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Minireview

Honey Bee Viruses: An Ongoing History of Discovery

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Abstract Numerous threats to honey bees' health exist, including climate change, pesticides, diseases, and pests, and their combined actions pose greater risks than a single factor. Viruses have been investigated for roughly 100 years since the first bee virus detection, *Sacbrood virus* from the United States in 1913. So far, seven viruses have been routinely included in honey bee health monitoring and surveillance systems in Korea, but new viruses have lately been found. However, understanding of viruses as a threat to honey bees remains insufficient. Although some of the threats to honey bee health posed by viruses and other factors have been identified, research is still in its initial step. In this paper, we have reviewed the diversity of honey bee viruses, virulence, mode of transmission, and potential molecular biological analysis approaches.

Keywords Honey bee viruses, Virome analysis, *Apis mellifera*, *Varroa destructor*, *Nosema*, High throughput sequencing

INTRODUCTION

Honey bees (*Apis mellifera*) are indispensable to the global agricultural ecosystem since their pollination affects the yield of numerous crops (Gallai *et al*., 2009). Moreover, honey bees produce honey, pollen, royal jelly, wax, and other products that significantly contribute to the agricultural economy (Popovska Stojanov *et al*., 2021; Zacepins *et al*., 2021). Winter mortality, which is higher than summer mortality, is one of the key challenges (Steinhauer *et al*., 2014). In summer, honey bee activity is so high that the exchange of various pathogens among honey bees occurs outside, increasing the load of pathogens (Runckel *et al*., 2011), but the nutrients that honey bees can take are abundant, which does not appreciably affect the health of honey bees (Di Pasquale *et al*., 2013). In winter, nutrients are limited, and the *Varroa* mite, a vector of pathogens, increases (Traynor *et al*., 2016). As a result of the lengthy lifespan and the dense structure (winter cluster) inside the hive, and pathogens continuously infect the honey bees in winter that cause more harmful than in summer (Jung and Bae, 2022).

The physiological ecology of honey bees can be divided into summer honey bees, which have a short lifespan of 15 to 45 days, and winter honey bees, which have a lifespan of approximately 150 days or more (Doeke *et al*., 2015). Honey bees are known to prepare for the winter season around the autumnal equinox (Jung and Bae, 2022). The strength of a honey bee colony influences the ability of honey bee to survive during overwintering (Jung and Bae, 2022). In Korea, winter honey bees are born beginning mid-October, and if they fail to develop into adults during this period, they overwinter with weakened colonies or continue to make winter honey bees until December (Jung and Bae, 2022). Throughout the winter, honey bee colonies remain overcrowded to form winter clusters for temperature management; as a result, winter honey bees have more antibiotic activity than summer honey bees, but they are more vulnerable to infectious diseases (Jung and Bae, 2022). Winter clusters begin to form when the external temperature drops to 10 to 14°C for more than three days (Stabentheiner *et al*., 2010). The inside of a winter

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cluster must be at least 13°C, and typically needs to be maintained between 20 to 25°C for honey bees to be able to carry out colony maintenance activities (Southwick and Mugaas, 1971). According to Steinhauer *et al*. (2014), honey bee mortality in overwintering colonies in the US, was caused by weak forces, a lack of food, unproductive queen honey bees, honey bee mites, and pesticides. Between 2011 and 2013, the average overwintering success rate in Korea was 82.6% (Jeong *et al*., 2016). Honey bee mites had the greatest influence on the mortality of winter colonies (Genersch *et al*., 2010; Guzman-Novoa *et al*., 2016). Winter honey bees infected with honey bee mites are reported to have a 20% higher overwinter mortality than healthy hives (Jung and Bae, 2022). If mite infection becomes severe during the winter honey bee breeding season, the risk of overwinter mortality increases due to losses of fat and vitellogenin, which are substances that enhance the resistance to cold in honey bees (Fries *et al*., 1994; Amdam *et al*., 2004). Viruses such as *Deformed wing virus* (DWV) and *Israeli acute paralysis virus* (IAPV) are closely associated with colony mortality, and the damage caused by these viruses can be exacerbated by honey bee mite infestations, leading to higher mortality rates in honey bee colonies (Gisder *et al*., 2009; Chen *et al*., 2014).

Worker honey bees are reduced by 10 to 20% in the average overwintering colony. In Korea, a drop of more than 30% is considered abnormal mass loss phenomenon (Kim, 2022). Colony collapse disorder (CCD), which first occurred in Pennsylvania in the US in 2006 (Cox-Foster *et al*., 2007; vanEngelsdorp *et al*., 2007), is a phenomenon similar to abnormal winter mortality in Korea. CCD is a phenomenon in which worker honey bees disappear with little evidence of mass mortality near the hive, leaving only the queen and some young honey bees in the colony despite having sufficient food in the colony (Johnson, 2010). In this review, we describe the viruses that have been reported thus far, as well as synergy between viruses and other factors and virome analysis.

HONEY BEE VIRUSES

Viruses are classified as DNA or RNA viruses depending on the nucleic acid genome, and can be single and double-stranded depending on the structure of the genome (Villarreal, 2004). In addition, RNA viruses are divided into positive-sense and negative-sense (Payne, 2017). Positive-sense viral RNA genomes can be translated in the same manner as mRNA, so they can be expressed immediately after the viral genome enters the cell, but negative-sense RNA viruses can only be expressed in cells after a transcription process to positive-sense RNA virus occurs (Nguyen and Haenni, 2003).

Viruses are highly mutable, but RNA viruses have a higher mutation rate than DNA viruses (Sanjuán *et al*., 2010). Positive-sense single-stranded RNA viruses are the most common viruses identified in honey bees (Brutscher *et al*., 2016). Recently, many DNA viruses have been discovered in honey bees (Kraberger *et al*., 2019). However, little is known about the impacts of DNA viruses other than *Apis mellifera filamentous virus* (Gauthier *et al*., 2015).

Thus far, 128 viruses found in honey bees have been reported in the NCBI GenBank database (Table 1). Viruses are mainly found in worker honey bees but are sometimes found in drones, queen honey bees, bumblebees, wasps, and honey bee mites. The pathways, symptoms, and risks of most viruses have not yet been uncovered. *Acute bee paralysis virus* (ABPV), *Black queen cell virus* (BQCV), *Chronic bee paralysis virus* (CBPV), DWV, IAPV, *Kashmir bee virus* (KBV), *Sacbrood virus* (SBV), *Apis rhabdovirus* (ARV) group, and *Lake Sinai virus* (LSV) group have been the focus of global research.

MAJOR TAXA OF HONEY BEE VIRUSES

The viruses discovered in honey bees reported to NCBI are divided into nine orders, 11 families, and six genera, with several unclassified viruses (Table 1). The major honey bee viruses are mainly found in *Nodamuvirales* and *Picornavirales*.

Nodamuvirales was named after the *Nodamura virus* found in Noda-mura, Tokyo, Japan (Scherer and Hurlbut, 1967). It includes two families, and the virion form has a non-enveloped icosahedral symmetric structure with a size of 25–33 nm and a genome of 4.5–6 kb. In the case of the family *Nodaviridae*, it consists of two molecules of positive-sense single-stranded RNA1 and RNA2 (Thiéry *et al*., 2022). However, viruses in the family *Sinhaliviridae* have one positive-sense single-stranded

Table 1. List of viruses found in honey bees (*Apis mellifera*) reported in the NCBI GenBank database

Order	Family	Genus	Organism	Molecular type	First reported sequence accession No. in NCBI GenBank database
Amarillovirales	*Flaviviridae*	Unclassified	*Apis flavivirus*	ssRNA(+)	KY354238
Articulavirales	*Orthomyxoviridae*	Unclassified	*Varroa orthomyxovirus-1*	ssRNA(−)	MK032465-MK032470
Bunyavirales	*Peribunyaviridae*	Unclassified	*Apis bunyavirus 1-2*	ssRNA(−)	KY354236-KY354237
			Duke bunyavirus	ssRNA(−)	KY094605-KY094607
Mononegavirales	*Rhabdoviridae*	Unclassified	*Apis rhabdovirus 1-2*, and *5*	ssRNA(−)	KY354230-KY354234, and MZ822106-MZ822108
Nodamuvirales	*Sinhaliviridae*	*Sinaivirus*	*Lake Sinai virus 1*	ssRNA(+)	HQ871931
			Lake Sinai virus 2	ssRNA(+)	HQ888865
			Lake Sinai virus 3	ssRNA(+)	JQ480620
			Lake Sinai virus 4	ssRNA(+)	JX878492
			Lake Sinai virus 5	ssRNA(+)	KC880121-KC880126
			Lake Sinai virus 6	ssRNA(+)	KR021357
			Lake Sinai virus 7	ssRNA(+)	KR021355
			Lake Sinai virus 8	ssRNA(+)	MZ821865-MZ821908
Picornavirales	*Caliciviridae*	Unclassified	*PNG bee virus 1-14*	ssRNA(+)	MT482483-MT482496
	Dicistroviridae	*Aparavirus*	*Acute bee paralysis virus*	ssRNA(+)	AF038361
			Aparavirus sp.	ssRNA(+)	MK431884-MK431886
			Israeli acute paralysis virus	ssRNA(+)	EU604006-EU604010
			Kashmir bee virus	ssRNA(+)	AF027125, AF034541, AF034542, AF035359, AF037591, and AF052566
		Triatovirus	*Black queen cell virus*	ssRNA(+)	AF125252
			Triatovirus sp.	ssRNA(+)	MK431878-MK431883
		Cripavirus	*Aphis gossypii virus*	ssRNA(+)	MT747981
			Cricket paralysis virus	ssRNA(+)	MH025822
			Rhopalosiphum padi virus	ssRNA(+)	MH025813-MH025820
			Apis cripavirus	ssRNA(+)	MZ822074
		Unclassified	*Apis dicistrovirus*	ssRNA(+)	KY354239
			Apis dicistrovirus 3 and *4*	ssRNA(+)	MZ822071 and MZ822072
			Big Sioux River virus	ssRNA(+)	JF423195-JF423198
	Iflaviridae	*Iflavirus*	*Deformed wing virus*	ssRNA(+)	AJ489744
			Iflavirus sp.	ssRNA(+)	MK431870-MK431877
			Apis iflavirus 1-2	ssRNA(+)	MZ822075-MZ822076
			Sacbrood virus	ssRNA(+)	AY230515-AY230518
			Slow bee paralysis virus	ssRNA(+)	GU079653
			Varroa destructor virus 1	ssRNA(+)	EU779940-EU779945
		Unclassified	*La Jolla virus*	ssRNA(+)	MH025824
			Moku virus	ssRNA(+)	MK829247-MK829256, MT251354, MT251355, and MT251361
			SI bee virus 1-3	ssRNA(+)	MT482497-MT482499

Table 1. Continued

Order	Family	Genus	Organism	Molecular type	First reported sequence accession No. in NCBI GenBank database
Picornavirales	Unclassified	Unclassified	*Apis picorna-like virus 1,2,* and *4*	ssRNA(+)	MZ822067, MZ822068, and MZ822094
			Bundaberg bee virus 1-8	ssRNA(+)	MG995700-MG995707
			Darwin bee virus 1-8	ssRNA(+)	MG995693-MG995699
			Hobart bee virus 1	ssRNA(+)	MG995722
			Perth bee virus 1-9	ssRNA(+)	MG995725-MG995733
			Renmark bee virus 1-5	ssRNA(+)	MG995708-MG995712
			Robinvale bee virus 1-9	ssRNA(+)	MG995713-MG995721
			Victoria bee virus 1	ssRNA(+)	MG995723
			Victoria bee virus 2	ssRNA(+)	MG995724
Tymovirales	*Tymoviridae*	Unclassified	*Bee Macula-like virus*	ssRNA(+)	KT162924, KT162925
Geplafuvirales	*Genomoviridae*	Unclassified	*Apis mellifera genomovirus 1-2*	ssDNA	MH973737-MH973741
Recrevirales	*Redondoviridae*	*Torbevirus*	*Apis mellifera virus-1-16*	ssDNA	MH973742-MH973774
Unclassified	Unclassified	Unclassified	*Chronic bee paralysis virus*	ssRNA(+)	AF375659
			Apis Nora virus	RNA	KY354240
			Apis nora virus 2	RNA	MZ822097
			Varroa destructor virus 3/5	RNA	MZ821938-MZ821941, MZ821946, MZ821951, and MZ821952
			Cloudy wing virus	Unknown	AF034543
			Thika virus	Unknown	MH025821
			Insect-associated ssDNA molecule	ssDNA	MH973775-MH973779
			Apis mellifera filamentous virus	dsDNA	JF304814

RNA genome (Runckel *et al*., 2011). Among the two families, the viruses found in honey bees belong to the family *Sinhaliviridae*. *Sinhaliviridae* was named after two phylogenetically similar virus groups, the virus found in the sweat bee (*Halictus scabiosae, Adlikon virus* (Bigot *et al*., 2017)) and the LSV found in honey bees.

Picornavirus is a combination of the words "pico", which means "small" in Spanish, and RNA virus. Several phylogenetically similar "picornavirus-like" viruses have been identified since the first identification of *Picornavirus* in 1963 and the identification of the entire genome sequence in 1980, and the family *Picornaviridae* are used to bind them (Le Gall *et al*., 2008). It has now been reported in ICTV as the order *Picornavirales*, which is a higher group (Sanfaçon *et al*., 2022). Picornaviruses are classified into five families, among which the bee viruses are found in family *Dicistroviridae* and *Iflaviridae*.

The *Dicistroviridae* family has a positive-sense single-stranded RNA genome of 8−10 kb, and the virion type has an icosahedral structure with a size of 30 nm without an envelope (Valles *et al*., 2017). It also has a characteristic dicistronic genome, from which it was named, which includes the genera *Aparavirus*, *Triatovirus*, and *Cripavirus*. *Aparavirus* is derived from the *Acute bee paralysis virus*, *Triatovirus* is derived from the *Triatoma virus*, and *Cripavirus* is derived from the *Cricket paralysis virus* (ICTV, 2022). Major honey bee viruses belonging to this order include ABPV, KBV, and IAPV belonging to the genus *Aparavirus*, and BQCV belonging to the *Triatovirus*, and several viruses belonging to the genus *Cripavirus* have also been found (Table 1).

Iflaviridae has an RNA genome of 9−11 kb, and the virion form is 22−30 nm in size, without an envelope, and has an icosahedral symmetrical structure. Derived

from the *Infectious flacherie virus*, both family and genus were named, and one genus was included (Chen *et al*., 2022). The major honey bee viruses are DWV, SBV, and *Varroa destructor virus* (Table 1).

CHARACTERISTICS OF HONEY BEE VIRUSES

1. *Acute bee paralysis virus* (ABPV)

ABPV is a positive-sense single-stranded virus belonging to the family *Dicistroviridae* and genus *Aparavirus*. ABPV, along with CBPV, was found in *A. mellifera* adult insects (Bailey *et al*., 1963). Honey bees infected with ABPV show paralysis within 2 to 4 days and die within 1 day (Bailey *et al*., 1963). The complete viral genome sequence for ABPV was first detected in *A. mellifera* in the United Kingdom (Govan *et al*., 2000). ABPV was found in *A. mellifera*, *A. cerana*, honey bee mites (MZ821785, and KY451691), *Bombus* sp. (MW196265), *Vespa* sp. (MN565031), and other insects (ON304226, ON304239, and MW442703). In Korea, the first ABPV was detected in 2009 (Yoo and Yoon, 2009b). Ultra-rapid PCR and nested ultra-rapid PCR methods for ABPV detection have been reported (Kim *et al*., 2014b; Lee *et al*., 2016; Kim *et al*., 2017; Kim *et al*., 2018). However, ABPV genome sequence has not yet been reported in Korea.

2. *Black queen cell virus* (BQCV)

BQCV is a positive-sense single-stranded RNA virus of the family *Dicistroviridae* and genus *Triatovirus*. It was first discovered in queen larvae and pupae. BQCV was named after the black cell wall color of the infected pupa (Bailey and Woods, 1977). Worker honey bees infected with severe BQCV exhibit symptoms of impaired orientation similar to those of DWV (Retschnig *et al*., 2019). In Korea, a complete viral sequence of BQCV was first reported in Anyang in 2012 (Reddy *et al*., 2013a). Infections have been documented in *Vespa* sp. (NCBI GenBank accession number MN902108), *Bombus* sp. (MN565034), *A. mellifera*, and *A. cerana* (MZ821802) (Dalmon *et al*., 2019). Because BQCV is a major diagnostic target among honey bee viruses in Korea, various diagnostic methods have been developed to detect BQCV, such as multi-point PCR, real-time PCR, ultra-rapid real-time PCR, and loop-mediated isothermal amplification (LAMP) (Cho *et al*., 2007; Yoo *et al*., 2008a; Lim *et al*., 2016; Kim *et al*., 2019c).

3. *Chronic bee paralysis virus* (CBPV)

CBPV is a positive-sense single-stranded virus with an unknown classification that belongs to the realm *Riboviria* (Chevin *et al*., 2012). Its official classification has yet to be established following its discovery with ABPV by Bailey *et al*. (1963). Infected honey bees exhibit the initial symptoms after approximately 6 days, after which they do not immediately die but continue to exhibit chronic paralysis symptoms (Bailey *et al*., 1963). The region estimated as the RNA-dependent RNA polymerase region of CBPV is similar to the families of *Nodaviridae* and *Tombusviridae*; however, at present, it is considered a new virus family with a positive RNA genome (Olivier *et al*., 2008). CBPV genome consists of two segments, and the complete viral genome sequence was first detected in *A. mellifera* in France (Olivier *et al*., 2008). The reported host species included *A. mellifera*, *A. cerana*, *Bumbus* sp. (ON448801), *Vespa* sp. (MZ 151447), honey bee mites (MN114562, MN114563), and other insects (ON448799, ON448803, and ON448 852). In Korea, a partial viral genome sequence has been reported in Cheongju (MH327931 and MH327932), whereas the complete viral genome sequence has not yet been reported. Diagnostic methods based on ultra-rapid PCR, RT-PCR, real-time PCR, and LAMP have been introduced to detect CBPV (Choi *et al*., 2008; No *et al*., 2010b; Yoo *et al*., 2010a, 2010b; Kim *et al*., 2019a).

4. *Deformed wing virus* (DWV)

DWV is a positive-sense single-stranded RNA virus belonging to the family *Iflaviridae* and genus *Iflavirus*. In honey bees, DWV infection causes immature development, wing deformity, and sometimes death (Bailey, 1968a). Bailey *et al*. (1979) named it the *Egypt bee virus* (EBV) after its first discovery during their research. In 1982, a virus similar to the EBV was discovered in malformed adults collected in Japan; the EBV was subsequently renamed DWV because of its similar symptoms (Ribière *et al*., 2008). Currently, there are three different types of DWV: DWV-A, DWV-B, and DWV-C. DWV-A

Fig. 1. Symptoms caused by the *Deformed wing virus*, such as deformed wing and shortened abdomen.

corresponds to the known DWV. DWV-A is 97% identical to *Kakugo virus* (KV), which is only found in the brains of nurse honey bees and foragers, and its infection symptoms are more aggressive than those of DWV (Fujiyuki *et al*., 2004). It has also been demonstrated experimentally that KV can infect tissues other than the brains of honey bees (Lanzi *et al*., 2006). DWV-B, also known as the *Varroa destructor virus-1* (VDV-1), was first detected in the *Varroa* mite, and it is 84% identical to DWV-A (Ongus *et al*., 2004). VDV-1 can be replicated in honey bees (Yue and Genersch, 2005). In temperate regions, DWV-B is a larger problem than other types of DWV (Natsopoulou *et al*., 2017). Recombination between type A and type B has also been reported (Moore *et al*., 2011). Overall, DWV-C shared 79% identity with type A and 78.9% identity with type B (Mordecai *et al*., 2016). In Korea, after a partial viral genome sequence (EU836051) was reported in 2008, a complete viral genome sequence was reported in 2012 (Reddy *et al*., 2013c). The documented hosts included *A. mellifera*, *A. cerana* (MH607198), *Varroa destructor* (MZ821838), *Bumbus* sp. (HQ655506 and MW222481), *Vespa* sp. (MN565036), and other insects (KF978606, KF314877, ON448657, KF314878, MF13482, and ON448672). DWV diagnostic manuals that include ultra-rapid PCR, ultra-rapid real time PCR, real time PCR, and LAMP methods have been developed (Lim, 2013; Lim and Yoon, 2013; Kim *et al*., 2014a; Kim *et al*., 2019b).

5. *Israeli acute paralysis virus* (IAPV)

IAPV was first reported in Israel as a positive-sense single-stranded RNA virus belonging to the family *Dicistroviridae* and genus *Aparavirus* (Maori *et al*., 2007). It is a significant virus that causes CCD and has symptoms similar to those of ABPV (Cox-Foster *et al*., 2007). Choi *et al*. (2007) discovered the first IAPV partial viral sequence (EU375538) in Korea. The complete viral genome sequence of IAPV in Korea was first reported by Andong, Guri, and Gangneung in 2013 (Reddy *et al*., 2013b). Its host species are *A. mellifera*, *A. cerana*, honey bee mites, *Bumbus* sp. (HQ655581), *Vespa* sp. (HQ655583), and other insects (LC581780, KT152165, and KT717338). Due to the significance of IAPV as a primary pathogen for honey bees in Korea, many diagnostic methods have been developed, including nested PCR, ultra-rapid PCR, RT-PCR, real-time PCR, and ultra-rapid real-time PCR techniques (Kang *et al*., 2008; Kim *et al*., 2009; Yoo *et al*., 2009; Yoo and Yoon, 2009a; No *et al*., 2010a; Lim *et al*., 2016).

6. *Kashmir bee virus* (KBV)

KBV is a positive-sense single-stranded virus belonging to the family *Dicistroviridae* and genus *Aparavirus*. A substance extracted from *A. cerana* collected in the Kashmir region was discovered through an injection experiment in *A. mellifera* (Bailey *et al*., 1976). Although no major symptoms appear after infection, external factors can result in death (Ward *et al*., 2007). Infection by the *Varroa destructor*, a vector that activates KBV, can result in sudden pupa and worker honey bee mortality (de Miranda *et al*., 2013). A complete viral genome sequence for KBV was first revealed in Pennsylvania, USA (de Miranda *et al*., 2004). The reported host was *A. mellifera*, *A. cerana*, *Bumbus* sp. (MF004374), *Vespa* sp. (MN565039), honey bee mites (AF200336 and MN 114614), and several insects (MT068450, MT068447, and MT068448). In Korea, a complete viral genome sequence for KBV was first identified in *A. mellifera* sample from Anyang (Reddy *et al*., 2014) and its diagnostic method was based on real-time PCR (Yoo *et al*., 2008b).

7. *Sacbrood virus* (SBV)

SBV is a positive-sense single-stranded virus belonging to the family *Iflaviridae* and genus *Iflavirus*. It was the first virus identified in honey bees and described in 1913 (White, 1913). Infected larvae do not become pupae; instead, the molting fluid gradually accumulates in the integument, turns brown, and dies (Bailey, 1975). Hosts are *A. mellifera*, *A. cerana*, *Varroa destructor* (MN

114616), *Bumbus* sp. (MH900073), *Vespa* sp. (MH133 361), and other insects (MW435746, ON448730, ON448 736, and MG737469). In Korea, a partial SBV viral genome sequence was first detected in *A. mellifera* (Kim *et al*., 2008), and its complete viral genome sequence was detected in *A. cerana* (HQ322114). SBV caused the large-scale extinction of *A. cerana* in Korea (Choi *et al*., 2010). Because of the substantial damage caused by SBV, the Animal and Plant Quarantine Agency in Korea strictly controls its occurrence. Various diagnostic methods based on nested PCR, Ultra-rapid PCR, RT-PCR, real-time PCR, Ultra-rapid real-time PCR, and LAMP techniques have been developed to detect SBV in Korea (Lee *et al*., 2011; Yoo *et al*., 2013; Lee *et al*., 2014; Wang *et al*., 2015; Truong *et al*., 2017).

8. *Apis rhabdovirus* (ARV) group

Apis rhabdoviruses are negative-sense single-stranded RNA viruses that have not been classified as a genus belonging to the family *Rhabdoviridae* (Remnant *et al*., 2017). Five ARV species have been reported. ARV1 (KY354230) and ARV2 (KY354233) were first reported in 2017 and ARV3 (MZ822104), ARV4 (MZ822105), and ARV5 (MZ822106) in 2021. ARV3 and 4 were only detected in *A. cerana* and have five open reading frames (N protein, P protein, M protein, G protein, and L protein) (Remnant *et al*., 2017). No symptoms have been identified yet. As of November 1st, 2022, viral genome sequences were reported to the NCBI GenBank database by New Zealand, South Africa, Tonga, Israel, USA, Sweden, China, Czech Republic, Austria, and Slovenia.

9. *Lake Sinai virus* (LSV) group

Lake Sinai viruses are positive-sense single-stranded viruses belonging to the family *Sinhaliviridae* and genus *Sinaivirus* (ICTV, 2019). They are classified into eight species. LSV1 (HQ871931) and LSV2 (HQ888865) were discovered for the first time in a sample from South Dakota, USA, where CCD occurred (Runckel *et al*., 2011). Thereafter, a partial LSV3 viral genome sequence was reported (Cornman *et al*., 2012), and its complete viral genome sequence was reported in 2018 (Thaduri *et al*., 2018). Ravoet *et al*. (2013) reported the partial viral genome sequences of LSV4 (JX878492) and LSV5 (KC880121), and a Chinese researcher reported the complete viral genome sequence for LSV4 (MZ821850). The complete viral genome sequence of LSV5 has not yet been confirmed. Daughenbaugh *et al*. (2015) reported partial viral genome sequences for LSV6 (KR021357) and LSV7 (KR021355). However, their complete viral genome sequences have not yet been identified. The complete viral genome sequence of LSV8 has been recently uncovered (PRJNA706851). However, in addition to the eight species, some viral genome sequences were reported under the names of unclassified LSV and LSV TO (KY354241), LSV NE (KY354242), LSV SA1 (KY354243), and LSV SA2 (KY354244). Several researchers have identified the full-length viral sequences of LSVs and proposed classification criteria among LSVs, but this classification has not been established yet (Roberts *et al*., 2017; Cornman, 2019). Because many recent studies have suggested that LSV may affect the occurrence of CCD, it has been reported as an important virus for honey bee health (Cornman *et al*., 2012; Daughenbaugh *et al*., 2015; Remnant *et al*., 2017; Thaduri *et al*., 2018; Faurot-Daniels *et al*., 2020). However, the symptoms of the LSV group have not yet been uncovered.

10. Other viruses

In addition to the main research subjects described above, many more viruses have been discovered, most of which lack data and pose unknown threats to honey bees. Recently, several new viruses have been reported in Australia, with the majority of the honey bee viruses belonging to the order *Picornavirales*. The symptoms of these novel viruses and whether they can be replicated in honey bees have not been determined yet; however, their nomenclature has been established, with novel viruses mainly being named "discovery area + honey bee virus".

NOSEMA

Nosema apis, a unicellular parasite belonging to *Microsporidia*, was first discovered in 1909 (Zander, 1909). Queen honey bees infected with *N. apis* have a reduced spawning potential owing to ovary degeneration, and queen honey bees located inside the bottom side of the hive during spring are predominantly infected with the *N. apis* (Fyg, 1945; Liu, 1992). In the case of worker

bees, infections impair the hypopharyngeal glands, reducing the feeding capacity of spring nurse honey bees and making it impossible to properly raise larvae, thereby weakening the bee population (Lotmar, 1936). Moreover, RNA synthesis decreases in infected cells, and digestive enzymes release may cease, resulting in digestive disorders (Hartwig and Przelecka, 1971; Liu, 1984). When infected, worker honey bees develop into foraging honey bees faster than healthy bees, resulting in faster aging of infected honey bees (Hassanein, 1953; Wang and Mofller, 1970). The average life expectancy of infected honey bees is 17−31 days, 11−27 days shorter than honey bees that were not exposed to *N. apis* for seven years (Revell, 1960). As a result, it can reduce honey production (Moeller, 1962; L'Arrivee and Geiger, 1966; Cantwell and Shimanuki, 1969; Fries *et al*., 1984; Farrar, 2014). *N. apis* affects the wintering ability of the colony; winter loss is associated with the *Nosema* infection, and accumulation begins in the spring after surviving the winter (Farrar, 1942). In addition, when infected honey bees clean their honeycomb, the *Nosema* spores spread to the honeycomb itself and are then transmitted through the wax (Bailey and Ball, 2013). Honey bees infected with *N. apis* are suspected to have higher incidences of *Malpighamoeba mellificae*, however, more research is needed to confirm this (Bailey, 1968b). Recently, a TaqMan probe-based RT-qPCR diagnosis method for *M. mellificae* has been developed to study the effects of *M. mellificae* on honey bees (Schäfer *et al*., 2022). Several honey bee viruses are related to *N. apis* (Bailey, 1982). Considering that BQCV has a shorter lifespan in honey bees infected with both *Nosema* and BQCV than in single-infected honey bees, the simultaneous infection of BQCV and *Nosema* has been found to have a synergistic effect on the lifespan of honey bees (Gajda *et al*., 2021). In an experimental co-infection study, CBPV and *Nosema* had synergistic effects, as the co-infection resulted in faster honey bee mortality than individual infection (Toplak *et al*., 2013). *Nosema* infection did not significantly increase the DWV titer in the pollen supply process, however, compared to control, the DWV titer did increase significantly after the pollen supply was stopped, confirming that *Nosema* infection has a synergistic effect on the amplification of DWV when pollination is not properly performed (Zheng *et al*., 2015). In 1995, *Nosema cerana* was detected in *A. cerana* in China (Fries *et al*., 1996). *N. cerana* is known to have a greater impact on bumble bees than honey bees (Graystock *et al*., 2013). *N. cerana* was also found in pollen, which can cause infections, indicating that forager honey bees are more vulnerable to infection than queen honey bees and drones (Higes *et al*., 2008). *N. cerana* can be transmitted through *N. apis*, and can be infected by chewing contaminated wax when leaving the honeycomb (Malone and Gatehouse, 1998). Honey bees infected with *N. cerana* may have trouble returning to their hive due to stress (Wolf *et al*., 2016). This return ability has been demonstrated to reduce the level of trehalose involved in flight regardless of the degree of infection in infected honey bees (Kurze *et al*., 2016). *Nosema*-infected honey bees are also closely related to pesticides, with studies showing that honey bees exposed to high levels of pesticides are more susceptible to *N. cerana* infection than honey bees with low exposure levels (Pettis *et al*., 2013). After 8 days, honey bees infected with 1×10^5 *N. cerana* spores showed a 100% mortality rate (Higes *et al*., 2007). As a result, it may have a synergistic effect on the CCD phenomenon, which is the biggest threat to honey bees, by inflicting various damage (Bromenshenk *et al*., 2010).

VARROA MITE

The *Varroa* mite is a honey bee pest known to cause considerable damage to honey bees (Fig. 2). To date, the *Varroa* mite comprises four species. *Varroa jacobsoni* Oudemans was discovered in 1904 in *A. cerana*, Java, Indonesia (Oudemans, 1904); *V. underwoodi* in *A. cerana*, Nepal (Delfinado-Baker and Aggarwal, 1987); and *V. rindereri* in *A. koschevnikovi*, Borneo, Malaysia (De Guzman and Delfinado-Baker, 1996). The fourth species, *V. destructor*, was recently separated as another species from being misclassified as *V. jacobsoni* (Anderson, 2000; Anderson and Trueman, 2000). Among these four *Varroa* mites, *V. destructor* is mostly distributed in mainland Asia, especially in the eastern part, and is the most destructive to honey bees (Rosenkranz *et al*., 2010). Several symptoms of *Varroa* infection in honey bees have been reported: first, some infected honey bees displayed shortened abdomens and a 6−25% weight loss compared to healthy honey bees, with the number of *Varroa* mites and the weight of the honey bees ex-

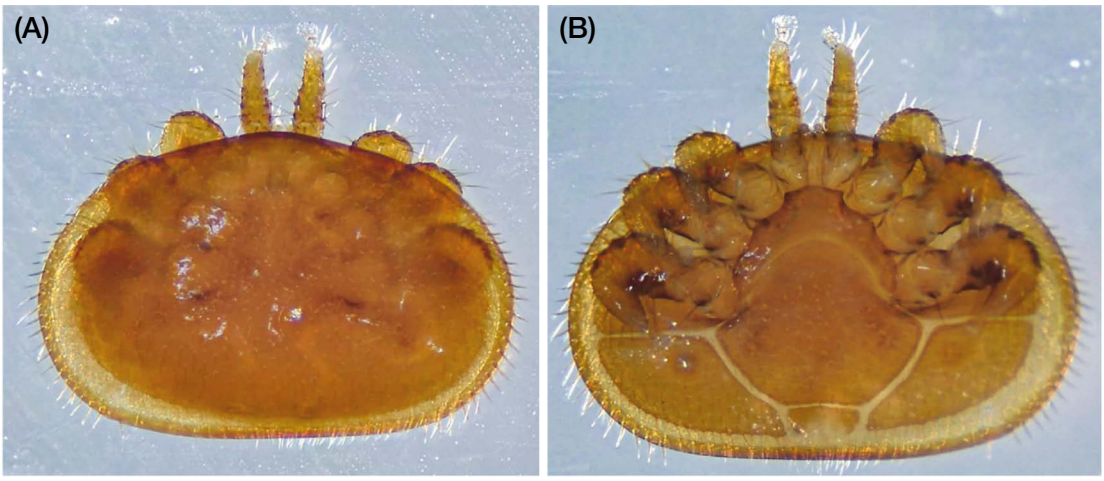

Fig. 2. *Varroa destructor*, reddish-brown in color, (A) dorsal view, (B) ventral view.

hibiting a negative correlation (De Jong *et al*., 1982). Second, the life span of honey bees varied according to the number of *Varroa* mites. The average life span of honey bees was 18.1 days when infected by one *Varroa* mite and 8.9 days when infected by two or more mites, and the number of *Varroa* mites was correlated with the honey bee life-span (De Jong and De Jong, 1983). Third, infected worker honey bees were less efficient in major activities; when infected during the larval stage, the size of the hypopharyngeal glands decreased by up to 31% and the adult stage decreased by an average of 14% (Schneider and Drescher, 1987). This reduction in the hypopharyngeal gland size makes it difficult for the nurse honey bees to feed the larvae, which interferes with honey bee growth and weakens the colony. As a result, the *Varroa* mite directly injures bee larvae and adults, injures hemolymph and fat bodies, and harms them, affecting their life duration, weight, and endocrine organs (Ramsey *et al*., 2019). Fourth, the *Varroa* mite has a large effect on honey bee's ability to fly. When infected by a *Varroa* mite in the larval stages, wing deformation can occur in some honey bees and the number of *Varroa*-infected honey bees that cannot return to the colony is twice that of healthy honey bees (Kralj and Fuchs, 2006). When a drone is infected by a *Varroa* mite, it has a great impact on the drone's flight ability. There is no difference in flight abilities between a healthy drone and an infected drone through a single *Varroa* mite, but a drone infected by two or more *Varroa* mites showed a maximum flight time of up to 6 min compared to a healthy drone with an average flight time of 27 min (Duay *et al*., 2002). As such, *Varroa* mites, which cause substantial damage, also act as a mediator for transferring pathogens to honey bees (Fig. 3). Currently, there are 22 viruses registered in the GenBank that are associated with *Varroa* mites. Among them, ABPV (Ball and Allen, 1988), BQCV (Locke *et al*., 2012), CBPV (Celle *et al*., 2008), IAPV (Di Prisco *et al*., 2011), SBV (Shen *et al*., 2005), KBV (Chen *et al*., 2004), SBPV (Santillán-Galicia *et al*., 2010), DWV, and VDV1 (Ryabov *et al*., 2017) are known to infect honey bees. As a result, direct damage to bees can reduce their immune systems, resulting in synergistic effects in causing CCD, which is the primary cause of honey bee mortality in the world (Le Conte *et al*., 2010).

VIROME ANALYSIS USING HIGH-THROUGHPUT SEQUENCING (HTS)

Recent studies have focused not only on the diagnosis of individual viruses, but also on the analysis of all viral nucleic acids present in individuals, communities, and the environment, confirming the diversity within these groups. The virus or viral nucleic acid information of such a group is referred to as a "virome" (Zárate *et al*., 2017).

Virome analysis using HTS began in 2002 using seawater samples (Breitbart *et al*., 2002). HTS has demonstrated broad capabilities for the detection of known and

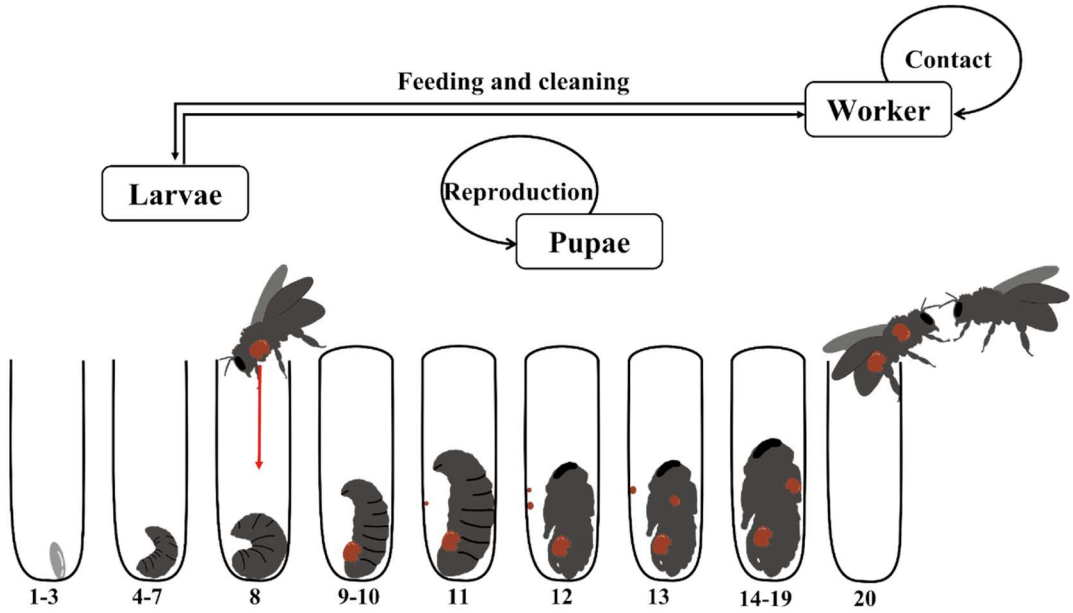

Fig. 3. *Varroa* mite infection pathway by honey bee life cycle, created by referring to de Miranda *et al*. (2011).

novel viruses in a variety of different sample types, including environmental, clinical, and biological samples such as cell lines and biological products (Goodacre *et al*., 2018). HTS technologies have also provided new insights into intraspecific viral diversity, thereby facilitating the characterization of virus variants and improving the disentanglement of viral population genetics (Maclot *et al*., 2020).

HTS technology-based virome analysis has been widely used by several researchers to study honey bees (Remnant *et al*., 2017; Roberts *et al*., 2018; Kadlečková *et al*., 2022; Lester *et al*., 2022). Various novel viruses have been identified using virome analysis. As a result, the number of viruses detected in honey bees has increased from 18 in 2007 to 128 in 2022 (Chen and Siede, 2007; NCBI, 2022). Although Virome analysis has already been actively conducted by many researchers around the world, and a virome analysis was recently performed for the first time in honey bees in Korea (Kwon *et al*., 2023).

FUTURE DIRECTIONS

Since the CCD outbreak in 2006, many researchers around the world have been interested in honey bees' health, with research on bees increasing annually. Several researchers in Korea have studied the effects of various factors on honey bee health, but research on viruses has not been conducted extensively. Countrywide, mass honey bee mortalities during the winter of 2021 were concluded to be caused by various factors (climate change, pesticides, and mites) without mentioning the influence of viruses (Lee and Choi, 2022). However, several studies have shown that viruses can have a significant impact on the health of bees, and further research is underway. Korea experienced severe damage from the SBV in *Apis cerana* during 2009–2010. Using past damage as a starting point, focusing on the risk of viruses in honey bees and accumulating data through various studies will lead to developments in Korean beekeeping.

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