Varroa destructor Biology:

Anatomy, Reproduction, Life History, & Genetics

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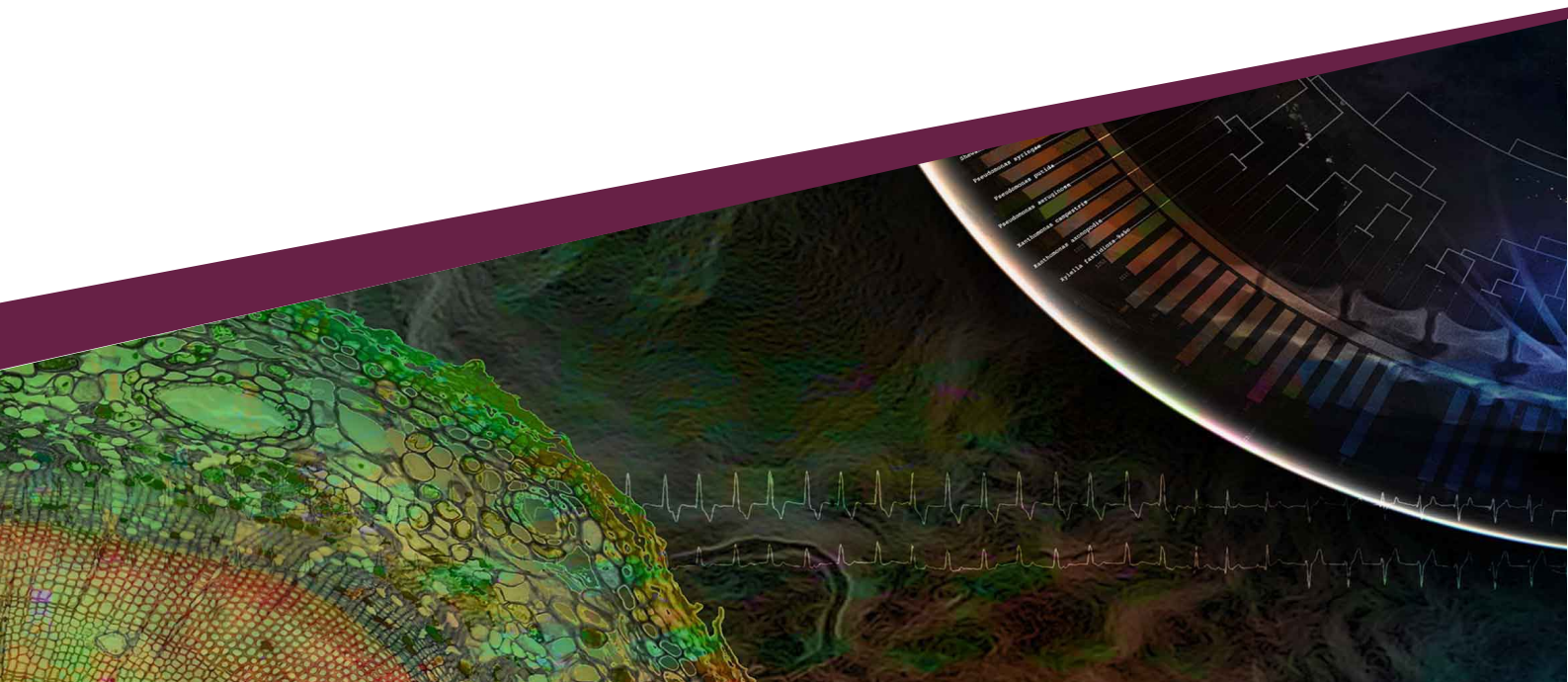
Introductory Research Essay
2025



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Anatomy, Reproduction, Life History, & Genetics

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Publisher:	Swedish University of Agricultural Sciences, Depatment of Ecology
Year of publication:	**2025**
Place of publication:	**Uppsala**
Keywords:	*Apis mellifera, Varroa destructor*, Anatomy, Reproduction, Parasite

Abstract

The ectoparasitic mite (*Varroa destructor)* is a parasitic species that has been scrutinized with increasing intensity due to its economic and ecologic impact on European honeybees (*Apis mellifera)*. With the plethora of research being produced it can be difficult to know what is or is not known about varroa mites. Previously, excellent reviews of the varroa have been written that focus on reproduction, disease transmission, and infestation dispersal. The goal of this review however is to gather both historic and modern research on the anatomy, life history, and genetic information of the varroa in detail, but to also point out gaps in the current field of research that should be investigated.

Keywords: *Apis mellifera, Varroa destructor*, Anatomy, Reproduction, Parasite

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Abbreviations

ABPV	Acute Bee Paralysis Virus
BEP	Brood Ester Pheromones
DWV	Deformed Wing Virus
J1	Japanese Haplotype
K1	Korean Haplotype
VG	Vitellogenin
SLU	Swedish University of Agricultural Sciences
VTP	Varroa Toxic Protein

1. Introduction

Varroa destructor (hence forth referred to as varroa) is an ectoparasitic mite that completes its entire life cycle within the hives of the European honeybee (Apis mellifera). The mite originally co-evolved as a parasite to the Asian honeybee (Apis cerana) before jumping to a new hosts in the mid-20th century. It is one of the major causes of colony mortality in A. mellifera through the vectoring of viruses to developing bee pupae while the mite is feeding off their fat bodies, known as Varroa disease, or Varroosis. These bees occlude (emerge from brood cell) with smaller bodies, lower weight, increased body malformations, along with a number of other symptoms leaving them less effective, or even unable, to contribute to the survival of the hive (Bowen-Walker and Gunn, 2001; Duay et al., 2003, 2002; Kralj et al., 2007; Kralj and Fuchs, 2006). When mite numbers reach a critical mass resulting in too many sick and malformed workers the hive can no longer support itself and dies (Boecking and Genersch, 2008). A general overview that looks at the current knowledge of mite biology and gaps that exist in our understanding, would be a beneficial resource for researchers, as well as apiarists trying to better understand the parasites that are affecting their colonies. While there has been an immense amount of effort and resources spent to eradicate this invasive threat, our understanding of the biology of the mite is still underdeveloped and in need of greater understanding.

1.1 Overview

Adult female varroa (foundresses) reproduce exclusively in the brood cells of developing honey bee pupae. Both adult and juvenile varroa feeds on the fat bodies of the developing pupae (Ramsey et al., 2018, 2019). When the adult bee emerges from the brood cell, the mite foundress and mated daughters escape as well, attaching themselves to the back of adult worker bees. The mite uses this dispersal phase for transport not only to new brood cells, but also to other colonies to begin the cycle again.

1.2 History

Varroa destructor originally was part of the species Varroa jacobsoni Oudemans which was first described on Apis cerana Fabricius bees in Java, Indonesia (Oudemans, 1904a). This species co-evolved with the Asian honeybee for thousands of years, with the species evolving into a stable host-parasite relationship. It is suspected that the first host jump occurred in in the 1940's when beekeepers moved their apiaries into Eastern Russia, resulting in contact between the European honeybee (Apis mellifera) and the Asian honeybee (Apis cerana). This contact allowed a subset of varroa to switch hosts and begin parasitizing A.

mellifera. As A. mellifera has not had the extended period of time to co-evolve as A. cerana, as well as not having preadaptation's that would contain varroa infestation, such as intense hygienic behavior, they were particularly susceptible (Oldroyd, 1999). V. destructor began spreading throughout Eurasia in the 1950's and 60's , arriving in South America in 1971, Africa in 1975, and finally reaching North America in 1987 (De Jong et al., 1982; Rinderer et al., 2010; Ruttner et al., 1984) and most recently in 2022 invading Australia. It is now found in all countries, with only a few select islands still mite free.

V. destructor was originally not viewed as a separate species, but instead just an expansion of the territory of V. jacobonsi for nearly 60 years. It was not until 2000 that they were identified as a unique species (Anderson and Trueman, 2000). Not only is V. destructor reproductively isolated from V. jacobonsi, but also significantly larger (Anderson and Trueman, 2000). Therefore, all research done before 2000 refers to the mite as V. jacobonsi, when it is now understood that they were looking at V. destructor.

1.3 Haplogroups

Since speciation occurred from V. jacobonsi, the varroa has been separated into different haplogroups, which are based on specific sequence polymorphisms in the mitochondrial DNA that correlate with geographic origins of the population (Kenney et al., 2013). Current analysis has found 10 different haplogroups, all in Southeast Asia, with four found in China, and one each in Sri Lanka, Nepal, India, Vietnam, Korea, and Japan (Traynor et al., 2020). Two of the most biologically and economically significant are the Korean (K1, called Russian or R type in previous studies) and Japanese (J1) haplogroup, as they are the only ones capable of reproducing on A. mellifera. A handful of genes have been found to be different between the two haplotypes, though it is currently unknown how these genes produce the phenotypic difference between K1 and J1 haplogroup. (Anderson and Fuchs, 1998; Solignac et al., 2005).

The K1 and J1 haplogroups are the only ones that have spread worldwide and are the only ones found to be pathogenic. The J1 haplotype is found only in Japan, Thailand and the Americas, while K1 is found worldwide, where it may be replacing the less destructive J1 (Figure 1). Through genetic research these two haplotypes were found to be partly isolated clones, due to the severe bottleneck that occurred at the time of the host switch (Solignac et al., 2005). The J1 haplotype was the first of the two discovered, and is considered less virulent and damaging than K1 due to reduced female reproductive capability (Anderson and Fuchs, 1998; Anderson and Trueman, 2000; de Guzman and Rinderer, 1999). J1 was imported to South America through Paraguay in 1971, where it spread to Brazil, and then 10 years later to North America (Anderson, 2000). K1 (originally known as Russian haplotype, or R) switched hosts from A. cerana sometime in the 1950's, most likely

around Vladivostok, Russia, just north-east of North Korea where it spread worldwide over the next 70 years (Traynor et al., 2020). K1 is much more virulent due to increased female reproductive capability, and is the haplotype of varroa almost exclusively associated with colony death (Anderson and Fuchs, 1998; Anderson and Trueman, 2000; de Guzman and Rinderer, 1999). Unless otherwise stated, K1 is exclusively used when referring to varroa, both in this paper and in a majority of other literature.

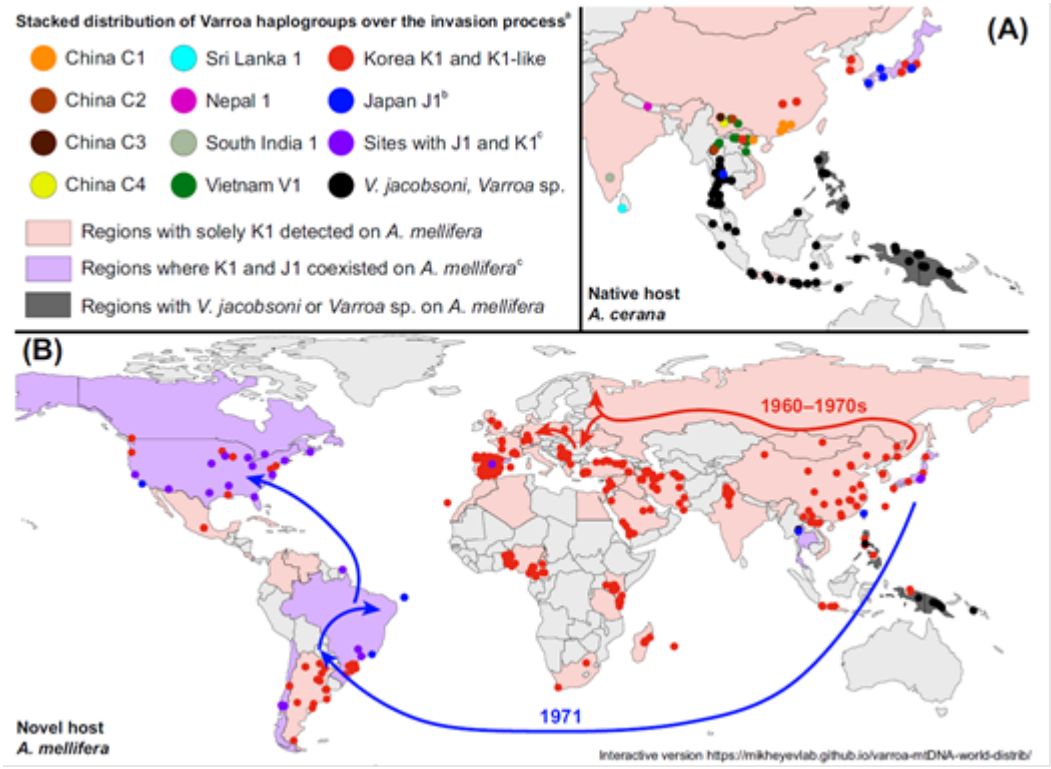

Figure 1. Haplogroup and distribution timeline of varroa (Traynor et al., 2020)

1.4 Mating in A. mellifera vs A. cerana

A major reason why A. cerana can coexist with varroa is due to mite-infestation only occurring in the drone brood, and not the worker brood (Lin et al., 2018). The commonly held understanding for this was that A. cerana is more hygienic compared to A. mellifera, meaning they clean out mites from the worker brood cells, ultimately lowering the colony's mite infestation pressure (Peng et al., 1987). This results in varroa only able to reproduce in around 8% of total brood cells compared to A. mellifera colonies, where they are able to reproduce in the remaining 92% of worker brood cells (Winston, 1991). This is further exacerbated due to drone rearing reaching its peak around May, with a slight increase again in August, compared to workers which are produced for most of spring and summer, depending on the environment (Winston, 1991). One documented method that A.

cerana employs is through the removal of infested brood at a higher rate than A. mellifera (Peng et al., 1987). Nurse bees remove developing brood from their cells which interrupts the feeding and reproduction of the mites, leaving them unmated. They also exhibit a behaviour known as entombing, where they plug the central pore in the cell cap that is necessary for gas exchange. This results in the drone death, and traps the mite preventing further spread and infestation (Boecking, 1999; Lin et al., 2018). While both of these methods results in the death of the brood, it may be necessary sacrifice to make in order to limit the spread of varroa. Further, A. cerana has been shown to have a much more thorough grooming behaviour that reduces the number of mites in the dispersal phase (Boecking and Spivak, 1999). All of these behaviours are at least partially mediated by semiochemical compounds released by the pupae that initiate hygienic behaviours (Rosenkranz et al., 1993).

A recent review of research on A. cerana however has pointed out that other factors may have exaggerated the hygienic behavior of A. cerana (Grindrod and Martin, 2023). This could mean that other factors are present that contribute to the stable host-parasite relationship.

One such factor is the significant preference of varroa to invade the worker and drone brood cells of A. mellifera over their original host A. cerana (Li et al., 2021). Research into this phenomenon found that a significant difference between the two brood was the cuticular hydrocarbons (BEP) released. A cerana brood produced higher levels of alkenes, while A. mellifera released higher levels of methyl-alkanes, which while not confirmed, may work as an attractant to varroa. Studies using glass dummies found that varroa significantly preferred the dummies coated with A. mellifera BEP's compared to A. cerana (Li et al., 2021). This could mean that A. mellifera is pre-maladapted to co-existing with varroa, further increasing their difficulties in surviving the host-parasite arms race.

Recent research from China shows that mites themselves may have adapted to only reproduce in the drone brood of A. cerana, instead of it being a product of worker bee action. A protein found in the saliva of the Varroa destructor mite, varroa toxic protein (VTP), was found to be toxic to A. cerana worker brood, significantly increasing their mortality rate, with no effect on drone brood (Zhang and Han, 2018). Previous research has proposed that parasites that rely on their hosts reproduction for transmission should become less virulent over time if that virulence factor severely negatively affects the hosts mating success (Knell, 1999). This may explain the evolutionary benefit of varroa producing VTP as it further encourages mites to only reproduce in the drone brood, thus lessening the negative impact on the hosts survival.

Zhang & Han 2018 in the same paper also found that VTP increases the levels of deformed wing virus (DWV) titers and resulting symptoms of deformed wing virus infection in adults. As the name implies, DWV is a virus transmitted from varroa that causes crippled, flightless adult honey bees (Fig 2.) with significantly

shortened life spans leading to the eventual loss of colony function (de Miranda and Genersch, 2010; Wilfert et al., 2016). This adds to what was stated previously that A. mellifera may be pre-maladapted to varroa infestation, further increasing their mortality and slowing the co-evolution that arose in A. cerana. Though further research is necessary to understand this completely.

A. B.

C.

Figure 2. A. mellifera with symptoms of deformed wing virus. Photo A & B courtesy of Barbara Locke, Photo C courtesy of Vitezslav Manak

1.5 Effect on Honeybee

Emerging adult honeybees that have been infested with varroa suffer from a variety of physiological issues compared to uninfested bees (Fig 3). On emergence, they have decreased body weight and water content, which is made worse by the presence of multiple foundresses (Bowen-Walker and Gunn, 2001; Duay et al., 2003). This reduces survival and in drones correlates with reduced sperm production resulting in reduced reproductive fitness (Duay et al., 2002; Schlüns et al., 2003).

Adult workers have decreased flight performance with less directionality and for shorter times compared to non-infested individuals, which results in reduced efficiency in collecting needed resources for the colony (Duay et al., 2002; Kralj and Fuchs, 2006). Infested individuals also have reduced non-associative (single stimuli) learning resulting in lower responsiveness and quicker habituation to sugar stimuli (Kralj et al., 2007). The result of reduced flying and non-associative learning may be beneficial to both parasite and host. With decreased foraging abilities worker bees are more likely to drift into a new hive, thus spreading the mite to a new population, but also lowering the rate of infestation due to the loss of the infested bee (Kralj et al., 2007; Kralj and Fuchs, 2006).

Varroa infestation also has an effect on honeybee immune responses that is just beginning to be understood. With the removal of hemolymph and hemocytes during feeding, as well as the transfer of immunosuppressing compounds, emerging individuals have significantly lower immune systems in addition to the previously stated issues (Annoscia et al., 2019; Řeřicha et al., 2021; Richards et al., 2011; Wegener et al., 2016; Yang and Cox-Foster, 2005) . Haemolymph functions as the circulatory system in insects and is responsible for water and chemical storage, as well as immune response using hemocytes (Arrese and Soulages, 2010; Strand, 2008). Emerging infested individuals have a downregulation of immune gene expression as well as changes in the proteomic pathways of the immune response (Erban et al., 2019; Marche et al., 2019; Słowińska et al., 2019; Surlis et al., 2018; Zaobidna et al., 2017). This could leave honeybees susceptible to non-varroa related diseases and further decrease their life span.

Significant changes also occur in the microfauna of infected honeybees with certain species becoming more or less prominent (Hubert et al., 2017; Marche et al., 2019, p. 201). Whether this is an adaptive response to infection or negative byproduct is yet to be seen and requires further research.

1.5.1 Viruses

Honey bee colonies naturally house a plethora of viruses such as Deformed Wing Virus (DWV), Acute Bee Paralysis Virus (ABPV), and Sacbrood Virus, among others at varying levels throughout the year (de Miranda and Genersch, 2010; Genersch and Aubert, 2010). They are normally transferred through a combination of vertical (drone → queen, queen → egg) and horizontal (oral, cell cleaning, cannibalism) transmission (Chen et al., 2006; Fries and Camazine, 2001). Infection biology hypothesizes that vertical transmission should select for less virulent strains leading to less deadly viruses over time (Chen et al., 2006). This is not the case with horizontal transmission however with there being reduced selection for lower virulence, and in some cases selection for increased virulence. With direct feeding on honeybee larvae a new horizontal transmission route is accessible to viruses resulting in much higher viral loads found in infected honey bee (Amiri et al., 2018; Chen et al., 2006; de Miranda et al., 2013; Fries and Camazine, 2001).

Recent research has found that viral infections can also cause more subtle changes in honeybee physiologies than was previous thought. Workers that are infected with DWV have impaired learning as well as begin foraging at a younger age, which both lead to colony loss as well as being less able to differentiate between varroa-infested and non-infested pupae (Mondet et al., 2015; Traniello et al., 2020). This alteration in behaviour may be due to a significant downregulation

of genes that code for neuron signaling (Pizzorno et al., 2021). With the majority of damage from varroa infestation coming from the viruses transmitted and not the mites themselves, this is an area of research that is receiving more attention in recent years. This will hopefully result in a better understanding of how honeybees are affected by these viruses as well as better ways to keep colonies healthy in the future.

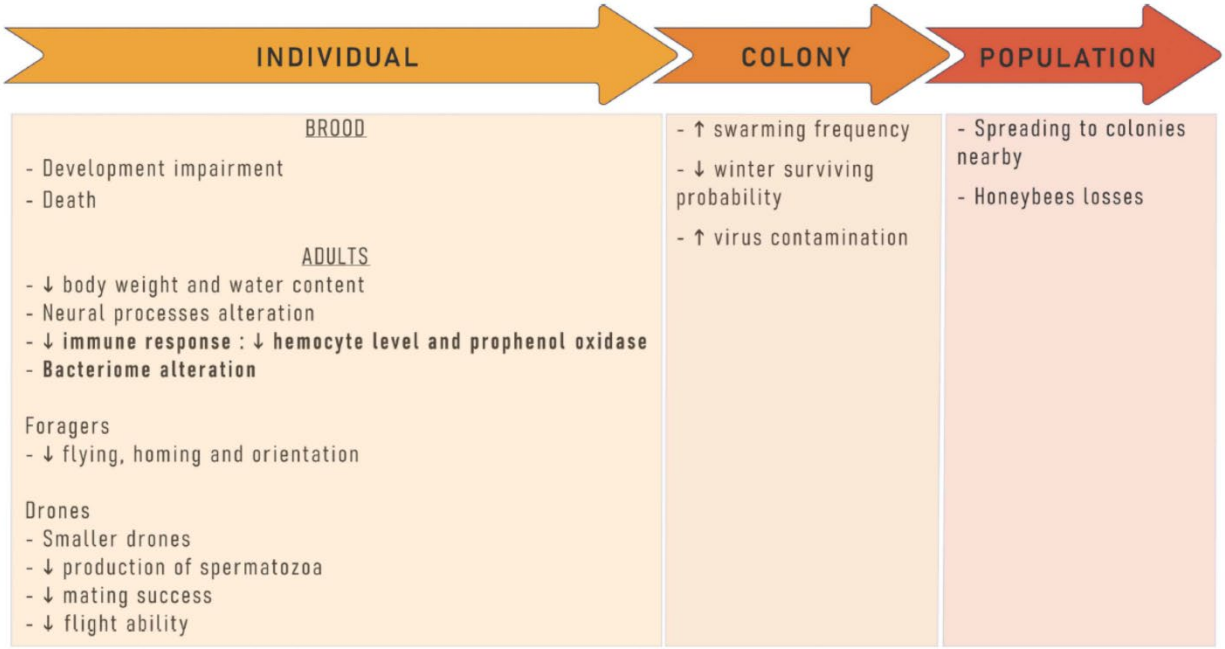

Figure 3. Effects of Mite on Hive Summary (Noël et al., 2020)

2. Anatomy

When fully grown, female varroa are 1.7 mm large, 1.1 mm long brown disc shaped mite with one large dorsal shield, and seven smaller ventral plates (Fig. 4) (Piou et al., 2021).

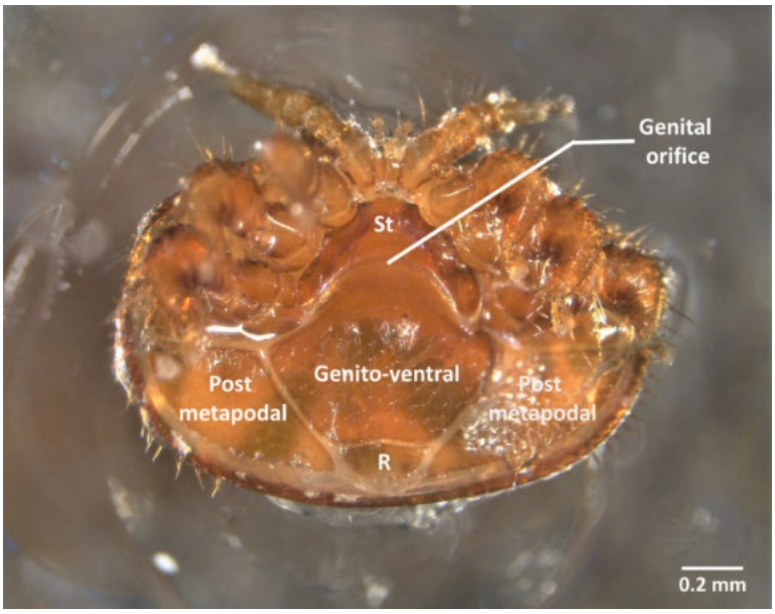

Figure 4. A. External view of Varroa destructor female dorsal plate. B. External view of Varroa destructor female ventral plates. R, rectal scutum; St, sernal scutum (Piou et al., 2021).

Being in the arachnid family, the mite has eight legs with the front two (chelicera) rarely being used for movement, but instead being used as mechano- and chemo receptors (Dillier et al., 2006). The mite is also covered in fine hairs of many different types, which are used for similar purposes as the chelicera (Dillier et al., 2006; Liu and Peng, 1990). Varroa has also been shown to be able to detect temperature and humidity, having a normal preference from 26 – 33 °C & 59 - 70% RH (Kraus and Velthuis, 1997; Le Conte et al., 1990a; Le Conte and Arnold, 1988). Directly behind the chelicera is a synganglion, comprising an ancestral brain and ventral nerve cord fused together (Fig. 5) (Piou et al., 2021; Sonenshine et al.,

2022). For more detailed description of the brain synganglion and nerve structure, see Soneshine et al. 2022.

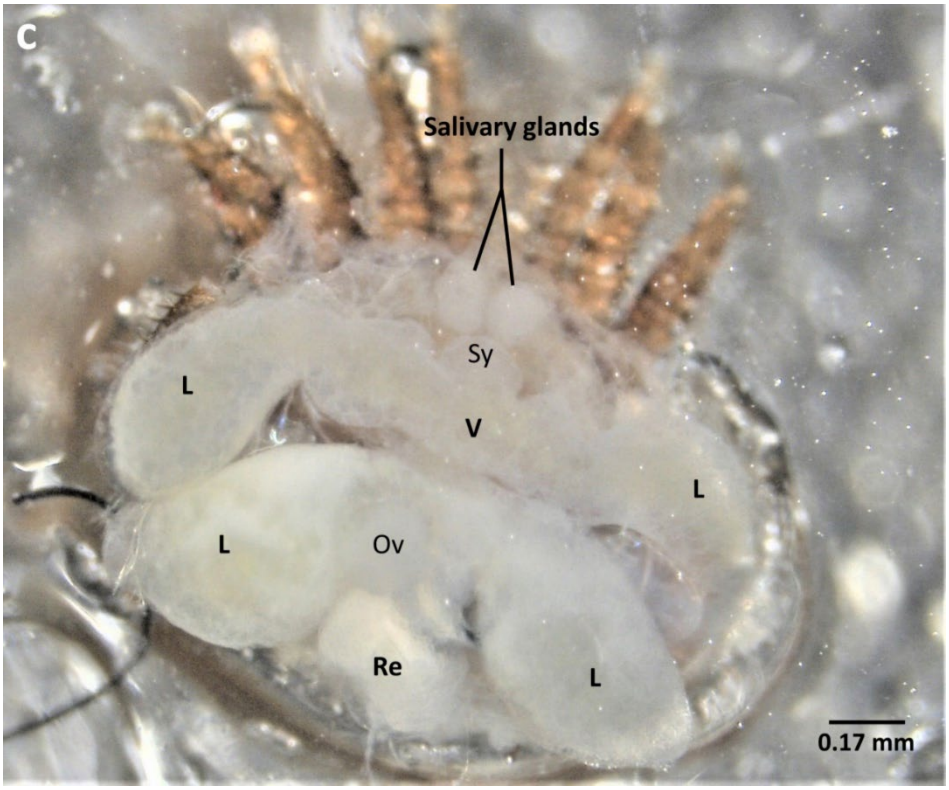

Figure 5. Internal anatomy of female Varroa destructor; dorsal view. Dorsal shield, trachea, fat bodies, and Malphighian tubules have been removed. L = caecal lobes; Ov = ovary; Re = rectum; SG = salivary glands; Sy = synganglion; V = ventriculus (Piou et al., 2

2.1 Legs

The legs are made up of multiple segments, ending in the pretarus. This consists of two main parts, the cuticular basal stalk, and an extrudable, membranous amulacral pad called the caruncle. When this is fully extruded and expanded, it becomes a bi-lobed sucker which can be used to attach to different surfaces such as the abdomen of honey bees or the walls of a brood comb (Fig. 6) (Liu and Peng, 1990).

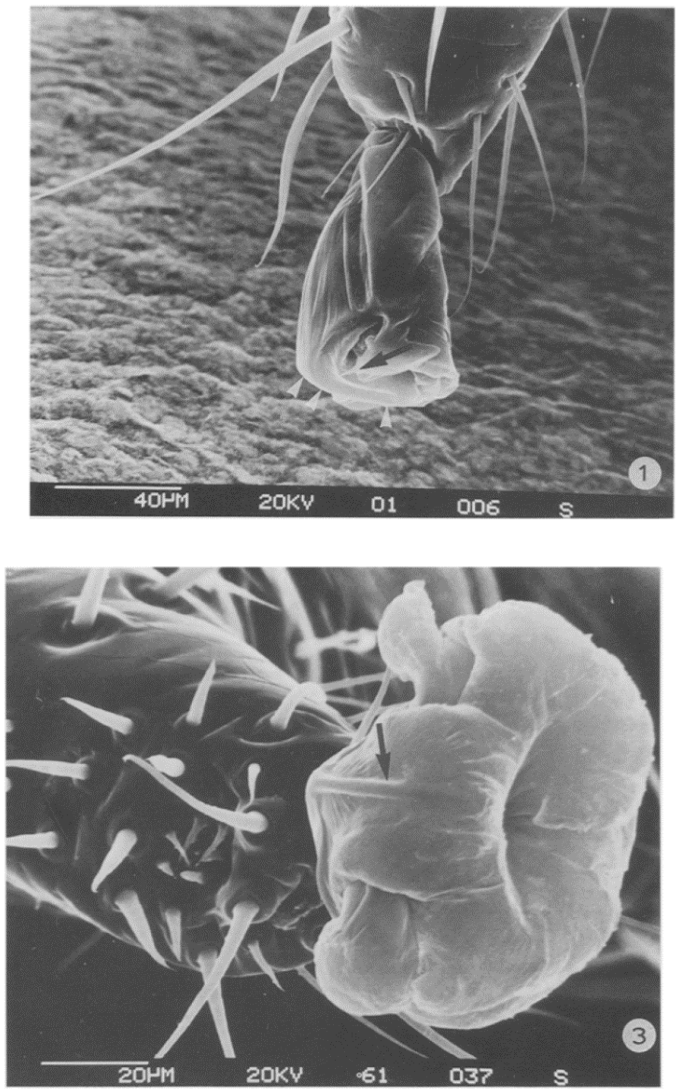

Figure 6. The sucker like structure on the leg of the varroa mite A) collapsed and B) fully expanded. The arrow points to plates used by varroa to collapse and fully open the structure (Liu and Peng, 1990).

2.2 Sensory Systems

The varroa mite is completely blind and deaf, with only a very limited number of light sensitive nerve cells (Kirchner, 1993), relying entirely on chemo and somatosensory system for direction, feeding, as well as timing and location for reproduction.

Chemo sensing is the dominant sense used by varroa mites, using their front two legs in a similar way that insects use their antennae (Dillier et al., 2006; Eliash et

al., 2019; Nganso et al., 2020). The olfactory organs are located near the dorsal section of each leg with nine chemosensing sensilla (s1-s9) located inside a pit, with nine longer sensila surrounding it (r1-r9) (Fig. 7). The S2-S6 sensilla appear to be used for olfactory detection, while S7-S9 do not contain chemo sensing pores and are used as hygro and thermo receptors which are crucial for mite reproduction, discussed below (Dillier et al., 2006). This pit organ is used prominently in both host and mate finding, with both actions being disrupted if the organ is blocked (Häußermann et al., 2015; Nganso et al., 2020). The pit organ is sensitive enough to be able to tell castes of honey bees apart based on the pheromones produced, with a particular preference for nurse bees (Eliash et al., 2014; Piccolo et al., 2010). This is at least partly due to a lower production of Z-8-heptadecene, geraniol and nerolic acid by nurse bees compared to foragers, all of which are repellents to varroa (Piccolo et al., 2010).

Varroa also uses somatosensory to orient themselves, with a majority of their body being covered in fine hairs of different types (Fig. 4, 7) (Dillier et al., 2006). They are quite sensitive to airflow, using its frontal legs to respond to air puffs for reorientation. This is seen in the form of detecting vibrations in a similar capacity to that of honey bees, as well as being sensitive to airflow (Dillier et al., 2006, 2002; Kirchner, 1993; Kuenen and Calderone, 1998). They have recently been found to produce ultra-short high magnitude vibrational pulses, though the exact purpose of this is not yet known, with the authors speculating that it may be used as a type of "sonar" probing function (Hall et al., 2022).

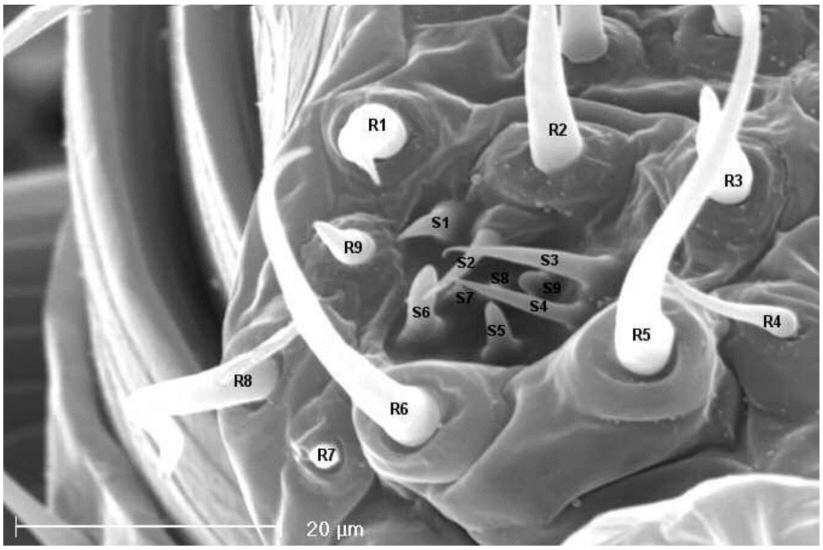

Figure 7. Photo showing both sets of chemosensing sensilla located in (S1-S9) and around (R1-R9) the pit organ on the front two legs of the varroa mite (Dillier et al., 2006).

2.3 Heart

The hearth is around 165 µm by 60 µm and consists of two lateral trunks (Koutouvela and Papachristoforou, 2019) (Fig. 8). Contractions of the ventruicula direct haemolymph into the heart while expansion directs haemolymph to other parts of the body. It contains 6 ostia (small openings that allow haemolymph to enter or leave the vessel) which is unique to the Acari standard of 4 (Heppner et al., 2008; Koutouvela and Papachristoforou, 2019). The heart resides in a sinus called the pericardial septim and haemolymph enters the myocardium heart from the ostia. Outside the heart cavity haemolymph flow is controlled using arterial vessels. Varroa heartbeat were on average 7.39 seconds in duration with an average frequency of the heart rate of 0.13 Hz (Koutouvela and Papachristoforou, 2019).

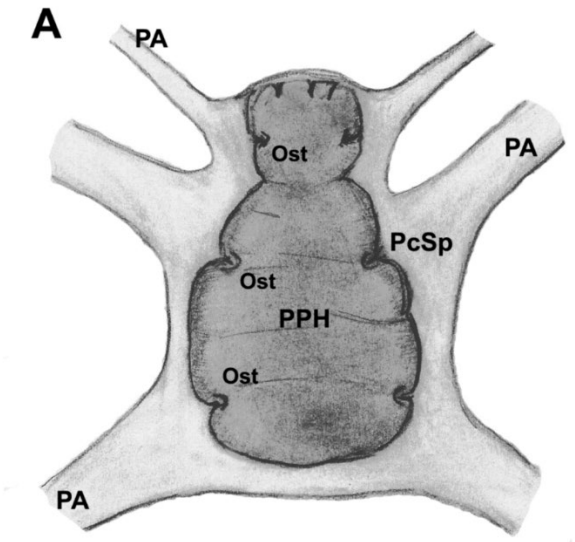

Figure 8. Drawing of Varroa destructor heart. PcSp: Pericardial septum PPH: Pulsative portion of heart, PA: Pedal arteries, Ost: Ostia (Koutouvela and Papachristoforou, 2019).

2.4 Trachea

Varroa breathes using a tracheal system similar to other Insecta and Arachnida. A main trunk extends from the atrium which divides into 5 anterior and 4 posterior tracheal branches (Richard et al., 1990) (Fig. 9). The anterior branch enters the region of the podosoma and gnathosoma of the mite where it subdivides further into the organs and anterior legs. The posterior branch enter the region of the opithosoma where it also subdivides further to enter the posterior organs and legs (Richard et al., 1990). Both left and right sides of the trachea are joined at multiple parts, but especially so at the gnathosoma, posterior of the nerve ganglia, and posterior area of the podosoma (Richard et al., 1990).

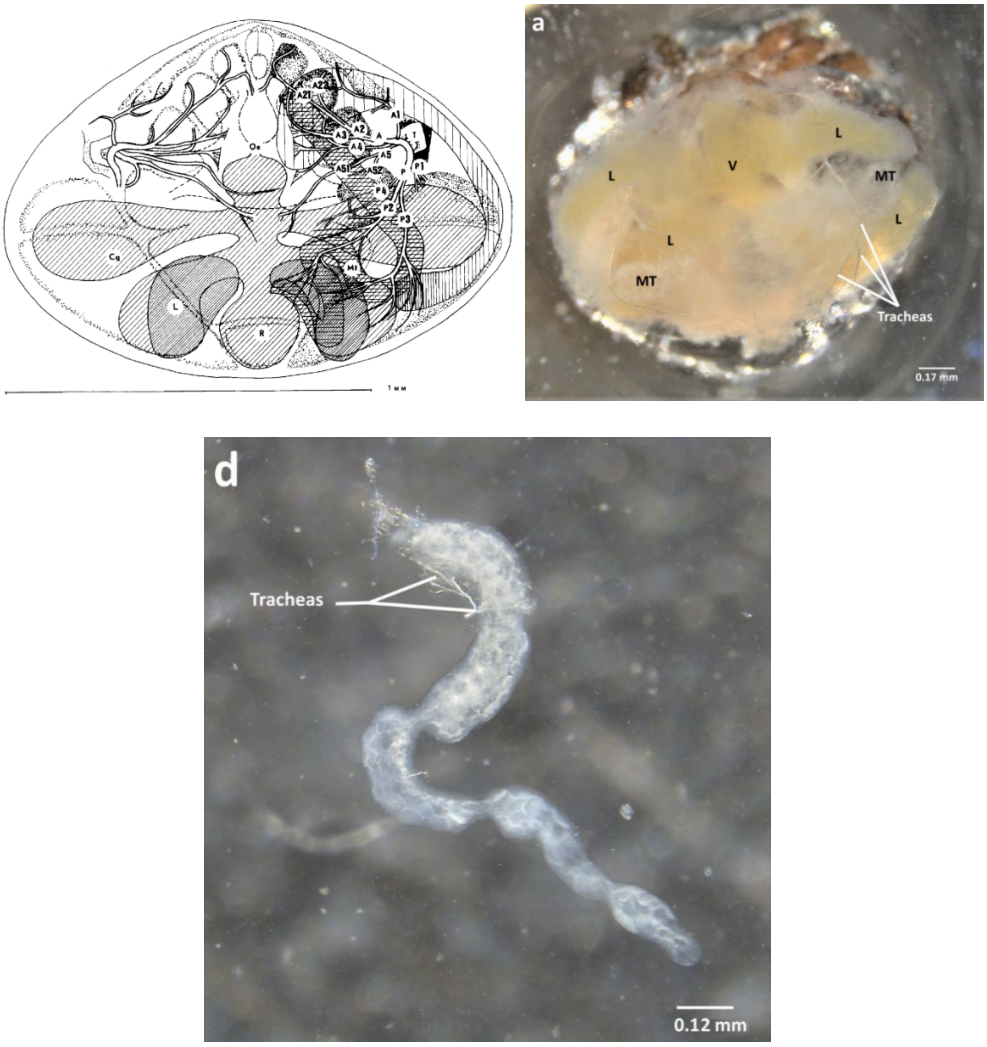

Figure 9. A. Drawing of general structure of trachea in female Varroa destructor. A, trachea of anterior branch; Oe, oesophagus; R, rectum; P, trachea of posterior branch; L, lyrate organ; Cg, caecal lobes; T, atrium; Mt, Malpighian tubule (Richard et al., 1990). B. Internal organs of female Varroa destructor after the dorsal shield has been removed. L = caecal lobes; MT = Malpighian tubules (Piou et al., 2021). C. Photo of female Varroa destructor trachea (Piou et al., 2021).

2.5 Feeding

A large amount of information regarding feeding and digestion is taken from Gorgol 1991, which in turn cites Reuter 1909, Ugolev 85, and Zavarsin 85 of which two are unavailable to read at this time and Reuter 1909 is only available in German. While modern research is needed to confirm these findings this article will cite what is reported in Gorgol 1991.

Varroa obtain nutrients in two different ways depending on their life stage. While in the protonymph stage the mite is lecithotrophic (feeding upon egg yolk reserves) (Ugolev 1985 in Gorgol 1991). Upon the deutonymph molt, feeding switches to heterotrophy, feeding on bee fat bodies (Gorgol 1991).

The mouthparts are structured similar to other fat-body consuming acari, with a gnathosoma comprised of two sensory pedipalps and two chelicera (Fig. 10). The chelicera are formed by the basal, the middle, and the distal digit segements (Ramsey et al., 2019). In females this last segment is movable with two small teeth, while this is a spermatodactyl in males (a thin tube-like structure used to transfer sperm into the female's genital tract). The females use these last two segments to pierce cuticle of the honeybee for feeding (Ramsey et al., 2019; Rosenkranz et al., 2010). At the base of the gnathostoma are well-developed paired salivary stylets which produce salivary fluid that mixes with the honeybee's tissue to begin extra-oral digestion (Fig. 5, 11, 12) (Cicero and Sammataro, 2010; Ramsey et al., 2019). Varroa can consume almost a microliter of host-fluids daily in this method (Posada-Florez et al., 2019).

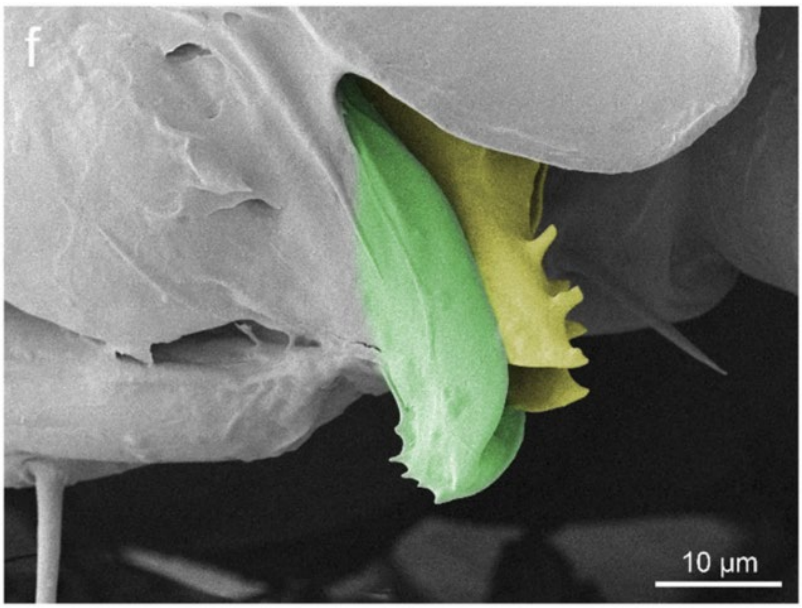

Figure 10. Chelicera of female varroa used for piercing honey bee cutical to feed on fat bodies (Ramsey et al., 2019).

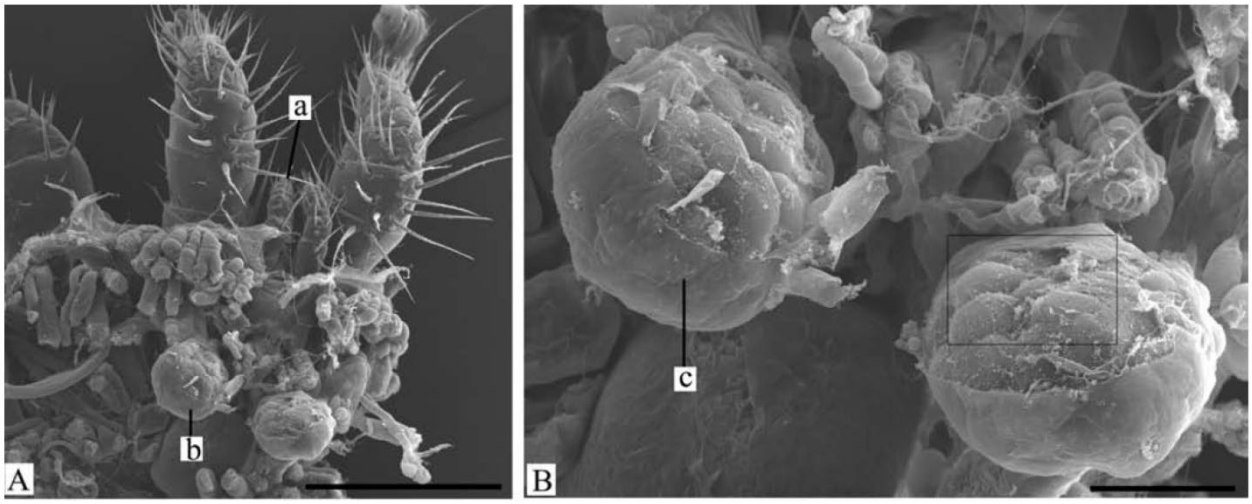

Figure 11.. Scanning electron micrograph of Varroa destructor gnathosoma and salivary glands. A. Dorsal view with dorsal shield removed. B. Magnification of salivary glands. Scale bars: A) 250 µl; B) 50 µl (Cicero and Sammataro, 2010).

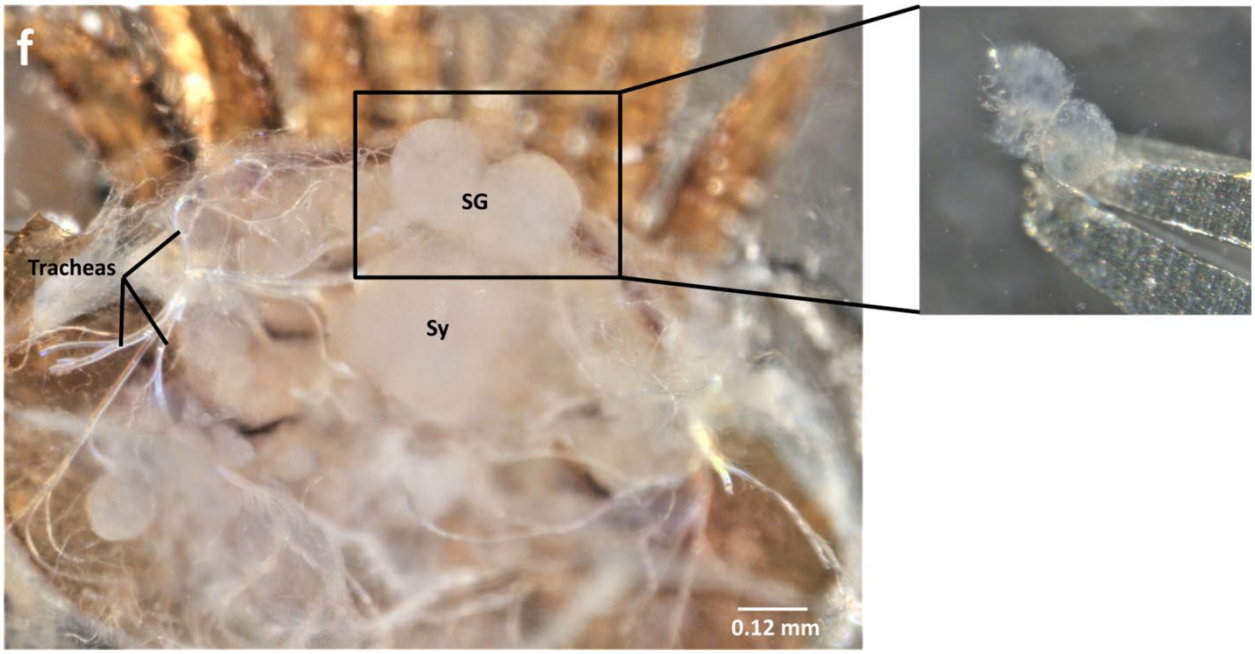

Figure 12. View of dissected female Varroa destructor salivary glands. SG, salivary glands; Sy, synganglion (Piou et al., 2021).

2.6 Digestion

Digestion occurs in varroa in three different ways: extra-intestinal, in the intestinal cavity, and in the intracellular cytosol and vesicles. Up to the deutonymph stage intact (absorption of intact proteins), intestinal, and intracellular cytolsolic (in the cytosol) digestion are predominantly used, only switching to intracellular vesicle (in the vesicle using lysosome) digestion in the final parts of the deutonymph stage. Fully mature adults mostly rely on vesicular and contact (intestinal membrane) digestion. The forms of different digestive prominence is not an abrupt changed with distinct stages but instead gradually change with a large amount of overlap (Gorgol 1991).

The gut is separated into two main systems: digestive and excretory (Gorgol, 1991; Reuter, 1909b in Gorgol 1991; Sonenshine et al., 2022). The digestive system

includes the extodermal anterior gut, consisting of the pharync and esophagus, and the entodermal middle gut, consisting of the stomach with diverticula, ceacal lobes, and colon. The excretory system is comprised of the entodermal rectal sac with Malpighian tubes as well as the extodermal rear gut (rectum) (Fig. 5, 13). Gut structure changes with female maturation, with males and immature females (proto & deutonymphs) having more vigorous development of the stomach with a shorted diverticula and mild colon development ((Reuter, 1909b in Gorgol 1991; Sonenshine et al., 2022). The pharynx, esophagus and rectum are lined with squamous epithelium and function passively only serving to transport food and digestion products (Gorgol, 1991). The stomach and diverticula are lined with two different cell types that change in dominance depending on the maturity of the mite. Undifferentiated cells represented by unipotent cambial element activities which are more pronounced in immature and weaken upon maturity. Functionally active cells are represented by single-type polymorphous and polyfunctional digestive cells and are present during all stages of maturity. The colon epithelium is lined with only a single-type of columnar epithelium cells ((Ugolev, 1979 in Gorgol 1991). The rectal sac and Malpighian tubes are lines with nephridial epithelial cells (Zavarsin, 1985 in Gorgol 1991) and function to process metabolism product excretion (guanine) as well as reabsorption of excretory fluid components. Mites excrete on average 18 times a day, with an average of 0.049nL ± 0.044 each excrement, averaging around 0.8 nL / day (Posada-Florez et al., 2019)

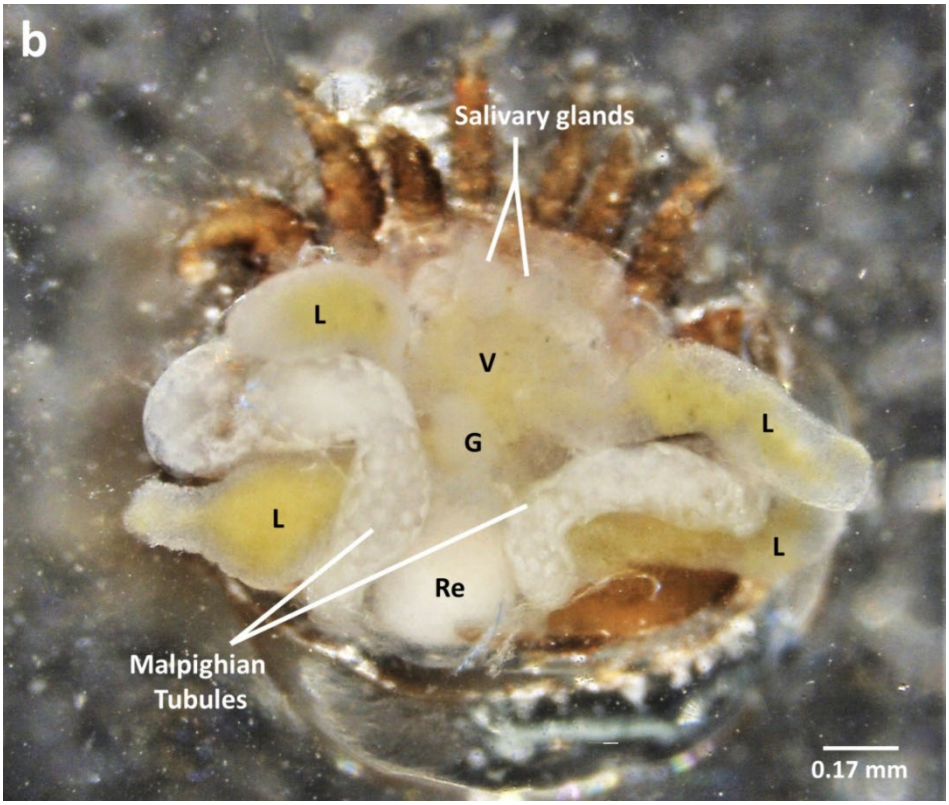

Figure 13. Dorsal view, internal anatomy of Varroa destructor female. Dorsal shield, trachea, & fat bodies removed. L, caecal lobes; MT, Malpighian tubules; Re, rectum; V, ventriculus (Piou et al., 2021).

2.7 Reproductive Organs

Varroa female reproductive organs consist of three main components: the ovary, lyrate organ, and sperm storage (Alberti and Hänel, 1986, 1986) (Fig. 14).

The ovary is located in the midsection of the body and is a large open organ containing oocytes and nurse cells, cells that assist other cells in their development (Reyes García and García Tamayo, 2013; Sonenshine et al., 2022) (Fig 15, 16). Protruding from the ovary is the paired lyrate organ (Fig. 15, 16) (Alberti and Zeck-Kapp, 1986; Sonenshine et al., 2022) which is believed to be have nutritive properties, transferring proteins, lipoproteins, and other nutrients into the ovary from the midgut though this has yet to be confirmed (Palma and Alberti, 2001; Sonenshine et al., 2022).

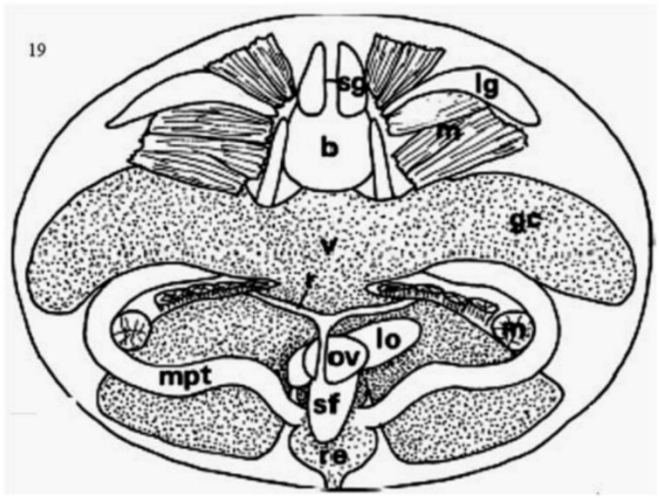

Figure 14. Drawing of Varroa destructor female organs. B, base of gnathosoma; gc, gastric caeca; lg, leg; lo, lyrate organ; m, muscle; mpt, malpighian tubule; ov, ovary; r, ramus (tubulus); re, rectal sac; sf , seminal receptacle; sg, chelicerae: V, ventriculus (De Ruijter and Kaas, 1983, Sibesgube et al, 2022

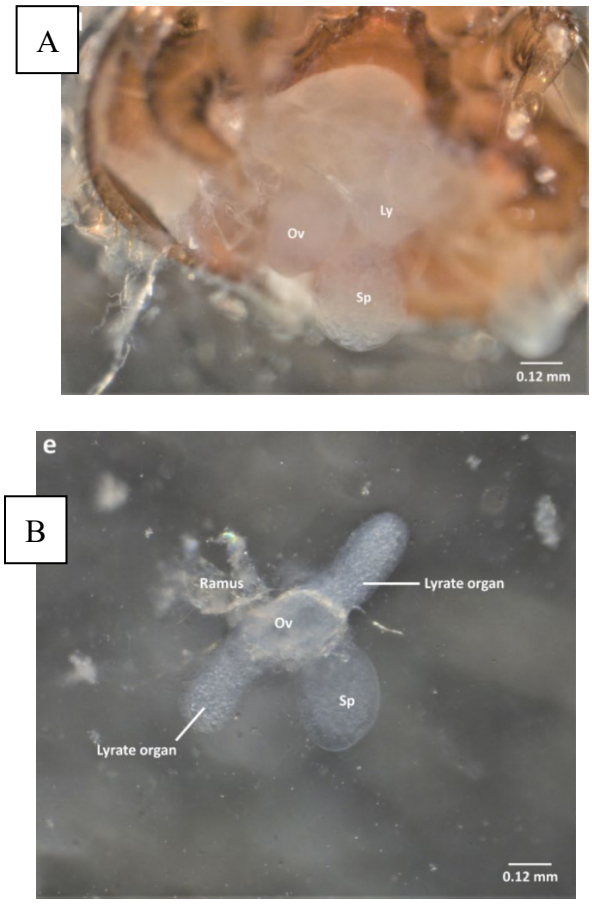

Figure 15. A. Picture dissected female Varroa destructor. Genito-ventral scutum, posterior metapodal scuta, trachea, fat bodies, and Malpighian tubules have been removes. B. Extracted

reproductive organs of female Varroa destructor. Ly, lyrate organ; Ov, Sp, spermathecal (Pious et al, 2021).

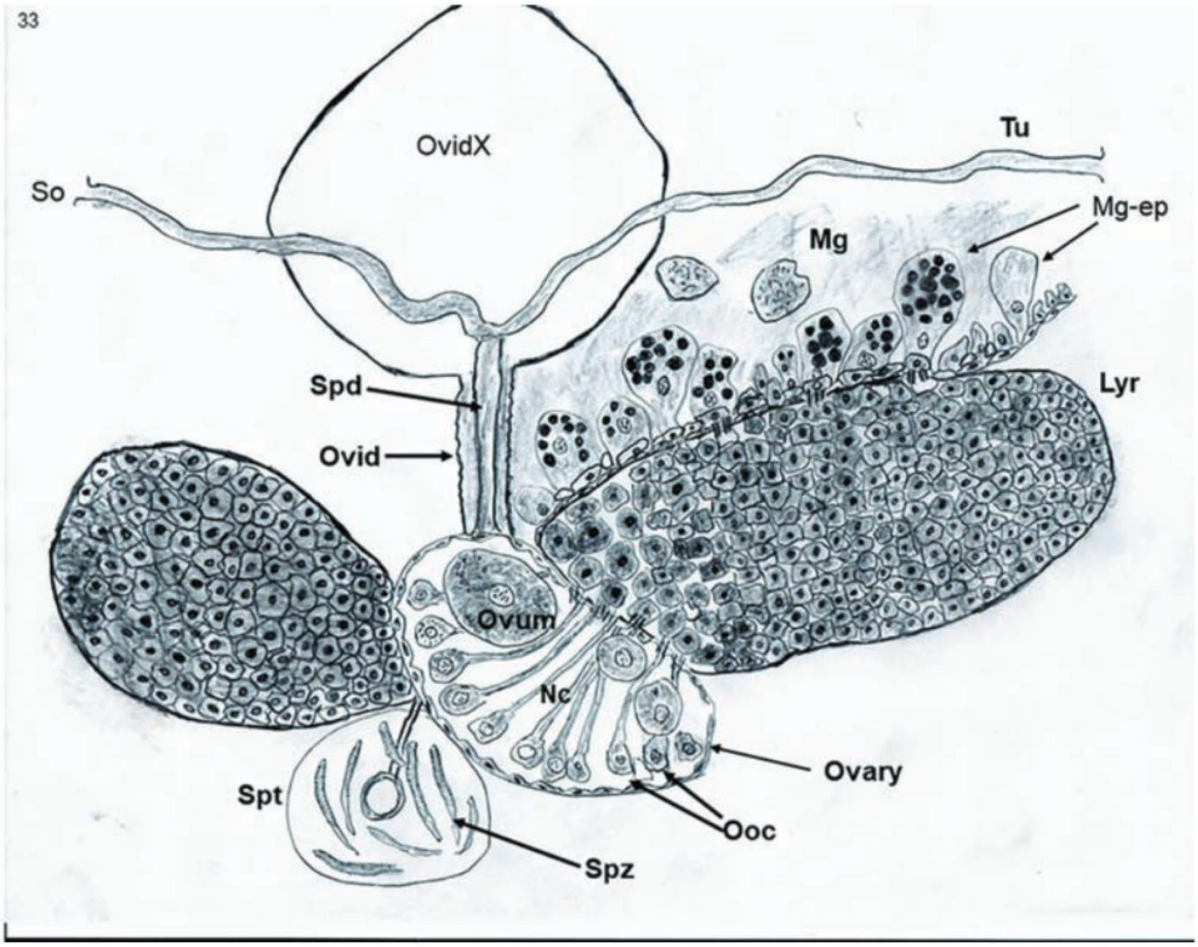

Figure 16. Drawing of adult female Varroa destructor reproductive system. Lyr, lyrate organ; Ovid, narrow section of oviduct; OvidX, larger main section of oviduct; Mg, midgut; Mg-ep, enlarged digestive cells with imbibed lipoproteins; Nc, nurse cells, with narrow, tubular extensions connected to developing ova; Ooc, ova in early stage of development, early stage of development; So, solenostome; Spd, sperm duct; Spz, spermatozoa; Spt, spermathecal; Tu, tubulus (Alberti and Hänel, 1986; Sonenshine et al., 2022).

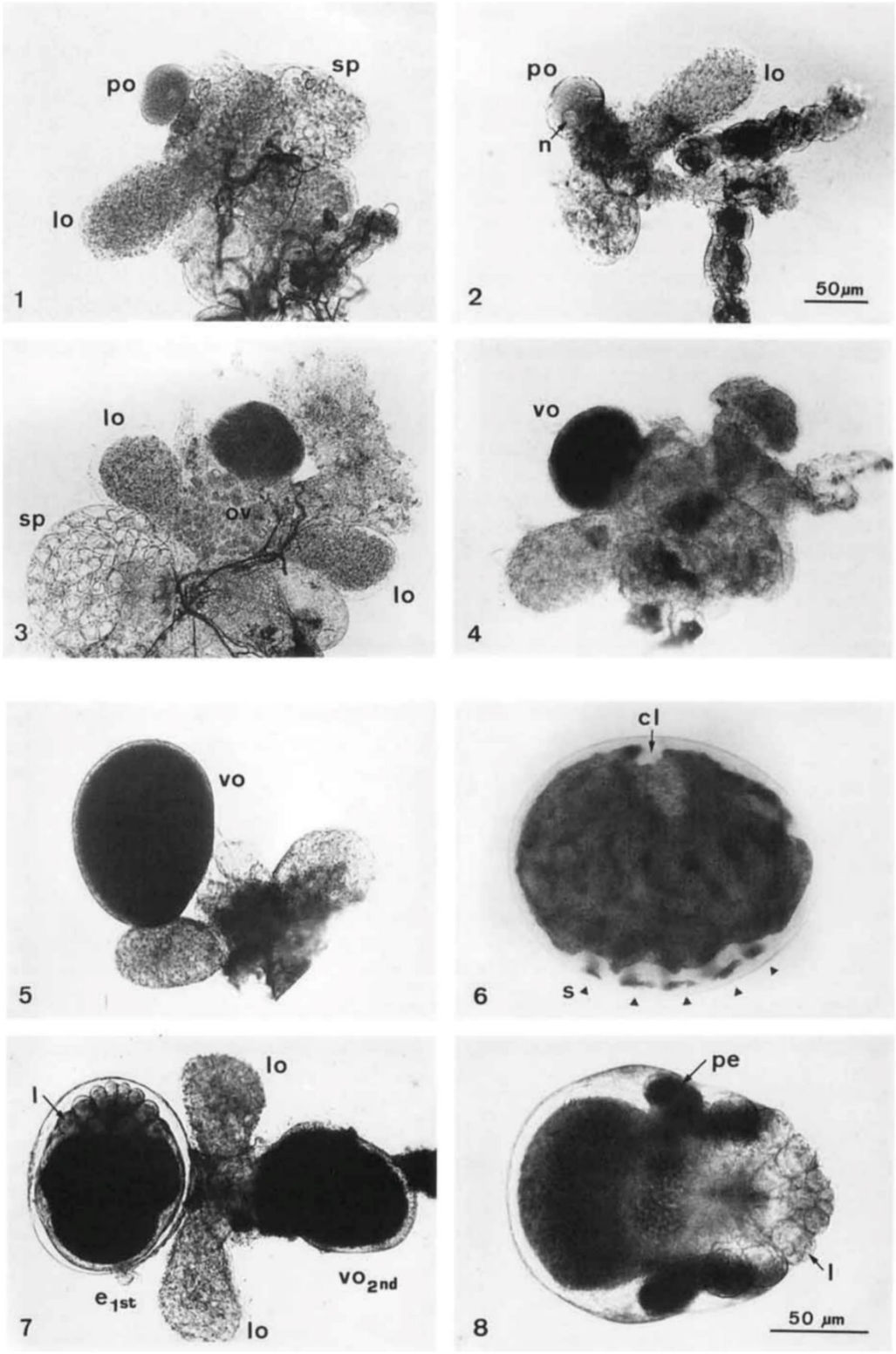

Figure 17. Reproductive system of adult female Varroa destructor. 2) Slightly enlarged oocyte with nucleus visible in the pre-vitellogenin phase (5 - 10 h). 3) Oocyte in early vitellogenin phase (10 – 15 h). 4) Medium sized oocyte in vitellogenin phase (15 – 20 h). 5) Oocyte in late vitellogenin phase (20 – 25 h). 6. Embryo showing early stages of segmentation (35 – 40 h). 7). Example of overlapping gonocycles with 1 embryo with visible legs, and 2nd oocyte in vitellogenin

phase (60 – 65h). 8) Pharate protonymph with peritreme anlagen C1, cleft; e, embryo; I, leg; lo, lyrate organ bilobed);n, nucleus; ov, ovary; pe, peritreme; po, previtellogenic oocyte; s, segment anlagen; sp, spermatheca; vo, vitellogenic oocyte." (Steiner et al., 1994).

The sperm storage system comprises a spermatheca, sperm duct, and paired solenostomes (Fig. 16) (Alberti and Hänel, 1986; Evans and Till, 1979; Michael, 1892). Spermatozoa enter through the solenostome, which are copulatory pores leading into a flat chamber called the tubulus. This feeds into the spermatheca, which is a large organ filled with spermatozoa where they are stored and matured. The sperm duct leads out of the spermatheca and into the ovary (Fig. 16) (Palma and Alberti, 2001; Sonenshine et al., 2022).

Male varroa genitals consist of a single testis in the posterior section of the body (Fig 18). From the testis two vasa deferentia emerge which eventually combine into a single tube, the ductus ejaculatorius, on top of small muscle cells which emerges at the front edge of the sternal shield (Alberti and Hänel, 1986). A single accessory genital gland is connected at the end of the ductus ejaculatorius and secrets what is thought to be proteins into the duct. The exact function of this protein is unknown, though it may be extra nutrients for the spermatozoa (Alberti and Hänel, 1986; Häußermann et al., 2018).

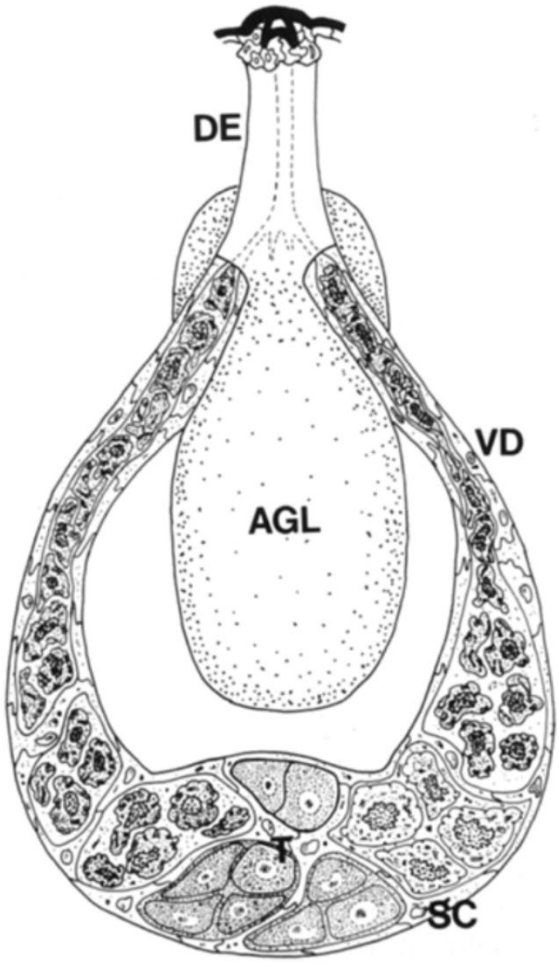

Figure 18. Drawing of Varroa destructor male genital system showing different stages of spermiogenesis. DE, ductus ejaculatorius ; VD, vas deferens; AGL, accessory gland; T, testis; SC, somatic cells (Alberti and Hänel, 1986).

3. Reproduction

Varroa mites reproduce exclusively in honeybee brood cells. If a cell is infested by multiple foundress's mating may occur between different families, but if there is only a single foundress as is most common, mating occurs between siblings (Donzé et al., 1996). Sib-mating is most common early in the brood season when there is a larger ratio of brood cells to mites, resulting in increased inbreeding. As brood numbers decline later in the season, the ratio of brood cells to mites decreases resulting in an increase in multiple foundress invasions and cross family matings (Beaurepaire et al., 2017). This can have consequences for acaricide resistance because if chemical treatment is applied early in the breeding season, inbreeding will accelerate the rate that resistant alleles will reach fixation (Beaurepaire et al., 2017). On the rare event that a cell is over-parasitized however (eg. 4 foundresses in one cell) reproduction may be halted entirely (Steiner et al., 1995).

Reproduction occurs in similar fashion to honeybees by arrhenotokous parthenogenesis, where fertilized eggs develop into females while unfertilized eggs become males (Häußermann et al., 2020). Oocyte activation occurs before egg-laying and is triggered 14 - 18 hours after capping with evidence pointing to this being at least partially due to cuticular volatiles produced by the larvae (Fig. 17) (Frey et al., 2013a; Garrido et al., 2000; Garrido and Rosenkranz, 2003; Rosenkranz and Garrido, 2004). Varroa females only mate once in their life cycle, receiving up to 35 spermatozoa from a male (Donzé et al., 1996; Donzé and Guerin, 1994). They are able to invade honeybee brood cells up to seven times with a maximum of 30 eggs being produced, though a modern study to confirm this number is required (De Ruijter, 1987).

3.1 Copulation

A male begins this process by finding a freshly molted female through the detection of six chemicals that she emits: palmitic acid, stearic acid, athyl palmitate, ethyl oleate, and ethyl stearate (Ziegelmann et al., 2013a). The male preferentially mates with younger molted females as the produce higher quantities of the attractive chemicals (Fahle and Rosenkranz, 2005; Ziegelmann et al., 2013a, 2013b). The male begins the mating process by cleaning his chelicerae and touching the female with his first pair of legs. He then ascends her dorsum, examining the frontal margins, before moving to her ventral side that the female has lifted for him. The male then searches for the gonopore, and transfers immature spermatophores out of his genital opening, into the gonopore (Alberti and Hänel, 1986; De Ruijter and Kaas, 1983). The spermatozoa take around 5 days to full mature beginning as a round prospermatozoa before move into the spermathecal and changing into a fusiform shape over 7 development stages (Fig. 19, Table 1) (Häußermann et al., 2016).

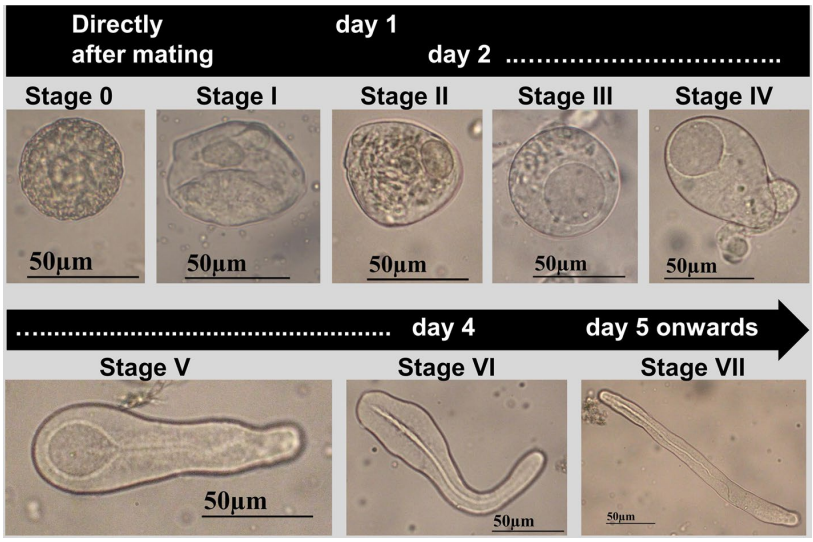

Figure 19. Time line of spermatozoa development of Varroa destructor found in female genital tract post mating (Häußermann et al., 2016).

Table 1. Description of spermatozoa morphology during development with mean (±SD) size (Häußermann et al., 2016).

Stage	Cell shape	Nucleus
0 (before the start of capacitation)	• roundish cell shape • nubby cell surface, that reminds of a raspberry • 48.5 (±3.1) µm (n = 8)	• cryptic cell nucleus
I	• cell shape still roundish but the surface seems to be crumpled • 56.0 (±6.6) µm (n = 10)	• clearly visible nucleus • oval shape • 15.2 (±4.2) µm (n = 10)
II	• roundish cell shape • cytoplasm seems to be dense with a lot of cell organelles • 61.0 (±3.3) µm (n= 10)	• nucleus with an oval shape • 19.6 (±3.8) µm (n = 10)
III	• clearly spherical in shape • 61.9 (±3.2) µm (n = 10)	• cell nucleus has expanded • 33.6 (±1.8) µm (n= 10) • size of the nucleus equates about 1/2 of the size of the spermatozoa
IV	• elongation of the spermatozoa begins • oval shape • 74 (±7.1) µm (n = 10)	• nucleus starts slightly to elongate • 29.8 (±2.3) µm (n = 10)
V	• elongation process is advanced • front of the spermatozoa with the cell nucleus is bigger in size than the tail • 113.7 (±23.9) µm (n = 10)	• elongation process is advanced: fine line leads from the cell nucleus up to the end of the spermatozoa • 27.6 (±2.4) µm (n = 10)
VI	• shape of the spermatozoa is clubbed • the front part is wider than the back • 155.7 (±13.4) µm (n = 10)	• cell nucleus is a completely fine line that lances the whole spermatozoa
VII	• spermatozoa are completely elongated • shape of the spermatozoa is fusiform • 227.9 (±17.5) µm (n = 10)	• cell nucleus is a completely fine line that lances the whole spermatozoa

A male can mate with up to five females, transferring a maximum of 35 spermatozoa each to fill her spermathecal (Donzé et al., 1996; Donzé and Guerin,

1994; Häußermann et al., 2018). They continues producing spermatozoa throughout their life, making an average of 125 spermatozoa (Häußermann et al., 2018).

3.1.1 1 - Oogenesis

1.1 - Previtellogenesis

During the dispersal phase, the mite caries previtellogenic oocytes (undeveloped eggs), though with one slightly larger and more developed than the others. This larger egg already has a visible nucleus and is ready to begin development. Six hours after capping the oocyte has continued to grow with the incorporation of either euplamatic components, yolk proteins, or both (Garrido et al., 2000). Further research is required to better understand this period. The previtellogenic phase completes around 10-15 hours after capping (Steiner et al., 1994).

1.2 - Vitellogenesis

The previtellogenic phase is followed immediately by the vitellogenic phase, which lasts around 10 hours. During this phase cells migrate onto the egg, which form a loose net with fibrous intercellular connections that later become a monolayer of cells (Steiner et al., 1994). Organelles such as mitochondria, free ribosomes, rough endoplasmic reticulum, golgi complexes, as well as lipid droplets are incorporated during this time. This phase also includes yolk accumulation, growing from around 0.8 µm diameter in early vitellogenesis, to around 9 µm in late vitellogenesis (Steiner et al., 1995).

1.3 - Egg shell formation

The development of the egg is completed around 20-25 hours after cell capping with the diameter of the egg reaching 250 – 300 pm, and is covered by a shell with small pores (Figure 20). Around this same time, the second egg to be oviposited begins developing, being in the previtellogenic phase for 15 hours, followed by the vitellogenic phase which is completed around 55-60 hours post capping. This continues with an overlap of subsequent egg development for an average of 4-5 eggs in total (Rosenkranz et al., 2010; Steiner et al., 1994).

3.1.2 2 - Embryogenesis

2.1 - Cleavage

Cleavage of the egg begins around 25-30 hours post capping, which is shortly after the completion of egg development. 35 hours post capping, the blastoderm has finished forming, with many small, round epithelial cells being present (Steiner et al., 1994).

2.2 - Segmentation

The beginning of segmentation happens around 35 – 40 hours post capping. Around 45-50 hours post capping, deep clefts are seen on the dorsal side of the embryo, which will eventually become the chelicera and pedipalps (Steiner et al., 1994).

2.3 - Limb Bud Formation

50-55 hours post capping all six segments with limb buds are clearly visible, along with the separation of the hypostome (mouth) from the ventral mass (Steiner et al., 1994).

2.4 - Limb differentiation

60-65 hours post capping, the legs have developed significantly, becoming much longer than the pedipalps or chelicera (Steiner et al., 1994).

2.5 - Embryonic moult

Shortly after limb differentiation the first molt occurs, with the legs being articulated and having fine tips and the cuticle beginning to have setae (Steiner et al., 1994).

2.6 - Oviposition

In vivo development finishes with oviposition that occurs between 60 – 72 hours post capping (Fig. 20) (Steiner et al., 1994). The first offspring is a haploid male and is glued to the upper cell wall as it is the safest area of the brood cell followed by females glued lower on the cell wall (Donzé and Guerin, 1994).

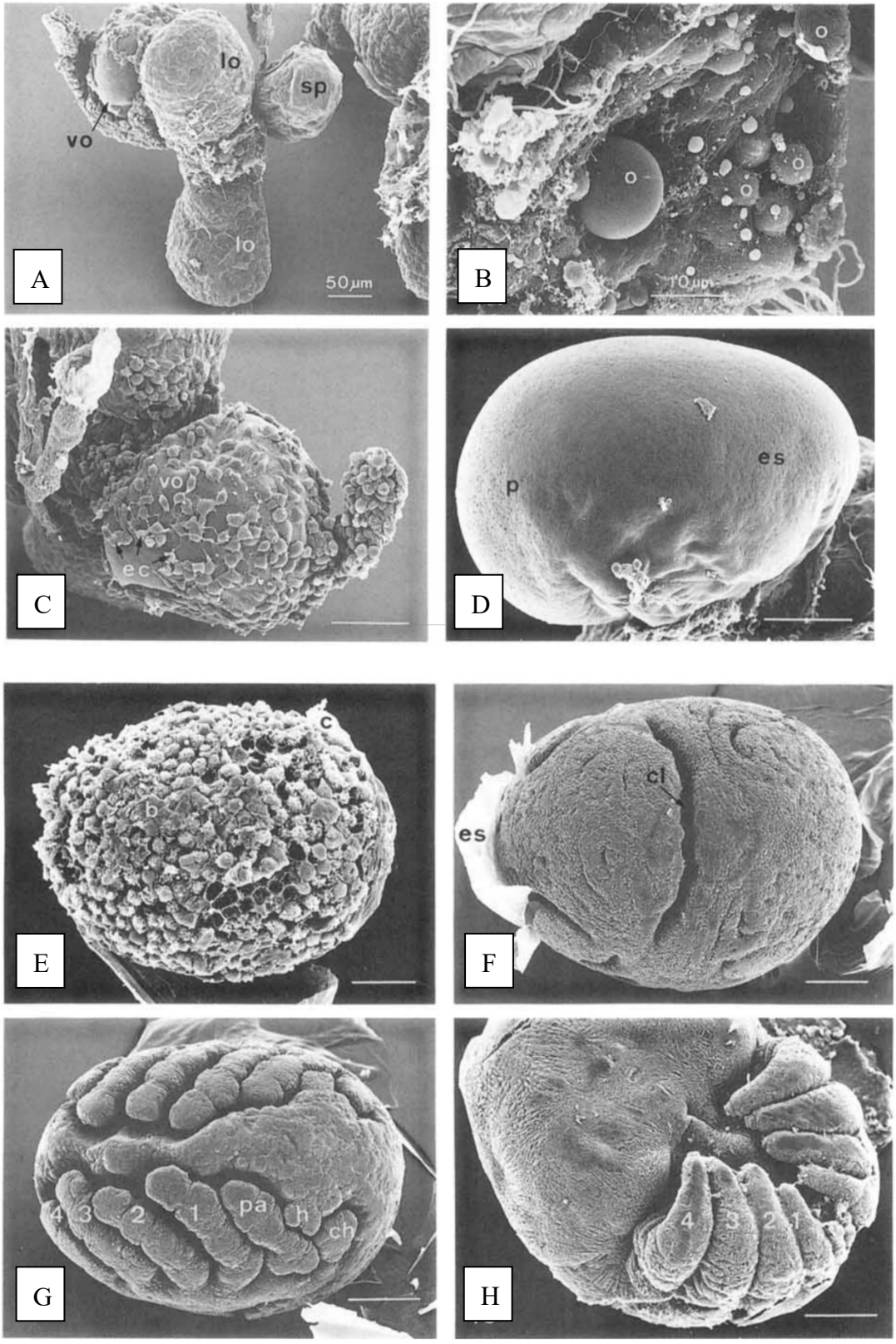

Figure 20. A. Ovary of a female from a worker brood cell (20-25 h). B. Detail showing a number of tiny primary oocytes. C. Vitellogenic oocyte with formation of a surrounding epithelium (20-25 h). D. Embryo covered with egg shell (25-30 h). E. Blastoderm stage with loosely packed cells

(30-35 h). F. Embryo in dorsal view with cleft separating proterosoma and hysterosoma (45-50 h). G. Embryo in ventral view with all (six pairs, 1-4 legs, palps and cheliceres) limb buds. Hypostome anlagen separating from the ventral mass (50-55 h). H. Embryo completely formed. Bent legs (four pairs) with the small pedipalps in front, chelicerae not visible (65-70 h). ec, epithelial cells; es, egg shell; p, pore; sp, spermatheca; vo, vitellogenic oocyte. lo, lyrate organ; o, oocyte; b, blastomeres; ch, chelicera; cl, cleft; es, egg shell; h, hypostome; pa, pedipalp (Steiner 1994).

Table 2. Timeline of mite oogenesis and embryogenesis (Steiner et al., 1994).

Stage of mite oogenesis/ embryogenesis	Time (h) after capping of the bee brood cell	
	Worker	Drone
Previtellogenesis	0–15	0–15
Vitellogenesis	15–30	15–25
Egg shell formation	30–35	25–30
Cleavage	35–40	30–35
Segmentation	40–45	35–40
Limb bud formation	45–50	40–45
Limb differentiation	50–65	45–60
Embryonic moult	65	60
Oviposition	70	65

3.2 Larval Development

The first female egg hatches around 1 day (27.4 ± 1.5 hours) after oviposition (1 d.a.o.) as protonymphs, measuring around 1 mm wide x 1.1 mm long and are translucent in color. Around 1 day (22.9 ± 1.7) after hatching (2 d.a.o.), they mature into the immobile protocrysalis stage, measuring around 1.13 x 1.15 mm where there color becomes slightly opaque. ¾ of a day later (17.0 ± 1.5) (2.75 d.a.o.) they enter the Deutonymph stage, measuring around 2 x 1.5 mm and their color begins to yellow. Around 1 day later (27.3 ± 3.0) (3.75 d.a.o.) they enter their penultimate stage of the immobile Deutocrisalis stage, where they reach their maximum size of

around 2.8 x 1.9 mm, with visible reproductive organs. Finally 2 days later (48.0 ± 2.2) (5.75 d.a.o.), females enter the mature adult stage, where become dark brown in color and are reproductively viable (Fig. 21, 22) (Donzé and Guerin, 1994; Rosenkranz et al., 2010). These numbers vary slightly with the 2^{nd} – 5^{th} eggs, with development generally taking less time (Fig 22, 23).

Males are born at around the same size as females, (roughly 1x1 mm), and are more or less indistinguishable to females in both the protonymph and protocrysalis phase. When males reach maturity, they are only 1.2 x 1.3 mm in size, and are distinguished from females by their leg arrangement being more spread around their body, and difference in visible reproductive organs (Fig. 21).

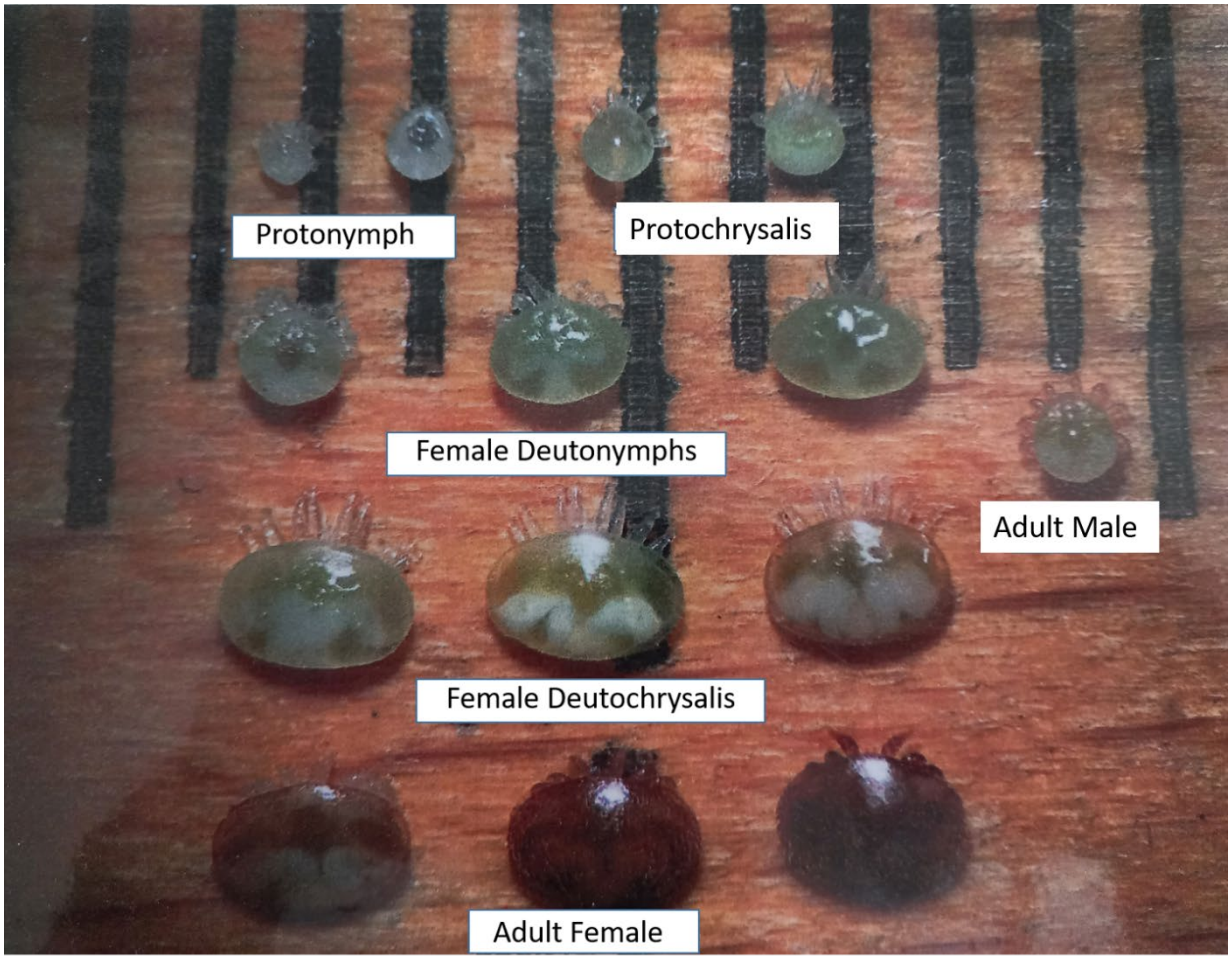

Figure 21. Different stages of Varroa destructor maturation. Scale lines 1mm apart. Photo courtesy of Barbara Locke.

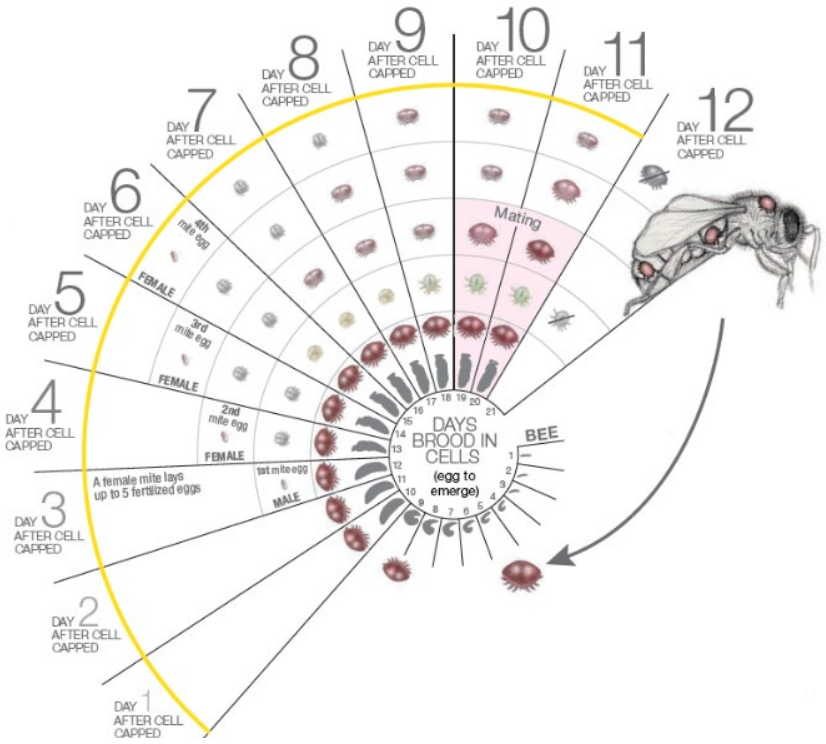

Figure 22. Varroa maturation cycle in brood cell (Trodtfeld et al., 2019).

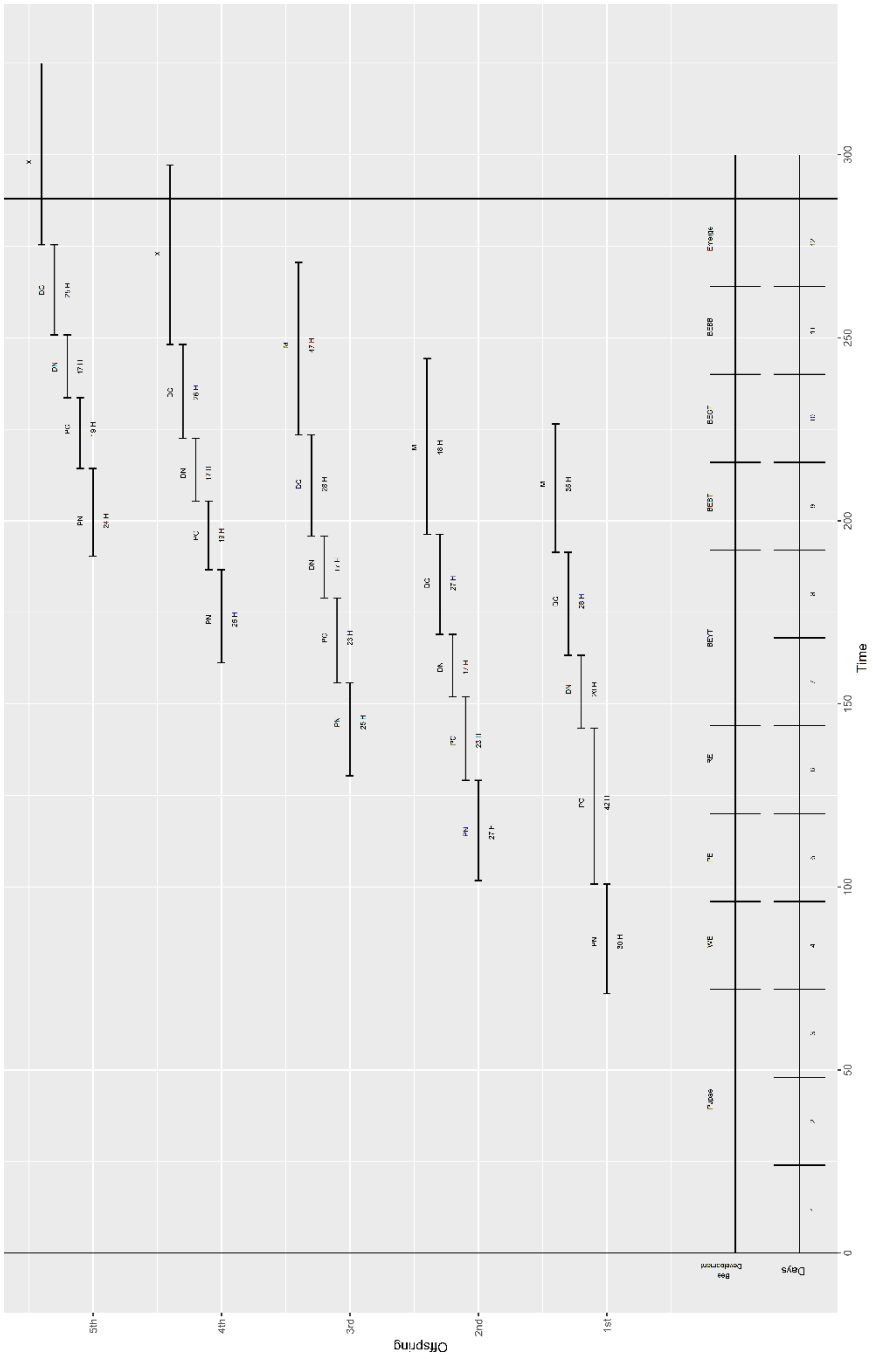

Figure 23. Time line of honeybee and mite offspring reproduction at the point of brood cell capping till emergence. PN Protonymph, PC = Protochrysalis, DN = Deutonymph, DC = Deutochrysalis, M = Mature, X = Failed to Mature, WE = White Eyes, PE = Pink Eye, RE = Red Eye, BEYT = Brown Eye Yellow Thorax, BEBT = Brown Eye Brown Thorax, BEGT = Brown Eye Gray Thorax, BEBB = Brown Eye Black Body. Data taken from Donze & Guerin 94, Martin 94, Traynor 2020, Remboldt & Ulrich 1980.

3.3 Vitellogenin

While there are many different parts of the egg needed to be synthesized, an important component is the yolk, which requires several yolk protein precursors to be synthesized. The most abundant of these is the glycolipoprotein vitellogenin (Vg). In varroa there are two different genes for Vg (VdVg1 & VdVg2) which produce two similar versions of VG that we see in other acarine (Cabrera Cordon et al., 2013; Hagedorn and Kunkel, 1979). Both varroa VdVg1 & 2 are more closely related to Vg 1 and 2 from other ticks than they are to each other, suggesting that a duplication event of the Vg gene occurred at some time before the split of mites and ticks.

In Varroa overall levels of Vg transcription are dependent not just on the age of the mite itself but also on if there is a honeybee pupae at the appropriate instar, and if there are appropriate environmental cues within the capped cell (Cabrera Cordon et al., 2013). Previous research looked at expression levels of Vg and large lipid transfer protein (LLTP), and found that Vg peaked during pre-laying and laying stages (Fig. 24) , while LLTP inversely lowered expression during these two stages (Mondet et al., 2018). LLTP allow hydrophobic & lipophilic molecules to be transported into the haemolymph (Cabrera et al., 2013). Overall Vg reached its max expression during oviposition, with Vg2 being expressed at a significantly higher value than Vg1 with LLTP reaching highest expression during the dispersal phase (Cabrera et al., 2013; Cabrera Cordon et al., 2013; Piou et al., 2016).

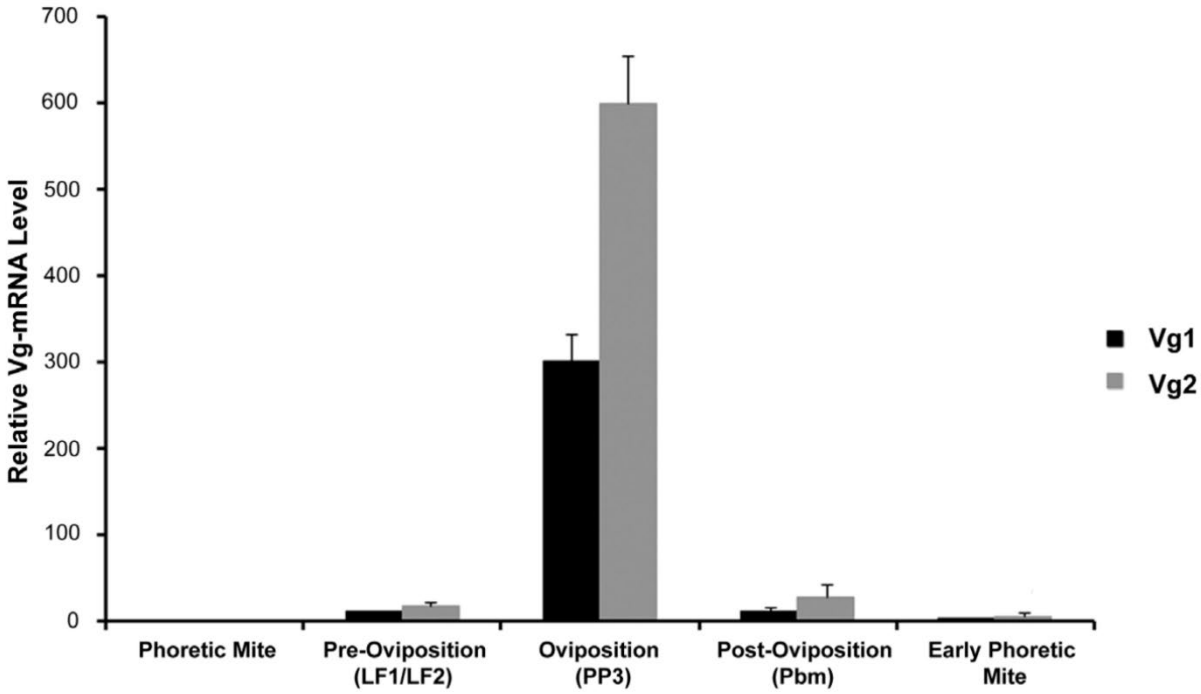

Figure 24. Relative expression levels during female Varroa destructor reproductive cycles (Cabrera Cordon et al., 2013).

4. Mature Life Stages

As adults females live on the back of honeybee workers where they feed on worker fat bodies (Ramsey et al., 2018, 2019). Once the worker bee nears a brood cell the mite detaches from the back of the bee and hides in the brood food, immobile, and using its peritreme like a snorkel to breath out of the food, until the brood cell is capped by nurse bees. Once the larva spins a cocoon around itself (5^{th} instar), the foundress mite punctures a hole (100 μm) into the larva to feed itself and future young. The foundress then lays her eggs, which when hatched, are cared for by the foundress by guiding them to the feeding spot as well as a designated defecation spot. Haploid male eggs are laid/hatched first, and are glued to the upper cell wall for protection (Donzé and Guerin, 1994). Diploid female eggs are laid every 30 hours after, depositing them further down the cell wall. Males have much shorter lifespans than females and are never found outside the brood cells. Males mate with females present in the cell (likely their sister) on the communal fecal pile, as soon as she has reached her first molt. If a male is not hatched or is killed, the female will not mate, as this is most likely the only opportunity for insemination. Around 12 days after the foundress invaded the brood cell, the worker emerges with both the foundress and any mature female offspring mites attached, to repeat the cycle. (Traynor et al., 2020).

As the mite does not have eyes, this process is significantly guided by kairomones emitted by the adult worker, the brood, and even food left for the brood (Nazzi et al., 2001). Fatty acid esters (such as methyl palmitate, ethyl palmitate, and methyl linolenate), which are used as pheromones to induce nurse bees to cap the cells, have been shown to also attract mites to the larvae. The mite also uses the

same molecule (ethyl oleate) that is released by both adult and larvae bees as its mating signal, further masking the mite signals (Nazzi and Le Conte, 2016). Volatiles produced by the larvae at specific ages also inform the mite when they should begin laying eggs, which the mites are sensitive too. If this timing is interrupted then the chance of successful reproduction is greatly decreased or halted completely (Frey et al., 2013b; Trouiller and Milani, 1999). Varroa is also sensitive to humidity and temperature during reproduction. In laboratory experiments, successful reproduction was found to be optimal between 36 & 38 °C, and at 70 % humidity. Interestingly, reproduction is completely halted at 80% humidity, and if temperatures exceed 38 °C mites die without reproducing. Both of these situations are survivable to bees which is a topic that can be looked into in the future for mite control (Kraus and Velthuis, 1997; Le Conte et al., 1990a; Vidal-Naquet et al., 2015).

4.1 Dispersal Stage

Previous studies referred to this stage as phoretic, however because the mite has been shown to feed during this stage, we have chosen to use the term dispersal. After emergence from brood cells, mites do not immediately breed again but instead enter a dispersal phase. This stage can last from a few days up to 6 months in winter where they attach themselves to adult workers. They do this by finding adults and attach using their pretarsal suckers to the lateral intetergites III or IV almost exclusively on the left side of the abdomen (Fig. 25) (Delfinado-Baker et al., 1992; Liu and Peng, 1990; Ramsey et al., 2019). While in this phase, they feed on the fat bodies of the honeybee (discussed above), and are transported to either new brood cells (nurse bees) or new hives (foragers). The length of time that a mite is in the

dispersal stage does not appear to affect the next reproduction of the mite in any way, though it appears that longer time spent in the dispersal stage resulted in higher rates of deformity for emerging honeybees as these mites had increased viral loads (Piou et al., 2016).

As mentioned above mites generally prefer nurse bees over foragers regardless of the mites life stage, further favoring younger nurse bees over older ones (Kraus, 1994; Kuenen and Calderone, 1998; Xie et al., 2016). This attraction was found to be at least partially attributed to lower levels of pheromones being produced by nurse bees. In particular two Nasonov pheromone components, geraniol and nerolic acid, as well as z-8-heptadecene were found in higher quantities in older worker bees that acted as repellents (Pernal et al., 2005; Piccolo et al., 2010; Xie et al., 2016). This preference disappears however when mites reach high abundance in a colony as the chemical signature of nurses and foragers become more uniform, leading to mites attaching to forager bees in similar rates to nurse bees. This increases the number of mites that are brought into contact with bees from other hives, allowing for dispersal. This increased uniformity in chemical signatures may be due to overall less bees in the hive as a result of mite-borne mortality, forcing forager bees to become nurse bees, obscuring the distinct signatures (Cervo et al., 2014).

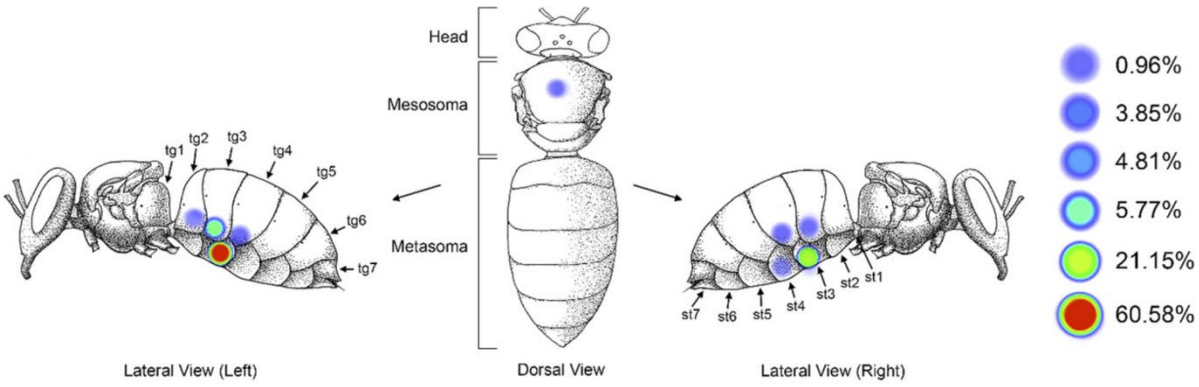

Figure 25. Heat map showing most common sites of mite attachment (Ramsey et al., 2019).

4.2 Camouflage

In order to avoid being detected and removed by honey bees, varroa can passively match their cuticular hydrocarbon (BEP) profile to match their host, making them much harder to detect by chemosensing (Nation et al., 1992). This is no easy task as the BEP profile of honey bees is made up of at least 50 different compounds (Martin et al., 2001; Salvy et al., 2001).Varroa requires direct access to the cuticle of the host in order to passively mimic its BEP profile. They can change their chemical profile within three to nine hours, apparently by absorbing the honeybees BEPs in a similar way to other arthropods either through active processes such as grooming, or passive absorption through close contact with the cuticle (Kather et al., 2015). This is particularly useful as different ages, sex, castes, and even colonies of honey bee have different BEP profiles, allowing the mite to readily adapt to its current host (Kather et al., 2015, 2011; Nation et al., 1992). This has even been shown between species, with individual varroa being able to mimic the BEP's of both their original host (*Apis cerana*) and their new host (*Apis mellifera*) (Le Conte et al., 2015).

4.3 Cell Invasion Cues

As varroa is functionally deaf and blind, it must rely on chemo and tactile sense to not only find brood cells, but also ensure the larvae have reached their 5th instar (L5) stage just before cell capping (Traynor et al., 2020).

Varroa uses volatiles such as methyl linoleate and ethyl palmitate produced by larvae as a trigger for cell invasion (Aumeier et al., 2002; Le Conte et al., 1990b; Liu et al., 2022; Rickli et al., 1992; Trouiller et al., 1994, 1992). As stated above, these pheromones are produced by the brood to signal to the nurse bees to initiate capping but are intercepted by varroa and used as kairomones. In addition to chemicals directly produced by the larvae, semiochemicals that are present in larval food are also attractants to varroa (Nazzi et al., 2001). In laboratory settings varroa are able to follow honey bee odor plumes to their source in a wind tunnel either by walking in a zigzag pattern or by following the edge of the odor plume (Kuenen and Calderone, 1998).

The sex and caste of honeybee larvae produce BEP's in different quantities as well as at timings. This has varying effects on how attractive a larva is to varroa as well as the length of time that this attractive window is open. Queen larvae for example were shown to be infested 15 times less often compared to worker cells (Calderone et al., 2002). This is in part due to queens producing larger quantities of mite repellent compounds compared to worker and drone larvae (Trouiller et al., 1994). This is compounded with queen cells containing more royal jelly which emit compounds that further repel mites (Le Conte et al., 1990b).

Drones on the other hand are highly attractive to mites with drone brood cells invaded almost up to nine times more frequently than worker brood cells (Boot et

al., 1995, p. 95; Calderone and Kuenen, 2003; Fuchs, 1990, p. 90). There are several factors that contribute to this such as drone cells having an attractive period lasting 2-3 times longer than worker cells while producing larger quantities of attractive kairomones during this time (Boot et al., 1992; Calderone et al., 2002; Calis, 2001). This is compounded with brood cells being visited more frequently by nurse bees, increasing the chance of mite exposure (Fuchs, 1990). There is also evidence that varroa are not only able to detect electrical charges such as those produced by the natural electrical fields of honey bees, but are attracted to them (Colin et al., 1992). However, further research is needed to determine if this a major contributor to locating brood and adults.

Once the cell has been located, the mite must determine if the larvae is of the appropriate age for reproduction. As larvae grow and fill more of the brood cell, they become more attractive to mite invasion. Once the distance between the larval head and top of the brood cell is around 7.0 – 7.5 mm varroa will begin invading (Boot et al., 1995; Goetz and Koeniger, 1993). This could be one reason that older comb is more attractive to mites than fresh comb (Piccirillo and De Jong, 2004). As pupae develop they molt six times, shedding their exoskeleton (Winston, 1991). This in combination of feces and cocoon silk build up on the cell surfaces results in a decrease of the overall size of the cell and bringing the larvae closer to the rim. (Piccirillo and De Jong, 2004). While reduced cell size was once thought to be a viable path forward in varroa control (Maggi et al., 2010; Martin and Kryger, 2002), it now appears that reduced cell size does not decrease mite reproduction, and may even exacerbate the problem (Berry et al., 2010; Coffey et al., 2010, p. 4). Though

this may also depend upon the subspecies of honey bee, and needs further research (de Guzman et al., 2008).

Population dynamics can also alter mite invasion and life stage preferences. An example of this is that as the number of available brood cells increase in the spring, so does the rate of mite invasion. This is also true in the reverse when the population of adult bees increase compared to the available brood cells the chance that a mite is brought to an available brood cell decreases (Boot et al., 1994). The total number of mites in a colony also changes invasion preferences, with an increase in mites resulting in an increased preference for worker cells. Once a threshold of mites has been surpassed it becomes more optimal to solely invade the more plentiful worker cells than sharing a drone cell that has already been infested (Fuchs, 1992; Reams and Rangel, 2022). Further as less drone brood becomes available, whether due to a decrease in uninfested cells or to the natural decrease in drone production later in the season, worker brood is infested at an increased rate (Fuchs, 1992, 1990).

4.4 Virgin Females & Parthenogenesis

Historically, if a female was found to be unmated (virgin) upon emergence due to a lack of male mite, that was viewed as a failed reproduction and the female was not counted towards future reproduction events. In a natural system, 8.2% of mites analyzed were virgins. Of those, 87.9% were fertile, producing an average of 1.7 male offspring per foundress where 34.5% of virgin foundresses mated with their own sons. In a laboratory experiment, 73.9% of virgin females were fertile, producing on average 1.4 male offspring per mite, which then proceeded to mate with their mother, enabling female offspring to be born in the next round of egg laying. While this is much lower than the average of 5-6 eggs laid by typical mated

females, it is still possible for this foundress to produce viable young. This study shows that the emergence of a virgin mite may slow the growth of the varroa population, it does not halt it completely, and must be accounted for (Häußermann et al., 020).

5. Genetics

Varroa genetics has been described in varying depth over the years (Campbell et al., 2016; Cornman et al., 2010; Lin et al., 2020; Navajas et al., 2002).Varroa, like honeybees, are arrhenotokous parthenogenetic individuals. This means that males develop from unfertilized eggs resulting in haploid individuals with seven chromosomes and females develop from fertilized eggs becoming diploid individuals with 14 chromosomes (Traynor et al., 2020).The varroa genome is around 565 Mbp, which is relatively large compared to insects, but small compared with some other Acari. (eg. 250 Mbp genome of *Apis mellifera* and 2.1 Gbp of the deer tick *Ixodes scapularis*) (Cornman et al., 2010; Ullmann et al., 2005; Wallberg et al., 2019).

Possibly due to a bottleneck effect that occurred when varroa switched host, as well as the large prominence of inbreeding due to their reproductive method of brothers commonly mating with sisters (Solignac et al., 2005), there is not the amount of genetic variation that would be otherwise expected in such a wide spread species (Kraus and Hunt, 1995; Solignac et al., 2005). However, a recent study has shown that it may be possible for mite populations to change their reproductive strategies in resistant populations (Moro et al., 2021). The study looked at artificially selected Dutch honeybees that once displayed VSH (Panziera et al., 2017), and found that they no longer showed signs of VSH only 4 years later (Moro et al., 2021). The mite itself can also change genetically over time, not requiring species level adaptations (Techer et al., 2019). This has occurred not only when they differentiated from their originally species, *Varroa jacobsoni*, but also temporally in the same population, with even more pronounced differences being

found in isolated populations (Beaurepaire et al., 2019; Techer et al., 2019). This suggests that despite previous research, co-evolution should be viewed as dynamic and researchers should use caution when considering a population resistant if it has not been verified recently.

While previously thought as not occurring, another possible introduction of genetic variation is through hybridization between *V. destructor* and *V. jacobsoni* in Asia, where the two species live in sympatry (Chiu et al., 2023; Dietemann et al., 2019). *V. jacobsoni* has been shown to have higher genetic diversity than *V. destructor*, meaning potential hybridization could result in an increase in *V. destructor* diversity. More research is required to know how often this is happening in sympatry and if this hybridization is affecting the host-parasite relationship between both varroa species and both honeybee species (*A. cerana*, *A. mellifera*) in Asia.

6. Future Research Needs

With the ever growing need for varroa research, a field that has garnered a large interest in the past 30 years is how to artificially rear varroa in a lab with little to no honeybee input (Bruce et al., 1991, 1988; Jack et al., 2020; Nazzi and Milani, 1994, 1994). Varroa studies typically need a large number of mites, requiring a highly infested hive. This forces researchers to walk the delicate line between high mite infestation and increased hive mortality. Further these "sick" research hives could act as a mite factory infesting colonies in the surrounding area (Dietemann et al., 2013). This also means that without a way to keep honeybees rearing brood over winter most varroa research involving living individuals must pause.

Varroa rearing in the lab on living honeybee brood has shown some promise, but all attempts to rear varroa without any honeybee presence whatsoever has so far been a failure. By better understanding the feeding and reproductive systems of the varroa mite we might be able to better replicate this in vitro. This would enable not only an easier collection of mites but also enable research to continue during cold winters and allow for more controlled variables in experimental design.

Select honeybee populations have been extensively researched in the last 20 years that have been labeled "naturally varroa resistant" (Le Conte et al., 2020; Locke, 2016a). In these populations, most research has focused on the traits and effects on the honeybees themselves (Behrens et al., 2011; Conlon et al., 2019; Grindrod and Martin, 2021; Locke, 2016b; Panziera et al., 2017). with only a small section of research focusing on the mites (Beaurepaire et al., 2019; Moro et al., 2021) The few studies that have been done however has found that mites in resistant populations can have unique genetic profiles (Beaurepaire et al., 2019; Moro et al.,

2021). Through further research into how not only the bees, but varroa are adapting in these natural host-parasite environments we can gain a better understanding of how this unique interaction adapts and evolves. This information would be useful as we attempt to artificially breed varroa-resistant honeybee populations in an efficient and sustainable way.

While an abundance of research has been done on VG in different egg laying species, besides the few studies mentioned above very little has been done on VG in the varroa mite and how it can be used for prediction of mite reproductive success. While the methodology has not yet been tested it could be possible to use VG to as a predictor if mites in a colony will reproduce successfully or not. This type of work has already been done on fish both to indicate reproductive success (Crago et al., 2011) and reproductive disruption (Cheek et al., 2001).

While there is a large cache of research already done on how *A. mellifera* affects, and is affected by varroa, there is still the question of how some colonies are able to resist high varroa infections while others succumb in only a few years. As discussed earlier, there is evidence of worker bees exhibiting behavioural traits such as increased grooming and removal of infested mites. This is not the case for all populations. An alternative solution could be an alteration in volatiles that are produced by the brood, which as discussed above, is tightly linked to varroa reproductive timing. This area has just begun to be investigated, which may provide important information in the host-parasite relationship.

An area that is still lacking is how the mite itself is affected by the viruses that it is host to. Recent research has found that viruses may affect the mites behaviour, as well as new species of virus that only infect varroa and not honey bees (Campbell

et al., 2016; Herrero et al., 2019). This opens-up another variable in the host-parasite relationship that must be considered and plays a pivotal role in the fundamental lack of understanding in the immune system of the mite. We know very little about how they defend themselves from microbial attacks, or even if they synthesize their own immune system. If we wish to fully understand the interplay between mite and host, this is an area that must not be neglected.

Finally, while we know much about how the mites reproduce both physically and chemically, there is still a lack of understanding for why some mites fail to reproduce, while others are successful given ideal circumstances. It is unknown if this is due to brood or worker effects, natural genetic variation in the mite population, or due to viral and bacterial infection levels. We see different levels of mite reproductive success in populations around the world and being able to determine exactly what is the cause could be beneficial to selective breeding efforts. Further, being able to take a sample of mites from a colony and perform a test to know if they would have reproduced successfully in the future would be beneficial for predicting future infestation levels. This would aid in informing beekeepers what steps need to be taken. Metrics such as vitellogenin as a predictor for reproductive success may be one of the options forward, but research into this is needed to make this a reality.

7. Conclusion

Varroa destructor is a species that has been intensely studied since its escape from Asia 70 years ago. While a large amount of research has been dedicated to effects on the honeybee as well as ways that the bee is or is not adapting, it is important to understand the mite itself. This review is a synthesis of that research, focusing on the mite's anatomy, reproduction, life history, and genetics. We hope this to be a useful tool to not only educate researchers and apiarists but also to highlight areas of varroa research that are as of now understudied. By learning what has been previously discovered and knowing what we don't know we hopefully can refine our varroa resistance efforts in an efficient and sustainable way.

8. Acknowledgments

I would like to thank my supervisor Barbara Locke for all of her help with research discussions as well as editing, as well as my colleagues Joachim Rodriguez de Miranda & Naomi Keehnen for excellent scientific discussions. I would also like to thank my sambo Tifaine for all of her love and support. Finally I would like to thank Sci-Hub for making science more open and accessible to all, regardless of monetary or social status.

9. References

Alberti, G., Hänel, H., 1986. Fine structure of the genital system in the bee parasite, *Varroa jacobsoni* (Gamasida: Dermanyssina) with remarks on spermiogenesis, spermatozoa and capacitation. Exp. Appl. Acarol. 2, 63–104. https://doi.org/10.1007/BF01193355

Alberti, G., Zeck-Kapp, G., 1986. The Nutrimentary Egg Development of the Mite, *Varroa jacobsoni* (Acari, Arachnida), an Ectoparasite of Honey Bees. Acta Zoologica 67, 11–25. https://doi.org/10.1111/j.1463-6395.1986.tb00845.x

Amiri, E., Kryger, P., Meixner, M.D., Strand, M.K., Tarpy, D.R., Rueppell, O., 2018. Quantitative patterns of vertical transmission of deformed wing virus in honey bees. PLoS ONE 13, e0195283. https://doi.org/10.1371/journal.pone.0195283

Anderson, D.L., 2000. Variation in the parasitic bee mite *Varroa jacobsoni Oud.* . Apidologie 31, 281–292. https://doi.org/10.1051/apido:2000122

Anderson, D.L., Fuchs, S., 1998. Two genetically distinct populations of *Varroa jacobsoni* with contrasting reproductive abilities on *Apis mellifera*. J. Apicult. Res. 37, 69–78. https://doi.org/10.1080/00218839.1998.11100957

Anderson, D.L., Trueman, J.W.H., 2000. *Varroa jacobsoni* (Acari: Varroidae) is more than one species. Exp. Appl. Acarol. 25.

Annoscia, D., Brown, S.P., Di Prisco, G., De Paoli, E., Del Fabbro, S., Frizzera, D., Zanni, V., Galbraith, D.A., Caprio, E., Grozinger, C.M., Pennacchio, F., Nazzi, F., 2019. Haemolymph removal by varroa mite destabilizes the dynamical interaction between immune effectors and virus in bees, as predicted by Volterra's model. P. Roy. Soc. B-Biol. Sci. 286, 20190331. https://doi.org/10.1098/rspb.2019.0331

Arrese, E.L., Soulages, J.L., 2010. Insect Fat Body: Energy, Metabolism, and Regulation. Annu. Rev. Entomol. 55, 207–225. https://doi.org/10.1146/annurev-ento-112408-085356

Aumeier, P., Rosenkranz, P., Francke, W., 2002. Cuticular volatiles, attractivity of worker larvae and invasion of brood cells by *Varroa mites*. A comparison of Africanized and European honey bees. Chemoecology 12, 65–75. https://doi.org/10.1007/s00049-002-8328-y

Beaurepaire, A.L., Krieger, K.J., Moritz, R.F.A., 2017. Seasonal cycle of inbreeding and recombination of the parasitic mite *Varroa destructor* in honeybee colonies and its implications for the selection of acaricide resistance. Infection, Genetics and Evolution 50, 49–54. https://doi.org/10.1016/j.meegid.2017.02.011

Beaurepaire, A.L., Moro, A., Mondet, F., Le Conte, Y., Neumann, P., Locke, B., 2019. Population genetics of ectoparasitic mites suggest arms race with honeybee hosts. Sci. Rep. 9, 11355. https://doi.org/10.1038/s41598-019-47801-5

Behrens, D., Huang, Q., Geßner, C., Rosenkranz, P., Frey, E., Locke, B., Moritz, R.F.A., Kraus, F.B., 2011. Three QTL in the honey bee *Apis mellifera L.* suppress reproduction of the parasitic mite *Varroa destructor*: QTL-Mapping of *Varroa* Resistance in Honeybees. Ecol. Evol. 1, 451–458. https://doi.org/10.1002/ece3.17

Berry, J.A., Owens, W.B., Delaplane, K.S., 2010. Small-cell comb foundation does not impede varroa mite population growth in honey bee colonies. Apidologie 41, 40–44. https://doi.org/10.1051/apido/2009049

Boecking, O., 1999. Sealing up and non-removal of diseased and *Varroa jacobsoni* infested drone brood cells is part of the hygienic behaviour in *Apis cerana*. J. Apicult. Res. 38, 159–168. https://doi.org/10.1080/00218839.1999.11101006

Boecking, O., Genersch, E., 2008. Varroosis – the Ongoing Crisis in Bee Keeping. J. Verbr. Lebensm. 3, 221–228. https://doi.org/10.1007/s00003-008-0331-y

Boecking, O., Spivak, M., 1999. Behavioral defenses of honey bees against *Varroa jacobsoni* Oud. Apidologie 30, 141–158. https://doi.org/10.1051/apido:19990205

Boot, W., Schoenmaker, J., Calis, J., Beetsma, J., 1995. Invasion of Varroa-Jacobsoni into Drone Brood Cells of the Honey-Bee, Apis-Mellifera. Apidologie 26, 109–118. https://doi.org/10.1051/apido:19950204

Boot, W.J., Beetsma, J., Calis, J.N.M., 1994. Behaviour of varroa mites invading honey bee brood cells. Exp. Appl. Acarol. 18, 371–379. https://doi.org/10.1007/BF00116318

Boot, W.J., Calis, J.N.M., Beetsma, J., 1992. Differential periods of varroa mite invasion into worker and drone cells of honey bees. Exp. Appl. Acarol. 16, 295–301. https://doi.org/10.1007/BF01218571

Bowen-Walker, P.L., Gunn, A., 2001. The effect of the ectoparasitic mite, *Varroa destructor* on adult worker honeybee (*Apis mellifera*) emergence weights, water, protein, carbohydrate, and lipid levels. Entomol Exp. Appl. 101, 207–217. https://doi.org/10.1046/j.1570-7458.2001.00905.x

Bruce, W.A., Chiesa, F., Marchetti, S., Griffiths, D.A., 1988. LABORATORY FEEDING OF VARROA JACOBSONI OUDEMANS ON NATURAL AND ARTIFICIAL DIETS (ACARI : VARROIDAE). Apidologie 19, 209–218. https://doi.org/10.1051/apido:19880209

Bruce, W.A., Henegar, R.B., Hackett, K.J., 1991. An artificial membrane for in vitro feeding of Varroa jacobsoni and Acarapis woodi, mite parasites of honey bees*. Apidologie 22, 503–507. https://doi.org/10.1051/apido:19910503

Cabrera, A.R., Shirk, P.D., Duehl, A.J., Donohue, K.V., Grozinger, C.M., Evans, J.D., Teal, P.E.A., 2013. Genomic organization and reproductive regulation of a large lipid transfer protein in the varroa mite, *V arroa destructor* (Anderson & Trueman): Varroa mite large lipid transfer protein gene. Insect Mol Biol 22, 505–522. https://doi.org/10.1111/imb.12040

Cabrera Cordon, A.R., Shirk, P.D., Duehl, A.J., Evans, J.D., Teal, P.E.A., 2013. Variable induction of vitellogenin genes in the varroa mite, *Varroa destructor* (Anderson & Trueman), by the honeybee, *Apis mellifera L* , host and its environment: varroa mite vitellogenin gene regulation. Insect Mol. Bio. 22, 88–103. https://doi.org/10.1111/imb.12006

Calderone, N.W., Kuenen, L.P.S., 2003. Differential tending of worker and drone larvae of the honey bee, *Apis mellifera* , during the 60 hours prior to cell capping. Apidologie 34, 543–552. https://doi.org/10.1051/apido:2003054

Calderone, N.W., Lin, S., Kuenen, L.P.S., 2002. Differential infestation of honey bee, *Apis mellifera*, worker and queen brood by the parasitic mite *Varroa destructor*. Apidologie 33, 389–398. https://doi.org/10.1051/apido:2002024

Calis, J.N.M., 2001. Parasite-host interactions between the varroa mite and the honey bee: a contribution to sustainable varroa control. s.n., S.l.

Campbell, E.M., Budge, G.E., Watkins, M., Bowman, A.S., 2016. Transcriptome analysis of the synganglion from the honey bee mite, *Varroa destructor* and RNAi knockdown of neural peptide targets. Insect Biochem. Molec. 70, 116–126. https://doi.org/10.1016/j.ibmb.2015.12.007

Cervo, R., Bruschini, C., Cappa, F., Meconcelli, S., Pieraccini, G., Pradella, D., Turillazzi, S., 2014. High varroa mite abundance influences chemical profiles of worker bees and mite–host preferences. J. Exp. Biol. 217, 2998–3001. https://doi.org/10.1242/jeb.099978

Cheek, A.O., Brouwer, T.H., Carroll, S., Manning, S., McLachlan, J.A., Brouwer, M., 2001. Experimental evaluation of vitellogenin as a predictive biomarker for reproductive disruption. Environ. Health Persp. 109, 10.

Chen, Y., Evans, J., Feldlaufer, M., 2006. Horizontal and vertical transmission of viruses in the honey bee, *Apis mellifera*. J. Invertbr. Pathol. 92, 152–159. https://doi.org/10.1016/j.jip.2006.03.010

Chiu, Y.-F., Nguyen, T.T.H., Yeh, P.-T., Cronin, A.L., Peng, P., Su, Y.-C., 2023. Genome-wide SNPs show hybridization of Varroa mites from different Apis hosts in Vietnam and Taiwan. Apidologie 54, 25. https://doi.org/10.1007/s13592-023-01001-3

Cicero, J.M., Sammataro, D., 2010. The salivary glands of adult female *Varroa destructor* (Acari: Varroidae), an ectoparasite of the honey bee, *Apis mellifera* (Hymenoptera: Apidae). International Journal of Acarology 36, 377–386. https://doi.org/10.1080/01647951003757961

Coffey, M.F., Breen, J., Brown, M.J.F., McMullan, J.B., 2010. Brood-cell size has no influence on the population dynamics of *Varroa destructor* mites in the native western honey bee, *Apis mellifera mellifera*. Apidologie 41, 522–530. https://doi.org/10.1051/apido/2010003

Colin, M.E., Richard, D., Fourcassie, V., Belzunces, L.P., 1992. Attraction of *Varroa jacobsoni*, parasite of *Apis mellifera* by electrical charges. J. Insect Physiol. 38, 111–117. https://doi.org/10.1016/0022-1910(92)90039-G

Conlon, B.H., Aurori, A., Giurgiu, A., Kefuss, J., Dezmirean, D.S., Moritz, R.F.A., Routtu, J., 2019. A gene for resistance to the varroa mite (Acari) in honey bee (*Apis mellifera*) pupae. Mol. Ecol. 28, 2958–2966. https://doi.org/10.1111/mec.15080

Cornman, R.S., Schatz, M.C., Johnston, J.S., Chen, Y.-P., Pettis, J., Hunt, G., Bourgeois, L., Elsik, C., Anderson, D., Grozinger, C.M., Evans, J.D., 2010. Genomic survey of the ectoparasitic mite *Varroa destructor*, a major pest of the honey bee *Apis mellifera*. BMC Genomics 11, 602. https://doi.org/10.1186/1471-2164-11-602

Crago, J., Corsi, S.R., Weber, D., Bannerman, R., Klaper, R., 2011. Linking biomarkers to reproductive success of caged fathead minnows in streams with increasing urbanization. Chemosphere 82, 1669–1674. https://doi.org/10.1016/j.chemosphere.2010.11.011

de Guzman, L.I., Rinderer, T.E., 1999. Identification and comparison of varroa species infesting honey bees. Apidologie 30, 85–95. https://doi.org/10.1051/apido:19990201

de Guzman, L.I., Rinderer, T.E., Frake, A.M., 2008. Comparative reproduction of *Varroa destructor* in different types of Russian and Italian honey bee combs. Exp. Appl. Acarol. 44, 227–238. https://doi.org/10.1007/s10493-008-9142-1

De Jong, D., Morse, R.A., Eickwort, G.C., 1982. Mite Pests of Honey Bees. Annu. Rev. Entomol. 27, 229–252. https://doi.org/10.1146/annurev.en.27.010182.001305

de Miranda, J.R., Bailey, L., Ball, B.V., Blanchard, P., Budge, G.E., Chejanovsky, N., Chen, Y.-P., Gauthier, L., Genersch, E., de Graaf, D.C., Ribière, M., Ryabov, E., De Smet, L., van der Steen, J.J.M., 2013. Standard methods for virus research in *Apis mellifera*. J. Apicult. Res. 52, 1–56. https://doi.org/10.3896/IBRA.1.52.4.22

de Miranda, J.R., Genersch, E., 2010. Deformed wing virus. J. Invertbr. Pathol. 103, S48–S61. https://doi.org/10.1016/j.jip.2009.06.012

De Ruijter, A., 1987. Reproduction of *Varroa jacobsoni* during successive brood cycles of the honeybee. Apidologie 18, 321–326. https://doi.org/10.1051/apido:19870403

De Ruijter, A., Kaas, J.P., 1983. The Anatomy of the Varroa mite Varroa jacobsoni Affecting Honey Bees: Present Status and Needs. Rotterdam : Published for the Commission of the European Communities by A.A. Balkema 45–47.
Delfinado-Baker, M., Rath, W., Boecking, O., 1992. Phoretic bee mites and honeybee grooming behavior. Int. J. Acarol 18, 315–322. https://doi.org/10.1080/01647959208683966
Dietemann, V., Beaurepaire, A., Page, P., Yañez, O., Buawangpong, N., Chantawannakul, P., Neumann, P., 2019. Population genetics of ectoparasitic mites *Varroa* spp. in Eastern and Western honey bees. Parasitology 146, 1429–1439. https://doi.org/10.1017/S003118201900091X
Dietemann, V., Nazzi, F., Martin, S.J., Anderson, D.L., Locke, B., Delaplane, K.S., Wauquiez, Q., Tannahill, C., Frey, E., Ziegelmann, B., Rosenkranz, P., Ellis, J.D., 2013. Standard methods for varroa research. Journal of Apicultural Research 52, 1–54. https://doi.org/10.3896/IBRA.1.52.1.09
Dillier, F.-X., Fluri, P., Guerin, P., 2002. Schlussbericht und Datenverzeichnisse.
Dillier, F.-X., Fluri, P., Imdorf, A., 2006. Review of the orientation behaviour in the bee parasitic mite *Varroa destructor*: Sensory equipment and cell invasion behaviour. Rev. Suisse Zool. 113, 857–877. https://doi.org/10.5962/bhl.part.80381
Donzé, G., Guerin, P.M., 1994. Behavioral attributs and parental care of varroa mites parasitizing honeybee brood. Behav. Ecol. Sociobiol 34, 305–319.
Donzé, G., Herrmann, M., Bachofen, B., Guerin, P.R.M., 1996. Effect of mating frequency and brood cell infestation rate on the reproductive success of the honeybee parasite *Varroa jacobsoni*. Ecol. Entomol. 21, 17–26. https://doi.org/10.1111/j.1365-2311.1996.tb00261.x
Duay, P., Jong, D.D., Engels, W., 2003. Weight loss in drone pupae (*Apis mellifera*) multiply infested by *Varroa destructor mites*. Apidologie 34, 61–65. https://doi.org/10.1051/apido:2002052
Duay, P., Jong, D.D., Engels, W., 2002. Decreased flight performance and sperm production in drones of the honey bee (*Apis mellifera*) slightly infested by *Varroa destructor* mites during pupal development. Genet. Mol. Biol.
Eliash, N., Singh, N.K., Kamer, Y., Pinnelli, G.R., Plettner, E., Soroker, V., 2014. Can We Disrupt the Sensing of Honey Bees by the Bee Parasite *Varroa destructor*? PLoS ONE 9.
Eliash, N., Thangarajan, S., Goldenberg, I., Sela, N., Kupervaser, M., Barlev, J., Altman, Y., Knyazer, A., Kamer, Y., Zaidman, I., Rafaeli, A., Soroker, V., 2019. Varroa chemosensory proteins: some are conserved across Arthropoda but others are arachnid specific. Insect Mol Biol 28, 321–341. https://doi.org/10.1111/imb.12553
Erban, T., Sopko, B., Kadlikova, K., Talacko, P., Harant, K., 2019. *Varroa destructor* parasitism has a greater effect on proteome changes than the deformed wing virus and activates TGF-β signaling pathways. Sci. Rep. 9, 9400. https://doi.org/10.1038/s41598-019-45764-1
Evans, G.O., Till, W.M., 1979. Mesostigmatic mites of Britain and Ireland (Chelicerata: Acari-Parasitiformes): An introduction to their external morphology and classification. The Transactions of the Zoological Society of London 35, 139–262. https://doi.org/10.1111/j.1096-3642.1979.tb00059.x
Fahle, N., Rosenkranz, P., 2005. Mate choice in *Varroa destructor*: male mites prefer young females. Presented at the IUSSI - Proceedings of the German Section Meeting at Halle.
Frey, E., Odemer, R., Blum, T., Rosenkranz, P., 2013a. Activation and interruption of the reproduction of *Varroa destructor* is triggered by host signals (*Apis*

mellifera). J. Invertbr. Pathol. 113, 56–62. https://doi.org/10.1016/j.jip.2013.01.007
Frey, E., Odemer, R., Blum, T., Rosenkranz, P., 2013b. Activation and interruption of the reproduction of *Varroa destructor* is triggered by host signals (*Apis mellifera*). Journal of Invertebrate Pathology 113, 56–62. https://doi.org/10.1016/j.jip.2013.01.007
Fries, I., Camazine, S., 2001. Implications of horizontal and vertical pathogen transmission for honey bee epidemiology. Apidologie 32, 199–214. https://doi.org/10.1051/apido:2001122
Fuchs, S., 1992. Choice in Varroa jacobsoni Oud. between Honey Bee Drone or Workerbrood Cells for Reproduction. Behavioral Ecology and Sociobiology 31, 429–435.
Fuchs, S., 1990. Preference for drone brood cells by Varroa jacobsoni Oud in colonies of *Apis mellifera* carnica. http://dx.doi.org/10.1051/apido:19900304 21. https://doi.org/10.1051/apido:19900304
Garrido, C., Rosenkranz, P., 2003. The reproductive program of female *Varroa destructor* mites is triggered by its host, *Apis mellifera*. Exp. Appl. Acarol. 31, 269–273. https://doi.org/10.1023/B:APPA.0000010386.10686.9f
Garrido, C., Rosenkranz, P., Stürmer, M., Rübsam, R., Büning, J., 2000. Toluidine blue staining as a rapid measure for initiation of oocyte growth and fertility in *Varroa jacobsoni Oud.* . Apidologie 31, 559–566. https://doi.org/10.1051/apido:2000146
Genersch, E., Aubert, M., 2010. Emerging and re-emerging viruses of the honey bee (*Apis mellifera* L.). Vet. Res. 41, 54. https://doi.org/10.1051/vetres/2010027
Goetz, B., Koeniger, N., 1993. The distance between larva and cell opening triggers broodcell invasion by *Varroa jacobsoni*. Apidologie 24, 67–72. https://doi.org/10.1051/apido:19930108
Gorgol, V.T., 1991. Morphological features of gut onotogeny in the parasitic mite *Varroa jacobsoni* . WIADOMOSCI PARAZYTOLOGICZNE 37, 95–97.
Grindrod, I., Martin, S.J., 2023. Varroa resistance in *Apis cerana*: a review. Apidologie 54, 14. https://doi.org/10.1007/s13592-022-00977-8
Grindrod, I., Martin, S.J., 2021. Parallel evolution of *Varroa* resistance in honey bees: a common mechanism across continents? P. Roy. Soc. B-Biol. Sci. 288, 20211375. https://doi.org/10.1098/rspb.2021.1375
Hagedorn, H.H., Kunkel, J.G., 1979. Vitellogenin and Vitellin in Insects. Annu. Rev. Entomol. 24, 475–505. https://doi.org/10.1146/annurev.en.24.010179.002355
Hall, H., Bencsik, M., Newton, M.I., Chandler, D., Prince, G., Dwyer, S., 2022. *Varroa destructor* mites regularly generate ultra-short, high magnitude vibrational pulses. Entomol. Gen 42, 375–388. https://doi.org/10.1127/entomologia/2021/1407
Häußermann, C.K., Giacobino, A., Munz, R., Ziegelmann, B., Palacio, M.A., Rosenkranz, P., 2020. Reproductive parameters of female *Varroa destructor* and the impact of mating in worker brood of *Apis mellifera*. Apidologie 51, 342–355. https://doi.org/10.1007/s13592-019-00713-9
Häußermann, C.K., Ziegelmann, B., Bergmann, P., Rosenkranz, P., 2015. Male mites (*Varroa destructor*) perceive the female sex pheromone with the sensory pit organ on the front leg tarsi. Apidologie 46, 771–778. https://doi.org/10.1007/s13592-015-0367-9
Häußermann, C.K., Ziegelmann, B., Rosenkranz, P., 2018. Spermatozoa production in male *Varroa destructor* and its impact on reproduction in worker brood of *Apis mellifera*. Exp. Appl. Acarol. 74, 43–54. https://doi.org/10.1007/s10493-018-0216-4

Häußermann, C.K., Ziegelmann, B., Rosenkranz, P., 2016. Spermatozoa capacitation in female *Varroa destructor* and its influence on the timing and success of female reproduction. v 69, 371–387. https://doi.org/10.1007/s10493-016-0051-4

Heppner, J.B., Heppner, J.B., Tzanakakis, M.E., Tzanakakis, M.E., Tzanakakis, M.E., Lawrence, P.O., Capinera, J.L., Nagoshi, R., Gerlach, G., Smith, H., Capinera, J.L., Heppner, J.B., Heppner, J.B., Nation, J.L., Berryman, A.A., Leather, S.R., Heppner, J.B., 2008. Ostia, in: Capinera, J.L. (Ed.), Encyclopedia of Entomology. Springer Netherlands, Dordrecht, pp. 2698–2699. https://doi.org/10.1007/978-1-4020-6359-6_1902

Herrero, S., Millán-Leiva, A., Coll, S., González-Martínez, R.M., Parenti, S., González-Cabrera, J., 2019. Identification of new viral variants specific to the honey bee mite *Varroa destructor*. Exp. Appl. Acarol. 79, 157–168. https://doi.org/10.1007/s10493-019-00425-w

Hubert, J., Bicianova, M., Ledvinka, O., Kamler, M., Lester, P.J., Nesvorna, M., Kopecky, J., Erban, T., 2017. Changes in the Bacteriome of Honey Bees Associated with the Parasite *Varroa destructor*, and Pathogens Nosema and Lotmaria passim. Microb. Ecol. 73, 685–698. https://doi.org/10.1007/s00248-016-0869-7

Jack, C.J., Dai, P.-L., van Santen, E., Ellis, J.D., 2020. Comparing four methods of rearing *Varroa destructor* in vitro. Exp. Appl. Acarol. 80, 463–476. https://doi.org/10.1007/s10493-020-00488-0

Kather, R., Drijfhout, F.P., Martin, S.J., 2011. Task Group Differences in Cuticular Lipids in the Honey Bee *Apis mellifera*. J. Chem. Ecol. 37, 205–212. https://doi.org/10.1007/s10886-011-9909-4

Kather, R., Drijfhout, F.P., Shemilt, S., Martin, S.J., 2015. Evidence for Passive Chemical Camouflage in the Parasitic Mite *Varroa destructor*. J. Chem. Ecol. 41, 178–186. https://doi.org/10.1007/s10886-015-0548-z

Kenney, M.C., Ferrington, D.A., Udar, N., 2013. Mitochondrial Genetics of Retinal Disease, 5th ed. ed. Saunders/Elsevier, London.

Kirchner, W., 1993. 15. Lichtsinn und Vibrationssinn der Varroa-Milbe. Apidologie 24, 490–492.

Knell, R.J., 1999. Sexually Transmitted Disease and Parasite-Mediated Sexual Selection. Evolution 53, 957–961.

Koutouvela, E., Papachristoforou, A., 2019. The heart of *Varroa destructor*: description, function and inhibition following acaricide application. saa 24, 638. https://doi.org/10.11158/saa.24.4.9

Kralj, J., Brockmann, A., Fuchs, S., Tautz, J., 2007. The parasitic mite *Varroa destructor* affects non-associative learning in honey bee foragers, *Apis mellifera L.* J. Comp. Physiol. A 193, 363–370. https://doi.org/10.1007/s00359-006-0192-8

Kralj, J., Fuchs, S., 2006. Parasitic *Varroa destructor* mites influence flight duration and homing ability of infested *Apis mellifera* foragers. Apidologie 37, 577–587. https://doi.org/10.1051/apido:2006040

Kraus, B., 1994. Factors influencing host choice of the honey bee parasite *Varroa jacobsoni Oud*. Exp. Appl. Acarol. 18, 435–443. https://doi.org/10.1007/BF00051525

Kraus, B., Hunt, G., 1995. Differentiation of *Varroa jacobsoni Oud* populations by random amplification of polymorphic DNA (RAPD). Apidologie 26, 283–290. https://doi.org/10.1051/apido:19950402

Kraus, B., Velthuis, H.H.W., 1997. High Humidity in the Honey Bee (*Apis mellifera L.*) Brood Nest Limits Reproduction of the Parasitic Mite *Varroa jacobsoni Oud.* Naturwissenschaften 84, 217–218. https://doi.org/10.1007/s001140050382

Kuenen, L.P.S., Calderone, N.W., 1998. Positive anemotaxis by varroa mites: responses to bee odour plumes and single clean-air puffs. Physiol. Entomol. 23, 255–264. https://doi.org/10.1046/j.1365-3032.1998.233085.x

Le Conte, Y., Arnold, G., 1988. ETUDE DU THERMOPRÉFÉRENDUM DE *VARROA JACOBSONI OUD*. Apidologie 19, 155–164. https://doi.org/10.1051/apido:19880205

Le Conte, Y., Arnold, G., Desenfant, P., 1990a. Influence of Brood Temperature and Hygrometry Variations on the Development of the Honey Bee Ectoparasite *Varroa jacobsoni*. Entymological Society of America 19, 1780–1785.

Le Conte, Y., Arnold, G., Trouiller, J., Masson, C., Chappe, B., 1990b. Identification of a brood pheromone in honeybees. Naturwissenschaften 77, 334–336. https://doi.org/10.1007/BF01138390

Le Conte, Y., Huang, Z.Y., Roux, M., Zeng, Z.J., Christidès, J.-P., Bagnères, A.-G., 2015. *Varroa destructor* changes its cuticular hydrocarbons to mimic new hosts. Biol. Lett. 11, 20150233. https://doi.org/10.1098/rsbl.2015.0233

Le Conte, Y., Meixner, M.D., Brandt, A., Carreck, N.L., Costa, C., Mondet, F., Büchler, R., 2020. Geographical Distribution and Selection of European Honey Bees Resistant to *Varroa destructor*. Insects 11, 873. https://doi.org/10.3390/insects11120873

Li, W., Zhang, Y., Peng, H., Zhang, R., Wang, Z., Huang, Z.Y., Chen, Y.P., Han, R., 2021. The cell invasion preference of *Varroa destructor* between the original and new honey bee hosts. Int. J. Parasitol. S0020751921002617. https://doi.org/10.1016/j.ijpara.2021.08.001

Lin, Z., Liu, Y., Chen, X., Han, C., Wang, W., Ke, Y., Su, X., Li, Y., Chen, H., Xu, H., Chen, G., Ji, T., 2020. Genome-Wide Identification of Long Non-coding RNAs in the Gravid Ectoparasite *Varroa destructor*. Front. Genet. 11, 575680. https://doi.org/10.3389/fgene.2020.575680

Lin, Z., Qin, Y., Page, P., Wang, S., Li, L., Wen, Z., Hu, F., Neumann, P., Zheng, H., Dietemann, V., 2018. Reproduction of parasitic mites *Varroa destructor* in original and new honeybee hosts. Ecol. Evol. 8, 2135–2145. https://doi.org/10.1002/ece3.3802

Liu, J., Zhang, R., Tang, R., Zhang, Y., Guo, R., Xu, G., Chen, D., Huang, Z.Y., Chen, Y., Han, R., Li, W., 2022. The Role of Honey Bee Derived Aliphatic Esters in the Host-Finding Behavior of *Varroa destructor*. Insects 14, 24. https://doi.org/10.3390/insects14010024

Liu, T.P., Peng, Y.-S., 1990. PALPAL TARSAL SENSILLA OF THE FEMALE MITE, *VARROA JACOBSONI* OUDEMANS (ACARI: VARROIDAE). Can Entomol 122, 295–300. https://doi.org/10.4039/Ent122295-3

Locke, B., 2016a. Natural varroa mite-surviving </i>*Apis mellifera* </i>honeybee populations. Apidologie 47, 467–482. https://doi.org/10.1007/s13592-015-0412-8

Locke, B., 2016b. Inheritance of reduced varroa mite reproductive success in reciprocal crosses of mite-resistant and mite-susceptible honey bees (*Apis mellifera*). Apidologie 47, 583–588. https://doi.org/10.1007/s13592-015-0403-9

Locke, B., Fries, I., 2011. Characteristics of honey bee colonies (*Apis mellifera*) in Sweden surviving *Varroa destructor* infestation. Apidologie 42, 533–542. https://doi.org/10.1007/s13592-011-0029-5

Maggi, M., Damiani, N., Ruffinengo, S., De Jong, D., Principal, J., Eguaras, M., 2010. Brood cell size of *Apis mellifera* modifies the reproductive behavior of *Varroa destructor*. Exp. Appl. Acarol. 50, 269–279. https://doi.org/10.1007/s10493-009-9314-7

Marche, M.G., Satta, A., Floris, I., Pusceddu, M., Buffa, F., Ruiu, L., 2019. Quantitative variation in the core bacterial community associated with

honey bees from *Varroa*- infested colonies. Journal of Apicultural Research 58, 444–454. https://doi.org/10.1080/00218839.2019.1589669
Martin, C., Salvy, M., Provost, E., Bagnères, A.-G., Roux, M., Crauser, D., Clement, J.-L., Le Conte, Y., 2001. Variations in chemical mimicry by the ectoparasitic mite *Varroa jacobsoni* according to the developmental stage of the host honey-bee *Apis mellifera*. Insect Biochem. Molec. 31, 365–379. https://doi.org/10.1016/S0965-1748(00)00130-2
Martin, S.J., Kryger, P., 2002. Reproduction of *Varroa destructor* in South African honey bees: does cell space influence Varroa male survivorship? Apidologie 33, 51–61. https://doi.org/10.1051/apido:2001007
Michael, A.D., 1892. On the Variations of the Internal Anatomy of the Gamasinae, especially in that of the Genital Organs, and on their Mode of Coition. Transactions of the Linnean Society of London. 2nd Series: Zoology 5, 281–324. https://doi.org/10.1111/j.1096-3642.1892.tb00175.x
Mondet, F., Alaux, C., Severac, D., Rohmer, M., Mercer, A.R., Le Conte, Y., 2015. Antennae hold a key to Varroa-sensitive hygiene behaviour in honey bees. Sci. Rep. 5, 10454. https://doi.org/10.1038/srep10454
Mondet, F., Rau, A., Klopp, C., Rohmer, M., Severac, D., Le Conte, Y., Alaux, C., 2018. Transcriptome profiling of the honeybee parasite *Varroa destructor* provides new biological insights into the mite adult life cycle. BMC Genomics 19, 328. https://doi.org/10.1186/s12864-018-4668-z
Moro, A., Blacquière, T., Panziera, D., Dietemann, V., Neumann, P., 2021. Host-Parasite Co-Evolution in Real-Time: Changes in Honey Bee Resistance Mechanisms and Mite Reproductive Strategies. Insects 12, 120. https://doi.org/10.3390/insects12020120
Nation, J.L., Sanford, M.T., Milne, K., 1992. Cuticular hydrocarbons from *Varroa jacobsoni*. Exp. Appl. Acarol. 16, 331–344. https://doi.org/10.1007/BF01218575
Navajas, M., Conte, Y.L., Solignac, M., Cros-Arteil, S., Cornuet, J.-M., 2002. The Complete Sequence of the Mitochondrial Genome of the Honeybee Ectoparasite Mite *Varroa destructor* (Acari: Mesostigmata). Molecular Biology and Evolution 19, 2313–2317. https://doi.org/10.1093/oxfordjournals.molbev.a004055
Nazzi, F., Le Conte, Y., 2016. Ecology of *Varroa destructor* , the Major Ectoparasite of the Western Honey Bee, *Apis mellifera*. Annu. Rev. Entomol. 61, 417–432. https://doi.org/10.1146/annurev-ento-010715-023731
Nazzi, F., Milani, N., 1994. A technique for reproduction of Varroa jacobsoni Oud under laboratory conditions. Apidologie 25, 579–584. https://doi.org/10.1051/apido:19940608
Nazzi, F., Milani, N., Vedova, G.D., Nimis, M., 2001. Semiochemicals from larval food affect the locomotory behaviour of *Varroa destructor*. Apidologie 32, 149–155. https://doi.org/10.1051/apido:2001120
Nganso, B.T., Mani, K., Altman, Y., Rafaeli, A., Soroker, V., 2020. How Crucial is the Functional Pit Organ for the Varroa Mite? Insects 11, 395. https://doi.org/10.3390/insects11060395
Noël, A., Le Conte, Y., Mondet, F., 2020. *Varroa destructor*: how does it harm *Apis mellifera* honey bees and what can be done about it? Emerg. Top. Life Sci. 4, 45–57. https://doi.org/10.1042/ETLS20190125
Oldroyd, B.P., 1999. Coevolution while you wait: *Varroa jacobsoni*, a new parasite of western honeybees. Trends Ecol. Evol. 14, 312–315. https://doi.org/10.1016/S0169-5347(99)01613-4
Palma, A.D., Alberti, G., 2001. Fine Structure of the Female Genital System in Phytoseiid Mites with Remarks on Egg Nutrimentary Development, Sperm-

Access System, Sperm Transfer, and Capacitation (Acari, Gamasida, Phytoseiidae). Experimental and Applied Acarology 25, 525–591.
Panziera, D., van Langevelde, F., Blacquière, T., 2017. Varroa sensitive hygiene contributes to naturally selected varroa resistance in honey bees. J. Apicult. Res. 56, 635–642. https://doi.org/10.1080/00218839.2017.1351860
Peng, Y.-S., Fang, Y., Xu, S., Ge, L., 1987. The resistance mechanism of the Asian honey bee, *Apis cerana* Fabr., to an ectoparasitic mite, Varroa jacobsoni Oudemans. Journal of Invertebrate Pathology 49, 54–60. https://doi.org/10.1016/0022-2011(87)90125-X
Pernal, S.F., Baird, D.S., Birmingham, A.L., Higo, H.A., Slessor, K.N., Winston, M.L., 2005. Semiochemicals Influencing the Host-finding Behaviour of *Varroa destructor*. Exp Appl Acarol 37, 1–26. https://doi.org/10.1007/s10493-005-1117-x
Piccirillo, G.A., De Jong, D., 2004. Old honey bee brood combs are more infested by the mite *Varroa destructor* than are new brood combs. Apidologie 35, 359–364. https://doi.org/10.1051/apido:2004022
Piccolo, F.D., Nazzi, F., Vedova, G.D., Milani, N., 2010. Selection of *Apis mellifera* workers by the parasitic mite *Varroa destructor* using host cuticular hydrocarbons. Parasitology 137, 967–973. https://doi.org/10.1017/S0031182009991867
Piou, V., Tabart, J., Urrutia, V., Hemptinne, J.-L., Vétillard, A., 2016. Impact of the Phoretic Phase on Reproduction and Damage Caused by *Varroa destructor* (Anderson and Trueman) to Its Host, the European Honey Bee (*Apis mellifera* L.). PLoS ONE 11, e0153482. https://doi.org/10.1371/journal.pone.0153482
Piou, V., Vilarem, C., Rein, C., Sprau, L., Vétillard, A., 2021. Standard Methods for Dissection of *Varroa destructor* Females. Insects 13, 37. https://doi.org/10.3390/insects13010037
Pizzorno, M.C., Field, K., Kobokovich, A.L., Martin, P.L., Gupta, R.A., Mammone, R., Rovnyak, D., Capaldi, E.A., 2021. Transcriptomic Responses of the Honey Bee Brain to Infection with Deformed Wing Virus. Viruses 13, 287. https://doi.org/10.3390/v13020287
Posada-Florez, F., Sonenshine, D.E., Egekwu, N.I., Rice, C., Lupitskyy, R., Cook, S.C., 2019. Insights into the metabolism and behaviour of *Varroa destructor* mites from analysis of their waste excretions. Parasitology 146, 527–532. https://doi.org/10.1017/S0031182018001762
Ramsey, S., Gulbronson, C.J., Mowery, J., Ochoa, R., vanEngelsdorp, D., Bauchan, G., 2018. A Multi-Microscopy Approach to Discover the Feeding Site and Host Tissue Consumed by *Varroa destructor* on Host Honey Bees. Microsc Microanal 24, 1258–1259. https://doi.org/10.1017/S1431927618006773
Ramsey, S.D., Ochoa, R., Bauchan, G., Gulbronson, C., Mowery, J.D., Cohen, A., Lim, D., Joklik, J., Cicero, J.M., Ellis, J.D., Hawthorne, D., vanEngelsdorp, D., 2019. *Varroa destructor* feeds primarily on honey bee fat body tissue and not hemolymph. P. Natl. A. Sci. USA 116, 1792–1801. https://doi.org/10.1073/pnas.1818371116
Reams, T., Rangel, J., 2022. Understanding the Enemy: A Review of the Genetics, Behavior and Chemical Ecology of *Varroa destructor* , the Parasitic Mite of *Apis mellifera*. J. Insect Sci. 22, 18. https://doi.org/10.1093/jisesa/ieab101
Rembold, H., Kremer, J.-P., Ulrich, G.M., 1980. CHARACTERIZATION OF POSTEMBRYONIC DEVELOPMENTAL STAGES OF THE FEMALE CASTES OF THE HONEY BEE, *APIS MELLIFERA L*. Apidologie 11, 29–38. https://doi.org/10.1051/apido:19800104

Řeřicha, M., Dobeš, P., Knapp, M., 2021. Changes in haemolymph parameters and insect ability to respond to immune challenge during overwintering. Ecol. Evol. 11, 4267–4275. https://doi.org/10.1002/ece3.7323
Reuter, E., 1909. Zur Morphologie und Ontogenie der Acariden. Acta Societatis Scientiarum Fennicae.
Reyes García, M.G., García Tamayo, F., 2013. The Importance of the Nurse Cells and Regulatory Cells in the Control of T Lymphocyte Responses. BioMed Research International 2013, 1–15. https://doi.org/10.1155/2013/352414
Richard, D., Colin, M.E., Lhomme, M., 1990. Anatomical organization of the tracheal system ofVarroa jacobsoni (Acari: Varroidae). Exp Appl Acarol 9, 63–72. https://doi.org/10.1007/BF01198983
Richards, E.H., Jones, B., Bowman, A., 2011. Salivary secretions from the honeybee mite, *Varroa destructor:* effects on insect haemocytes and preliminary biochemical characterization. Parasitology 138, 602–608. https://doi.org/10.1017/S0031182011000072
Rickli, M., Guerin, P.M., Diehl, P.A., 1992. Palmitic acid released from honeybee worker larvae attracts the parasitic mite *Varroa jacobsoni* on a servosphere. Naturwissenschaften 79, 320–322. https://doi.org/10.1007/BF01138711
Rinderer, T.E., Harris, J.W., Hunt, G.J., de Guzman, L.I., 2010. Breeding for resistance to *Varroa destructor* in North America. Apidologie 41, 409–424. https://doi.org/10.1051/apido/2010015
Rosenkranz, P., Aumeier, P., Ziegelmann, B., 2010. Biology and control of *Varroa destructor*. J. Invertbr. Pathol. 103, S96–S119. https://doi.org/10.1016/j.jip.2009.07.016
Rosenkranz, P., Garrido, C., 2004. Volatiles of the honey bee larva initiate oogenesis in the parasitic mite *Varroa destructor*. Evolutionary, Mechanistic and Environmental Approaches to Chemically-Mediated Interactions 14. https://doi.org/10.1007/s00049-004-0278-0
Rosenkranz, P., Tewarson, N.C., Singh, A., Engels, W., 1993. Differential hygienic behaviour towards *Varroa jacobsoni* in capped worker brood of *Apis cerana* depends on alien scent adhering to the mites. J. Apicult. Res. 32, 89–93. https://doi.org/10.1080/00218839.1993.11101292
Ruttner, F., Marx, H., Marx, G., 1984. BEOBACHTUNGEN ÜBER EINE MÖGLICHE ANPASSUNG VON *VARROA JACOBSONI* AN *APIS MELLIFERA L.* IN URUGUAY. Apidologie 15, 43–62. https://doi.org/10.1051/apido:19840105
Salvy, M., Martin, C., Bagnères, A.G., Provost, É., Roux, M., Le Conte, Y., Clément, J.L., 2001. Modifications of the cuticular hydrocarbon profile of *Apis mellifera* worker bees in the presence of the ectoparasitic mite *Varroa jacobsoni* in brood cells. Parasitology 122. https://doi.org/10.1017/S0031182001007181
Schlüns, H., Schlüns, E.A., van Praagh, J., Moritz, R.F.A., 2003. Sperm numbers in drone honeybees (*Apis mellifera*) depend on body size. Apidologie 34, 577–584. https://doi.org/10.1051/apido:2003051
Słowińska, M., Nynca, J., Bąk, B., Wilde, J., Siuda, M., Ciereszko, A., 2019. 2D-DIGE proteomic analysis reveals changes in haemolymph proteome of 1-day-old honey bee (*Apis mellifera*) workers in response to infection with *Varroa destructor* mites. Apidologie 50, 632–656. https://doi.org/10.1007/s13592-019-00674-z
Solignac, M., Cornuet, J., Vautrin, D., Le Conte, Y., Anderson, D., Evans, J., Cros-Arteil, S., Navajas, M., 2005. The invasive Korea and Japan types of *Varroa destructor* , ectoparasitic mites of the Western honeybee (*Apis mellifera*), are two partly isolated clones. P. Roy. Soc. B-Biol. Sci. 272, 411–419. https://doi.org/10.1098/rspb.2004.2853

Sonenshine, D.E., Posada-Florez, F., Laudier, D., Gulbronson, C.J., Ramsey, S., Cook, S.C., 2022. Histological Atlas of the Internal Anatomy of Female *Varroa destructor* (Mesostigmata: Varroidae) Mites in Relation to Feeding and Reproduction. Annals of the Entomological Society of America 115, 163–193. https://doi.org/10.1093/aesa/saab043

Steiner, J., Diehl, P.A., Vlimant, M., 1995. Vitellogenesis in *Varroa jacobsoni*, a parasite of honey bees. Exp. Appl. Acarol. 19, 411–422. https://doi.org/10.1007/BF00145158

Steiner, J., Dittmann, F., Rosenkranz, P., Engels, W., 1994. The first gonocycle of the parasitic mite (*Varroa jacobsoni*) in relation to preimaginal development of its host, the honey bee (*Apis mellifra carnicar*). Invertbr. Reprod. Dev. 25, 175–183. https://doi.org/10.1080/07924259.1994.9672384

Strand, M.R., 2008. INSECT HEMOCYTES AND THEIR ROLE IN IMMUNITY, in: Insect Immunology. Elsevier, pp. 25–47. https://doi.org/10.1016/B978-012373976-6.50004-5

Surlis, C., Carolan, J.C., Coffey, M., Kavanagh, K., 2018. Quantitative proteomics reveals divergent responses in *Apis mellifera* worker and drone pupae to parasitization by *Varroa destructor*. J. Insect Physiol. 107, 291–301. https://doi.org/10.1016/j.jinsphys.2017.12.004

Techer, M.A., Rane, R.V., Grau, M.L., Roberts, J.M.K., Sullivan, S.T., Liachko, I., Childers, A.K., Evans, J.D., Mikheyev, A.S., 2019. Divergent evolutionary trajectories following speciation in two ectoparasitic honey bee mites. Commun Biol 2, 357. https://doi.org/10.1038/s42003-019-0606-0

Traniello, I.M., Bukhari, S.A., Kevill, J., Ahmed, A.C., Hamilton, A.R., Naeger, N.L., Schroeder, D.C., Robinson, G.E., 2020. Meta-analysis of honey bee neurogenomic response links Deformed wing virus type A to precocious behavioral maturation. Sci. Rep. 10, 3101. https://doi.org/10.1038/s41598-020-59808-4

Traynor, K.S., Mondet, F., de Miranda, J.R., Techer, M., Kowallik, V., Oddie, M.A.Y., Chantawannakul, P., McAfee, A., 2020. *Varroa destructor*: A Complex Parasite, Crippling Honey Bees Worldwide. Trends Parasitol. 36, 592–606. https://doi.org/10.1016/j.pt.2020.04.004

Trodtfeld, P., Rogers, D., Dempster, J., Huntzinger, K., 2019. A Deadly Honey Bee Parasite: The Varroa Mite.

Trouiller, J., Arnold, G., Chappe, B., Le Conte, Y., Billion, A., Masson, C., 1994. The kairomonal esters attractive to the *Varroa jacobsoni* mite in the queen brood. Apidologie 25, 314–321. https://doi.org/10.1051/apido:19940306

Trouiller, J., Arnold, G., Chappe, B., Le Conte, Y., Masson, C., 1992. Semiochemical basis of infestation of honey bee brood by *Varroa jacobsoni*. J. Chem. Ecol. 18, 2041–2053. https://doi.org/10.1007/BF00981926

Trouiller, J., Milani, N., 1999. Stimulation of *Varroa jacobsoni Oud.* oviposition with semiochemicals from honeybee brood. Apidologie 30, 3–12. https://doi.org/10.1051/apido:19990101

Ugolev, A., 1979. Evoliutsiia pishchevareniia i nekotorye printsipy évoliutsii funktsiĭ [Evolution of digestion and several principles of the evolution of functions]. Zh Evol Biokhim Fiziol 15, 239–248.

Ullmann, A.J., Lima, C.M.R., Guerrero, F.D., Piesman, J., Black, W.C., 2005. Genome size and organization in the blacklegged tick, Ixodes scapularis and the Southern cattle tick, Boophilus microplus. Insect Mol Biol 14, 217–222. https://doi.org/10.1111/j.1365-2583.2005.00551.x

Vidal-Naquet, N., Vallat, B., Lewbart, G., 2015. Honeybee veterinary medicine: *Apis mellifera L.*, First edition. ed. 5M Publishing, Sheffield, United Kingdom.

Wallberg, A., Bunikis, I., Pettersson, O.V., Mosbech, M.-B., Childers, A.K., Evans, J.D., Mikheyev, A.S., Robertson, H.M., Robinson, G.E., Webster, M.T., 2019. A hybrid de novo genome assembly of the honeybee, *Apis mellifera*, with chromosome-length scaffolds. BMC Genomics 20, 275. https://doi.org/10.1186/s12864-019-5642-0

Wegener, J., Ruhnke, H., Scheller, K., Mispagel, S., Knollmann, U., Kamp, G., Bienefeld, K., 2016. Pathogenesis of varroosis at the level of the honey bee (*Apis mellifera*) colony. J. Insect Physiol. 91–92, 1–9. https://doi.org/10.1016/j.jinsphys.2016.06.004

Wilfert, L., Long, G., Leggett, H.C., Schmid-Hempel, P., Butlin, R., Martin, S.J.M., Boots, M., 2016. Deformed wing virus is a recent global epidemic in honeybees driven by varroa mites. Science 351, 594–597. https://doi.org/10.1126/science.aac9976

Winston, M.L., 1991. The biology of the honey bee, 1. Harvard Univ. Press paperback ed. ed. Harvard Univ. Press, Cambridge, Mass.

Xie, X., Huang, Z.Y., Zeng, Z., 2016. Why do varroa mites prefer nurse bees? Sci. Rep. 6, 28228. https://doi.org/10.1038/srep28228

Yang, X., Cox-Foster, D.L., 2005. Impact of an ectoparasite on the immunity and pathology of an invertebrate: Evidence for host immunosuppression and viral amplification. P. Natl. A. Sci. USA 102, 7470–7475. https://doi.org/10.1073/pnas.0501860102

Zaobidna, E.A., Żółtowska, K., Łopieńska-Biernat, E., 2017. *Varroa destructor* induces changes in the expression of immunity-related genes during the development of *Apis mellifera* worker and drone broods. Acta parasitol. 62. https://doi.org/10.1515/ap-2017-0094

Zavarsin, A.A., 1985. Bases of Comparative Histology. Leningrad University.

Zhang, Y., Han, R., 2018. A Saliva Protein of Varroa Mites Contributes to the Toxicity toward *Apis cerana* and the DWV Elevation in *A. mellifera*. Sci. Rep. 8, 3387. https://doi.org/10.1038/s41598-018-21736-9

Ziegelmann, B., Lindenmayer, A., Steidle, J., Rosenkranz, P., 2013a. The mating behavior of *Varroa destructor* is triggered by a female sex pheromone: Part 1: Preference behavior of male mites in a laboratory bioassay. Apidologie 44, 314–323. https://doi.org/10.1007/s13592-012-0182-5

Ziegelmann, B., Tolasch, T., Steidle, J.L.M., Rosenkranz, P., 2013b. The mating behavior of Varroa destructor is triggered by a female sex pheromone. Part 2: Identification and dose-dependent effects of components of the varroa sex pheromone. Apidologie 44, 481–490. https://doi.org/10.1007/s13592-013-0198-5