected to microscopic and molecular analysis to determine the presence of *V. apis* and/or *V. ceranae* infections. Analysis of data on the prevalence of infection with *Vairimorpha* spp. showed a significant increase in *V. ceranae* infections over the past 12 years in samples collected in autumn (reflecting summer development) and spring (reflecting winter development). Assuming the gradual replacement of *V. apis* by *V. ceranae* at the population level, it was therefore expected that the prevalence of *V. apis* infection should have decreased simultaneously during the study period.

However, a significant decrease in the prevalence of *V. apis* infections was observed only in autumn, and the results speak against the fundamental displacement of the originally endemic pathogen from northeastern Germany. Moreover, the long-term stability of *V. apis* infection frequency in the spring suggests that any mechanisms acting on *V. apis* during the summer and causing its decline in colony populations are compensated for and reversed during the winter. It was found that there is a balanced ratio of prevalences for both species in the spring period, and

in the long-term study, mixed infections in the colonies were found surprisingly often, indicating that there is no interspecies competition at the colony or population level during the wintering of the host. Rather, coinfection levels suggested infection with either of the two microsporidia already existing in the colony, favoring further infection of the colony by a second *Vairimorpha*.

These data do not support a general advantage of *V. ceranae* over *V. apis*, and the total replacement of *Vairimorpha apis* by *Vairimorpha ceranae* in the investigated honey bee population was not confirmed in the climatic conditions of northeastern Germany [37].

Similar conclusions were reached by the authors of a study where the prevalence of *Vairimorpha* spp. in Turkey was monitored for 7 years, despite the fact that this region is located in a warmer climate zone. They found that the number of *V. ceranae* spores significantly decreases at low temperatures (≤ 5 °C), however, statistical analyzes also revealed that there is also a significant relationship between warm weather conditions in winter and high spore levels and high prevalence of *V. ceranae* infection in bee colonies.

The level of co-infection was lowest during the first two years of observation (2009–2010), when average winter temperatures were highest (5.3 °C and 6.5 °C), and at the same time the highest level of *V. ceranae* infection was observed. In the following 5 years (2011 to 2016), the average winter temperatures were lower, ranging between 3.1 °C and 4.3 °C (never exceeding 5 °C), which was reflected by an increase in the level of co-infection (*V. apis* + *V. ceranae*) and at the same time a significant decrease in the infection by *V. ceranae* itself compared to the first two years [59].

They found that the winter season is the main factor influencing the level of *Vairimorpha* infection and the dominance of *V. ceranae* and also that winter temperatures are a significant indicator of co-infection of both species. This study suggests that there is no replacement of *V. apis* by *V. ceranae* under the conditions of Turkey, but there is a dynamic prevalence among *Vairimorpha* species depending on the average winter temperature [59].

In Slovakia, the species *V. ceranae* were confirmed for the first time in 2008 [68] and in 2009–2010 a study was carried out, the aim of which was to monitor the prevalence of mono-infection and co-infection of both species *V. apis* and *V. ceranae* in Slovakia using the polymerase

chain reaction (PCR). Already in 2010, mono-infection with the *V. apis* species was not recorded, and either co-infection of both species or mono-infection of *V. ceranae* prevailed [67].

Thus, a significant increase in the prevalence of *V. ceranae* and a decrease in *V. apis* were confirmed, and this trend was also shown by the results of the examinations of bee colonies, which we carried out 10 years later, in 2020 and 2021, where in none of the examined samples, using PCR examination, we did not detect the presence of *V. apis* [45]. However, this does not mean that this species is completely replaced and displaced by *V. ceranae*. For an objective evaluation of the current epidemiological situation, it would be necessary to examine a larger number of samples and take them twice a year, in spring and autumn. The samples came from bee colonies from queen breeders, they were taken in the spring, all regions of Slovakia were equally represented there, and the examination was carried out on the basis of mandatory periodic control of colonies for the presence of *Vairimorpha* spp. Sampling in the spring showed the development of *Vairimorpha* spp. in the winter period, however, there is a lack of data on the development of the prevalence in the summer, which would be shown during the collection of samples in the fall.

However, these results indicate that the prevalence of *Vairimorpha* spp. in Slovakia is closer to the situation in southern European countries.

CONCLUSIONS

As it turns out, the clarification of the shift in the prevalence of infection in favor of *V. ceranae* will require a more accurate data analysis and further long-term monitoring at the level of the population of bee colonies in different geographical areas. A number of findings obtained from experimental trials cannot be easily extrapolated to the situation at the population level, which was also shown by the results of several long-term observations in different climatic conditions. Factors affecting interspecific competition were experimentally explained mainly at the level of individual bees, while the obtained epidemiological data relate to bee colonies and populations. The concept of intrahost interspecific competition in obligate intracellular parasites such as *V. apis* and *V. ceranae* due to competition for a limited energy resource cannot be easily transferred

to the colony level, where a limited resource (in the case of a colony, new hosts) is not yet a problem.

The replacement of *V. apis* by *V. ceranae* at the colony level during the summer, but not during the winter period, points to different mechanisms acting or affecting these two microsporidian parasites and means that there is a variable prevalence between the two species depending on the average winter temperature. The exact mechanisms responsible for replacement at the population level are still not fully explained, but it is clear that climatic factors play an important role. So “replacement” may not be the right term to describe the change in the distribution of *V. apis* and *V. ceranae* in the world, the term “dynamic prevalence” better describes the situation.

Another point of interest when evaluating the results of the studies is the fact that on a purely molecular basis it is not possible to distinguish true infection from contamination, there is no correlation between a positive PCR test result and the presence of infection.

Regarding *Vairimorpha* spp. only a few spores of the pathogen may result in a positive molecular finding, but this evidence is of little or no significance. In principle, only the combination of clinical and laboratory diagnostic findings with expertise in pathogenesis can reduce the likelihood of confusion and minimize incorrect results in interpretation and diagnosis. The aforementioned inconsistencies between studies emphasize the need for standardized protocols for collection, examination of samples and evaluation of subclinical and clinical manifestations of infection. When evaluating the results of the study, the infection of *Vairimorpha* spp. it is necessary to take into account, in addition to climatic factors, above all the sublethal effects of insecticides, the synergistic effect of infection with other pathogens, nutritional conditions, different beekeeping techniques, and possibly also genetic differences. This comprehensive view of the problem of *Vairimorpha* spp. infections can significantly contribute to its control and the design of the necessary measures.

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