

# Chapter 16

## Asian Honeybee Mites

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### 16.1 Introduction

In honeybees, brood parasitism by parasitic mites (Acari) has evolved in every lineage except *A. mellifera* (Eickwort 1994). Despite the fact that all parasitic mites of honeybees are native to Asia, except for one tracheal mite species, we rarely encounter cases where these mites cause serious damage to their native hosts (Boot et al. 1997; Oldroyd 1999). Natural selection for benign host–parasite interactions might play a role in these relationships to allow co-existence between the bees and the mites (Fries and Camazine 2001; cf. Chap. 15). However, the more domesticated *A. mellifera* is not as fortunate as its relatives. As in many cases with horizontal transmission of a parasite to a new host, the host is ill-equipped behaviourally and physiologically to defend itself and may succumb to the novel invader (Lipsitch et al. 1995a, b). Thus, *A. mellifera* falls victim to these mites of Asian origin, which frequently results in the disintegration of colonies.

In Asia, two families of parasitic mesostigmatid mites are represented: Varroidae and Laelapidae. The tracheal mite, *Acarapis woodi*, in another family of parasitic mites from the order Prostigmata, is native to Europe and is considered to be an introduced parasitic species of Asian honeybees. Since the end of World War II, westerners introduced large numbers of *A. mellifera* colonies into Asia for commercial purposes (Crane 1988). These events provided the opportunities for the mites to find new hosts. Most of the time, cross-infections of the mites from their

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native hosts to *A. mellifera* occur as the result of robbing or drifting of foraging bees carrying mites from nearby colonies (Cook 1987; Rath et al. 1991; Fries and Camazine 2001). The moving of mite-infested colonies back to Europe from Asia introduced the parasites that eventually established themselves in apiaries in new locations throughout the world.

The most well-known case of an Asian mite introduction into Europe and the Americas is the notorious *Varroa* mite that switched hosts from its native Asian cavity-nesting species, *Apis cerana* to *Apis mellifera*, which later spread to almost every part of the world (Griffith and Bowman 1981; De Jong et al. 1982; de Guzman et al. 1997, 1998; Sammataro et al. 2000; Zhang 2000). Vast resources and attention have been invested in studies of chemical and biological treatments of *Varroa* on *A. mellifera*, despite numerous reports on the problems of differential resistance of the mites to these treatments (cf. Gerson et al. 1991; Lodesani et al. 1995; Colin et al. 1997; Eischen 1998a, b; Elzen et al. 1998). However, almost a century after the discovery of *Varroa*, we learned that the variations in resistance to *Varroa* stem from the genetic variations in different populations of these superficially similar mites (Anderson and Trueman 2000).

For the past decade, molecular genetics combined with classical taxonomic studies have shed light and revealed a lack of homogeneity in the populations of the parasitic mites of the honeybees in Asia. We are only beginning to learn about these differences and the potential they hold for *A. mellifera*. To understand the biology of Asian bee mites, and hence their control, can best be understood by reference to their native hosts. This chapter attempts to discuss the diversity, not only at the species level, but also the variations in different mite populations on Asian honeybees in the hopes of emphasising the importance of population genetic studies in research on honeybee mite epidemiology. The focus of this chapter is on the parasitic mesostigmatid mites of honeybees, Varroidae and Laelapidae, because they are the major groups of parasitic mites in Asia that also have an impact on beekeeping worldwide.

A list of currently described parasitic mesostigmatid mites and their native hosts in Asia is given in Table 16.1, as well as an identification key to the honeybee mites in Appendix 16.1. To avoid as much duplication as possible of other texts regarding Asian bee mites, we provide only short descriptions of the mites' life history traits for *Varroa* and *Tropilaelaps*. For more details, readers should consult other resources on topics such as life cycles, pathological conditions and treatments (cf. Morse and Nowogrodzki 1990; Sammataro et al. 2000; Webster and Delaplane 2001). In addition, the current situation on the tracheal mites in *A. cerana* in Asia is briefly discussed in Sect. 16.5 along with a section on honeybee non-parasitic mites in Sect. 16.6.

## 16.2 *Varroa* Mites

One of the prominent parasitic mites that have a long history with beekeepers around the world is the genus *Varroa* (Family Varroidae). The type species of the genus was

**Table 16.1** Mesostigmatid species of parasitic honeybee mites, their native hosts and geographic distributions in Asia. Data presented here were compiled from references cited in the text

Mite species	Native hosts	Geographical distributions
<i>Family Varroidae</i>		
<i>Genus Varroa</i> Oudemans (1904)		
<i>V. destructor</i> Anderson and Trueman (2000)	Mainland <i>A. cerana</i> <sup>a</sup>	India, Pakistan, Nepal, China, Japan, Korea, Taiwan, northern Thailand, Vietnam
<i>V. jacobsoni</i> Oudemans (1904)	Sundaland <i>A. cerana</i> <sup>a</sup>	Central and southern Thailand, Malaysia, Indonesia, Palawan Island
<i>V. underwoodi</i> Delfinado-Baker and Aggarwal (1987a)	<i>A. nigrocincta</i>	Sulawesi Island
	<i>A. cerana</i>	Presumably in <i>A. cerana</i> range except for China, Vietnam, Philippine Islands
<i>V. rindereri</i> de Guzman and Delfinado-Baker (1996)	<i>A. nigrocincta</i> <sup>b</sup>	Sulawesi Island
	<i>A. nuluensis</i> <sup>b</sup>	Mt. Kinabalu, Borneo
	<i>A. koschevnikovi</i>	Malaysia, Indonesia except islands beyond east of the Wallace line
<i>Genus Euvarroa</i> Delfinado and Baker (1974)		
<i>E. sinhai</i> Delfinado and Baker (1974)	<i>A. florea</i>	The Middle East, Pakistan, India, Nepal, Burma, Indochina, Malay Peninsula
<i>E. wonsirii</i> Lekprayoon and Tangkanasing (1991)	<i>A. andreniformis</i>	Burma, Indochina, Malaysia, Indonesia except islands beyond east of the Wallace line, Palawan Island
<i>Family Laelapidae</i>		
<i>Genus Tropilaelaps</i> Delfinado and Baker (1961)		
<i>T. mercedesae</i> Anderson and Morgan (2007)	<i>A. dorsata</i>	India, Nepal, Burma, south China, Indochina, Malaysia, Indonesia except Sulawesi, Palawan Island
<i>T. clareae</i> Delfinado and Baker (1961)	<i>A. breviligula</i>	Philippines except Palawan Island
	<i>A. dorsata binghami</i>	Sulawesi Island
<i>T. koenigerum</i> Delfinado-Baker and Baker (1982)	<i>A. laboriosa</i>	Nepal
	<i>A. dorsata</i>	India, Thailand, Borneo
<i>T. thaii</i> Anderson and Morgan (2007)	<i>A. laboriosa</i>	Nepal
	<i>A. laboriosa</i>	North Vietnam

<sup>a</sup>*A. cerana* populations in Asia can be categorised as belonging to four major mitochondrial lineages (Smith and Hagen 1996; Smith et al. 2000). Two of the four of these lineages have wide distributions. The so-called “Mainland” *A. cerana* is distributed throughout the India–Pakistan subcontinent, China, Japan, Laos, Cambodia, Vietnam, north and central Thailand. The “Sundaland” population occupies southern Thailand, Malaysia and Indonesia. The other two lineages occur in the Philippines

<sup>b</sup>The records of *V. underwoodi* on *A. nigrocincta* and *A. nuluensis* have never been confirmed. However, the probability of finding *V. underwoodi* on these bees is high (Oldroyd and Wongsiri 2006)

described early in the twentieth century and named *V. jacobsoni* Oudemans 1904, from a colony of *A. cerana* in Java, Indonesia. *Varroa* mites later spread into *A. mellifera* colonies that were introduced into Asia and have since infected many commercial bee colonies around the world due to transcontinental shipments of bee colonies (de Guzman et al. 1997, 1998). *Varroa* has now spread into most parts of the world except for Australia and the Antarctica (Sammataro et al. 2000). A decade ago, New Zealand and Hawaii were considered to be *Varroa*-free zones; however, recent reports have shown that the mites have already become established in those areas (Zhang 2000; HDOA 2010).

*Varroa* mites are generally elliptical and flattened dorso-ventrally, which provides the mites with the ability to attach themselves inconspicuously to sclerites of bees or to hide between areas where it is difficult for the bees to groom such as the propodeum (Yoder et al. 1999). The colour of *Varroa* ranges from reddish-brown to bright red. In an *A. cerana* colony, *Varroa* can reproduce only in the drone brood cells (Peng et al. 1987; Büchler et al. 1992; Fries et al. 1996; Boot et al. 1997; Rath 1999) because the bees can detect, groom and remove the mites from worker bees and worker brood cells. This bee behaviour reflects a co-adaptation between the host and parasite during their evolutionary history (Oldroyd 1999; Rath 1999; Sasagawa et al. 1999).

All species of the genus *Varroa* are native to Asia. Current knowledge on *Varroa* taxonomy recognises four valid species: *V. jacobsoni* Oudemans, *V. destructor* Anderson and Trueman, *V. underwoodi* (Delfinado-Baker and Aggarwal 1987a) and *V. rindereri* (de Guzman and Delfinado-Baker 1996). However, at least one population in the Philippine Islands has a distinct genetic composition different from others in mainland Asia and Indonesia that may also be valid as a separate species (Anderson and Trueman 2000; Anderson 2004). Only *V. destructor* is reported to colonise and wreak havoc on *A. mellifera* (Anderson and Trueman 2000; Warrit et al. 2006; Navajas et al. 2010). *A. cerana* is the primary host to at least three species of *Varroa* in Asia, except for *V. rindereri*. As to current knowledge, we know that *A. koschevnikovi* is parasitised only with *V. rindereri* (de Guzman and Delfinado-Baker 1996). A congeneric of *A. cerana* in Sulawesi, *A. nigrocincta*, is reported to harbour *V. jacobsoni* (Anderson and Trueman 2000), while there is speculation that *V. underwoodi* may infest this bee, and also *A. nuluensis* on Mt. Kinabalu, Malaysia (Otis and Kralj 2001).

*V. jacobsoni* was once believed to have as wide a distribution as *A. cerana* ranging throughout Asia; however, before 2000, there were numerous reports on pathological and genetic variations of *V. jacobsoni* in both *A. cerana* and *A. mellifera* worldwide (Moritz and Haenel 1984; Camazine 1986; Delfinado-Baker 1988; Delfinado-Baker and Houck 1989; Ritter et al. 1990; Moretto et al. 1991; Anderson 1994; Eguaras et al. 1995; Kraus and Hunt 1995; Anderson and Sukarsih 1996; De Jong and Soares 1997; de Guzman et al. 1997, 1998; Anderson and Fuchs 1998). Subsequently, Anderson and Trueman (2000) published a breakthrough paper that revealed that *V. jacobsoni* is in fact a complex of at least two species – *V. jacobsoni* sensu stricto (s. str.) and *V. destructor*. This finding was based on genetic variations of the cytochrome *c* oxidase I (COI) gene and the results of

reproductive isolation experiments of both mites on *A. cerana* and *A. mellifera*. The study revealed that *V. destructor* is a native parasite of *A. cerana* in mainland Asia.

The natural distribution of *V. destructor* ends in northern Thailand (Anderson and Trueman 2000; Warrit et al. 2006), while further down the Malay Peninsula and the Indonesia archipelago, the mite that reproduces in native *A. cerana* is *V. jacobsoni*. This finding also suggested that the mite species in Asia might have co-evolved with certain *A. cerana* mitochondrial DNA lineages (Anderson and Trueman 2000; Warrit et al. 2006). Only populations of *V. destructor* from Korea and Japan (designated by Anderson and Trueman (2000) as “K” and “J” haplotypes) are known to reproduce successfully in *A. mellifera*. The “K” haplotype was reported to be far more virulent than the “J” counterpart (de Guzman et al. 1997; de Guzman and Rinderer 1999; Anderson and Trueman 2000; Garrido et al. 2003). Navajas et al. (2010) suggested that the unique genetic make-up of Japanese and Korean *V. destructor* may be a factor facilitating their colonising of *A. mellifera* and might have stemmed from a genetic “bottleneck” event in the *Varroa* population in mainland Asia. They also added that the “K” and “J” haplotypes have variants that are well established in *A. mellifera* colonies in China, Taiwan, Vietnam and Thailand that have never been reported in *A. mellifera* in Europe and the Americas and might pose a new threat to apiculture worldwide.

Little is known about the basic biology of the more obscure *V. underwoodi* and *V. rindereri*. It is widely understood that *V. underwoodi* can be found with *A. cerana* throughout its range and sometimes living sympatrically with *V. destructor* or *V. jacobsoni* depending upon the locality of *A. cerana* (Oldroyd and Wongsiri 2006). With the distribution of *A. koschevnikovi* in the Malay Peninsula and the Indonesian archipelago, one can assume that *V. rindereri* is spread along with this bee in the region, except for the islands east of the Wallace line (Otis 1996).

### 16.2.1 Life Cycle of Varroa

The life cycle of *V. destructor* on *A. mellifera* is well studied and can be related to an understanding of this mite on *A. cerana* (cf. De Jong 1997; Donzé and Guerin 1994, 1997; Sammataro et al. 2000; Oldroyd and Wongsiri 2006). *Varroa*'s life cycle consists of two phases: phoretic and parasitic (Oldroyd and Wongsiri 2006). In the parasitic phase, the gravid adult female mite enters the prepupal brood cell 1 or 2 days before cell-capping by the nurse bees. The mite conceals itself, submerged in the liquid brood food until the cell is capped. The peritreme structure of the mite is used like a snorkel to help the mite breathe under the liquid food (Donzé and Guerin 1997). After the cell is capped and the prepupa is formed, the mite starts feeding on the bee haemolymph. About 60 h after the cell is capped, the mother mite produces her first egg, which develops into a male. All of the subsequent eggs (usually 3 or 4), which are laid at 30 h intervals, are destined to become females.

Immature mites (nymphs) feed on the haemolymph of the prepupa at the site where the mother mite usually feeds (Donzé and Guerin 1994). Male mites require slightly less time than females (5–6 and 6–7 days, respectively) to develop into adults. Mating occurs between siblings of the same brood. The life cycle of the male mite is short compared to the females. The male mite dies in the brood cell after the last female sister is fertilised and before the cell is uncapped. After the brood cell is uncapped, the female mite begins its phoretic phase. However, if the bee colony is not in its reproductive cycle, the mite will seek for a newly emerged adult bee as its short-term host. The mite stays on the bee's metasoma, or the area behind the head, and feeds continuously most of the time. The phoretic phase of the mite is shortened if the infested colony is full of new eggs and larvae that have recently been laid by the queen bee. Le Conte et al. (1989) suggested that, because of the higher levels of fatty acid esters produced by drone larvae, the female mites prefer invading drones more than worker cells.

### 16.2.2 Impact of *Varroa* on *A. cerana*

Tewarson et al. (1992) provided the first insights into the life cycle of *V. destructor* on an *A. cerana* colony in India. The mite population growth rate in an *A. cerana* colony is significantly slower than in *A. mellifera* (Boot et al. 1997). Most of the time, the mites infest the drone brood, and it is rare to observe the mites invading worker cells. Thus, the damage to the colony of the mite's native host is not as severe as we observe in *A. mellifera*, where mites are found reproducing successfully in worker cells. The defensive behaviours of *A. cerana* against the mites can explain the low growth rate of the mite population. The worker bees can groom each other to remove mites, a behaviour that is lacking in *A. mellifera* (Peng et al. 1987; Büchler et al. 1992; Fries et al. 1996; Rath 1999), and can detect capped cells that are infested with mites, which are later uncapped and the mites removed or both the bee prepupae and the mites are buried together (Büchler et al. 1992; Fries et al. 1996; Boot et al. 1997; Boecking and Spivak 1999).

### 16.3 *Eugarroa* Mites

A sister genus to *Varroa*, *Eugarroa* is a genus of parasitic mites that has been reported to colonise the Asian dwarf honeybees. *Eugarroa sinhai* Delfinado and Baker 1974 (the type species of the genus *Eugarroa*; Varroidae) was originally described from its host, *A. florea*, in India (Delfinado and Baker 1974). It can be

found throughout the distribution area of *A. florea* in Asia from the Middle East to the Malay Peninsula (Otis 1996). A second species, *E. wongsirii* Lekprayoon and Tangkanasing 1991, was later discovered from *A. andreniformis* in Thailand (Lekprayoon and Tangkanasing 1991) and has a distribution ranging from south China to Palawan Island of the Philippines (Otis 1996). The two mite species share an overlap of distribution in South East Asia. Both *Eugarroa* mites superficially resemble one another but can be easily distinguished from *Varroa* by their more or less similar body lengths and widths. Thus, *Eugarroa* is more triangularly shaped than *Varroa* which is more oval. *E. wongsirii* can be distinguished morphologically from *E. sinhai* by the broader triangular body and anal plate bearing 47–54 long lanceolate setae on a wider posterior end (where *E. sinhai* has 39–40 setae) (Lekprayoon and Tangkanasing 1991, 1993; Morin and Otis 1993).

The biology of *Eugarroa* is similar to that of *Varroa*. The mites are only capable of reproducing in the drone brood cells of their hosts and disperse to other colonies via both drones and worker bees (Akranakul and Burgett 1976; Mossadegh and Birjandi 1986; Aggarwal 1988; Kapil and Aggarwal 1989; Morin and Otis 1993). As with *Varroa*, *Eugarroa* causes little damage to their endemic host colonies. This may be because of the intensive grooming behaviour of the worker bees and the seasonal presence of drone brood cells that reduces the population of the mite to a minimal. However, evidence suggests that *E. sinhai* can reproduce in worker brood cells of *A. mellifera* (Mossadegh 1990). Also, Koeniger et al. (1993) reported that *E. sinhai* can survive in adult workers of *A. mellifera* and *A. cerana* in Thailand.

However, the impact of the *Eugarroa* infestation in apiary colonies of *A. mellifera* or *A. cerana* has not been determined. There are suggestions about why *Eugarroa* does not colonise *A. mellifera* colonies successfully. Sihag (1988) reported that competition among *Varroa*, *Eugarroa* and *Tropilaelaps* in the same *A. mellifera* colonies in Haryana, India, has an effect that reduces the population of *Eugarroa* in the colonies dramatically. The construction of queen cells may also reduce the population of the mites as well (Aggarwal and Kapil 1988). Thus far, reports on the occurrences of *E. wongsirii* outside of its native host are scarce, coming only from debris of *A. dorsata* colonies in Sabah, Malaysia, which were found to have *E. wongsirii* along with *Tropilaelaps* and *Varroa* (Koeniger et al. 2002).

Recent molecular and biogeographical studies of *A. florea* and *A. andreniformis* suggest that populations of the dwarf honeybees in Asia may not be as homogenous as previously thought (cf. Chaps. 2 and 4). This finding raises questions about the genetic homogeneity of the *Eugarroa* associated with these bees. Morin and Otis (1993) found some morphological differences in *E. sinhai* (e.g. number of setae on metatarsus I–IV) collected from India/Sri Lanka compared to specimens collected in Thailand. There is a great possibility of finding genetic and morphological variations among populations of both *E. sinhai* and *E. wongsirii* from different locations in the distribution areas of their hosts in Asia. This line of study will further our knowledge of *Eugarroa* diversity in Asia.

## 16.4 *Tropilaelaps* Mites

Twenty-five years ago, Burgett and Akwatanakul (1985) predicted that in the near future *Tropilaelaps clareae* would play a major role in the destruction of commercial honeybee colonies far greater than that caused by *A. woodi* and *Varroa* mites. Since then, *T. clareae* has been reported in countries beyond its primary host distribution (Kumar et al. 1993; Matheson 1996; Sammataro et al. 2000; Otis and Kralj 2001), but still no account of its presence in Europe and the Americas has been reported. Because of the absence of *T. clareae* in western countries and the great interest in *Varroa* mites, the importance of *Tropilaelaps* mites has not been sufficiently recognised by bee researchers. Nevertheless, after the introduction of *A. mellifera* into Asia, cross-infection of *T. clareae* from its original Asian honeybee hosts occurred resulting in a significant loss to commercial honey production (De Jong et al. 1982; Burgett et al. 1983; Bailey and Ball 1991). Burgett and Akwatanakul were not far off their prediction, particularly when one considers Asian apicultural industries.

Recently, many western bee researchers have expressed concerns about the cross-infestation of *Tropilaelaps* from its original host to *A. mellifera* in Europe and the Americas (Matheson 1996, 1997; Waite 2003; Sammataro 2004; Baker et al. 2005). The trepidation of *Tropilaelaps* was soon recognised by the Office International des Epizooties (OIE) in Paris who declared *Tropilaelaps* to be emerging parasite for honeybees worldwide in 2004. The relatively rapid developmental time of *Tropilaelaps* when it is established and starts reproducing in the brood cells of the host concern many beekeepers and researchers. When a colony is infected with *Tropilaelaps*, the mite populations can build up quickly and lead to the sudden collapse of colonies (Sammataro et al. 2000). Moreover, albeit the mites cannot feed and damage adult bees (because the mouthparts of *Tropilaelaps* are only suitable for feeding on soft tissue – Griffiths 1988), they are phoretic and can hitch-hike with adult bees foraging outside the hives, which can distribute the mites to other bees and colonies.

In Asia, reports on colony losses of *A. mellifera* due to *Tropilaelaps* infestations, specifically *T. clareae*, are not uncommon (Laigo and Morse 1968; Burgett et al. 1983, 1990; Tangkanasing et al. 1988; Otis and Kralj 2001). Beekeepers describe deformed adult bees with shortened abdomens, missing legs, and wrinkled wings as common pathological symptoms for colonies parasitised by *T. clareae*. Other symptoms include brood malformation and bees which crawl rather than fly (Sammataro 2004). Two recent separate reports considered the possibility of *Tropilaelaps* as a potential vector for the Deformed Wing Virus (Dainat et al. 2009; Forsgren et al. 2009), which is suggested as a culprit for the maladies observed in adult bees from infected colonies.

There are many review articles and books available (cf. De Jong et al. 1982; Morse and Nowogrodzki 1990; Sammataro et al. 2000; Webster and Delaplane 2001) that deal with much of the life history and host–parasite relationships between *Tropilaelaps* and its hosts. Because there have been some new and exciting

discoveries regarding the diversity of *Tropilaelaps* species and their host specificities in recent years, we focus this part of the chapter on the morphological and genetic variations of *Tropilaelaps* and their associations with their honeybee hosts to clarify and give the reader a better understanding of the identity of this emerging threat to honeybees. A brief description of the *Tropilaelaps* life cycle is given in Sect. 16.4.2, but readers should consult Sammataro et al. (2000) and Oldroyd and Wongsiri (2006) for more comprehensive details.

### 16.4.1 Identity of *Tropilaelaps clareae* and its Host Ranges

*Tropilaelaps* mites (Family Laelapidae) are obligate ectoparasites that feed on the haemolymph of larval honeybees. Both sexes of the mites are elongated and their bodies are covered with numerous, short, spine-like setae. *Tropilaelaps* are reddish-brown in colour, though the males are less sclerotised. Compared to *Varroa* mites, *Tropilaelaps* are smaller, flatter and more oval-shaped than round. The type species of the genus *Tropilaelaps* is *T. clareae* Delfinado and Baker 1961. *T. clareae* was first described from *A. mellifera* colonies in the Philippines and from rats living near bee colonies (Delfinado and Baker 1961). Its primary host species was later revealed to be *A. dorsata* from the Philippines (Bharadwaj 1968; Laigo and Morse 1968). Although current molecular evidence suggests that “*A. dorsata*”, host of *T. clareae* in the Philippines, is a distinct but closely related species, *A. breviligula* (Lo et al. 2010; cf. Chap. 1). *T. clareae* has been reported throughout most of the *A. dorsata* distribution in Asia (Matheson 1996; Anderson and Morgan 2007).

In 1982, Delfinado-Baker and Baker described a second *Tropilaelaps* species, *T. koenigerum*, from *A. dorsata* colonies in Sri Lanka. Later on, *T. koenigerum* was reported in colonies of *A. dorsata* in India, Thailand and Borneo (Delfinado-Baker and Baker 1982; Koeniger et al. 2002; Tangjingjai et al. 2003) and in colonies of *A. laboriosa* in Nepal (Delfinado-Baker et al. 1985), which lives sympatrically with *T. clareae* in the same colonies. There are also reports on the occurrence of *T. clareae* on *A. cerana* and *A. florea* in Asia, though the impact on these honeybees is not severe (Delfinado-Baker 1982; Aggarwal 1988; Sihag 1988; Delfinado-Baker et al. 1989; Abrol and Putatunda 1995; Woyke 2005; Anderson and Morgan 2007).

Before 2007, it was assumed that the mite that had become established in *A. mellifera* colonies in South Asia and the Oriental region and spread into Iran, Afghanistan, Kenya, South Korea and the Western Pacific Island of New Guinea was *T. clareae* (Burgett et al. 1983; Woyke 1984; Matheson 1996; Delfinado-Baker and Aggarwal 1987b; Kumar et al. 1993; Anderson 1994; Sammataro et al. 2000; Otis and Kralj 2001). However, Anderson and Morgan (2007), by examining the genetic variations, morphological variations and host associations of *Tropilaelaps* mites and their endemic hosts in Asia, showed that the once well-recognised “*T. clareae*” that infected *A. dorsata* and *A. mellifera* colonies throughout Asia and beyond was in fact comprised of two distinct species – *T. mercedesae*, which colonised *A. dorsata* and the introduced *A. mellifera*

inhabiting mainland Asia and Indonesia (excluding Sulawesi Island), and *T. clareae* (s. str.), which parasitised *A. breviligula*, *A. dorsata binghami* (Sulawesi Island) and *A. mellifera* on the Philippine Islands. Also stemming from this work is the recognition of another *Tropilaelaps* species, *T. thaii*, collected from *A. laboriosa* in the mountainous eastern region of the Himalayas in northern Vietnam.

Adult females of *T. mercedesae* can be distinguished morphologically from *T. clareae* (s. str.) by their sheer size (a longer and wider dorsal plate) and variations in the shape of the apex of the epigynial plate, which varies from bluntly to sharply pointed, whereas in *T. clareae* s. str. it is always bluntly pointed. Adult males of *T. mercedesae* are also significantly larger than males of *T. clareae* (s. str.); however, comparative morphological studies of the nymphal stages of the two mites have not been carried out. In addition to the morphological characters used in distinguishing the four *Tropilaelaps* species, the amplified fragments of the mitochondrial DNA (mtDNA) of cytochrome *c* oxidase subunit I (COI) and a region between nuclear internal transcribed spacers and rDNA (ITS1-5.8S-ITS2) gene sequences of *T. mercedesae*, *T. clareae* s. str., *T. koenigerum* and *T. thaii* are proved to be useful as molecular markers for differentiating the species utilising the RFLP technique (Anderson and Morgan 2007).

Adult females of *T. koenigerum* are relatively more easily distinguishable morphologically from *T. mercedesae* and *T. clareae* (s. str.) by the presence of a pear-shaped anal plate, whereas in the latter two mites the anal plates are more rectangular (Delfinado-Baker and Baker 1982). In adult males of *T. mercedesae* and *T. clareae* (s. str.), the moveable digit of the chelicerae, which acts as a spermatodactyl organ appears a long “corkscrew-like” coiled structure, whereas in *T. koenigerum* the spermatodactyl is shorter, not coiled and has a “pig-tail-like” loop at the apex (Delfinado-Baker and Baker 1982). Specific molecular diagnostic markers have also been developed using ITS sequence and RAPD primers to assist in taxonomic identification of *T. mercedesae* (described under *T. clareae*) and *T. koenigerum* in Thailand (Tangjingjai et al. 2003). Adult females of *T. thaii* possess somewhat pear-shaped or bell-shaped anal plates, more or less similar to *T. koenigerum*, but can be distinguished from other *Tropilaelaps* species by the absence of a subapical tooth on the moveable chela, and its unique RFLP profile compared to other *Tropilaelaps* (Anderson and Morgan 2007).

The taxonomy of *Tropilaelaps*' primary host, *A. dorsata*, is in question as to whether it is comprised of only a single species. Historically, Ruttner (1988) recognised four subspecies of *A. dorsata* based on a morphometric study – *A. d. dorsata*, *A. d. laboriosa*, *A. d. breviligula* and *A. d. binghami*, which are geographically isolated, except for the sympatry of *A. d. dorsata* and *A. d. laboriosa* in the Himalayan areas. It is now suggested by a number of authors that the once widely recognised single species is a complex species based on current DNA evidence and differential mating times (Arias and Sheppard 2005; Raffiudin and Crozier 2007; Lo et al. 2010; cf. Chap. 1). As in the case of *Varroa* mites and populations of *A. cerana* in Asia, the biogeography of *Tropilaelaps* spp. and their hosts reflect a pattern of coevolution between the two groups – distributions of the giant honeybee species complex are

broadly congruent with the distributions of the *Tropilaelaps* species. *A. dorsata* s. str., which is distributed in mainland Asia and Indonesia, is parasitised by *T. clareae* and sometimes with *T. koenigerum* living sympatrically in the same colonies, whereas *A. breviligula* and *A. d. binghami* harbour *T. clareae* in the Philippines and Sulawesi. One colony of *A. laboriosa* in North Vietnam was found to be infected by its unique mite, *T. thaii*. However, *T. mercedesae* was also found in the same colony where *T. thaii* was present. This might be a result of a cross-infection of *T. mercedesae* from *A. dorsata* s. str. cohabitating with *A. laboriosa* in the Himalayan trail.

The notion of the congruence of the patterns of distributions of the *A. dorsata* species complex and their *Tropilaelaps* mites provides evidence for co-evolution and may prove useful in future experimental studies on the host specificities and level of pathogenicity of different *Tropilaelaps* species on other *Apis*. This would be particularly so in the cavity-nesting species, as has been demonstrated with *Varroa* in *A. cerana* and *A. mellifera* (Anderson 1994; Anderson and Sukarsih 1996), which may lead to the understanding of *Tropilaelaps* biology that relates to their host immune systems and/or defence mechanisms.

#### 16.4.2 *Tropilaelaps* Life Cycle

The life cycle of *Tropilaelaps* is similar to that of *Varroa*, except that *Tropilaelaps* can invade both worker and drone brood cells (Kapil and Aggarwal 1987, 1989), which can increase the mite population in a bee colony drastically compared to *Varroa* (Sammataro et al. 2000). The following description of the *Tropilaelaps* life cycle is summarised from previous literature (e.g. Sammataro et al. 2000; Oldroyd and Wongsiri 2006) under circumstances where *T. clareae* (according to D. Anderson in Oldroyd and Wongsiri 2006) infected an *A. mellifera* colony. Studies of the life cycles of different *Tropilaelaps* species on their native hosts are yet to be investigated.

In an established bee colony, a gravid female mite enters a brood cell before capping, feeds on larval haemolymph for about 2 days or less and then lays her first egg. Three or four eggs can be found in a brood cell per reproductive cycle. Normally, the first egg will develop into an adult male. The developmental time from egg to adult takes about 6–7 days. The mother mite and her offspring will emerge from the brood with the adult bee and can enter other brood cells directly (for the mother mite) or mate with the opposite sex in the bee colony (for the virgin offspring). In a period when the host queen bee does not lay eggs, adult *Tropilaelaps* will adopt a phoretic stage and stay on the bees' sclerites until there are brood cells to parasitise, though no more than 3 days (Koeniger and Muzaffar 1988; Rinderer et al. 1994; Wilde 2000). This might explain the mechanism by which *A. dorsata* and its related giant honeybee species have a reduced load of *Tropilaelaps* through seasonal migration (Kavinseksan et al. 2003).

## 16.5 Tracheal Mites of the Genus *Acarapis*

*Acarapis woodi* (Prostigmata; Tarsonemidae) invades the tracheal system of adult honeybees and feeds on the haemolymph by piercing the tracheal wall (Hirschfelder and Sachs 1952). In North America, colonies that are infested with *A. woodi* suffer symptoms such as brood decline, decreases in worker bees and low honey production (Royce and Rossignal 1989; Morse and Nowogrodzki 1990; Bailey and Ball 1991; Mussen 2001). In serious cases, an *A. woodi* population can overwhelm and kill the entire colony. In *A. mellifera*, the entire life cycle of *A. woodi* from egg to adult can be completed in about 2 weeks with males maturing a couple of days earlier than females, which contributes to the explosion of *A. woodi* population in a colony in a short period of time (Pettis and Wilson 1996; Wilson et al. 1997). All life stages of *A. woodi* are spent living inside the tracheal system of the bees, except for the adult females that sometimes venture out to find a new host (Sammataro and Needham 1996). Most dispersing female mites are attracted to the prothoracic spiracle of the adult bees and will eventually reside and lay her eggs in the trachea (Hirschfelder and Sachs 1952; Phelan et al. 1991). Adult female mites can survive outside of the host for only a few hours (Hirschfelder and Sachs 1952).

Since the discovery of *A. woodi* in the Isle of Wight, England, during the early twentieth century (Clark 1985; Sammataro 1995), there have been few reports on the occurrence of *A. woodi* in Asian honeybees. Until now, there are reports from the subcontinent of India–Pakistan where *A. woodi* was found infesting *A. cerana* and *A. dorsata* (Dhaliwal and Sharma 1974; Adlakha 1976; Delfinado-Baker et al. 1989; Abrol 2000). Accounts on the demise of managed *A. mellifera* colonies in Asia as a result of *A. woodi* have never been reported. We hypothesise two possible explanations, based on previous studies of the tracheal mite's natural history and biology, for the absence or the lack of reports on *A. woodi* in most parts of Asia. First, *A. woodi* has already resided in *A. mellifera* colonies in apiaries throughout Asia and might possibly have cross-infected other Asian honeybee species already, particularly the congeneric cavity-nesting *A. mellifera* and *A. cerana*.

However, because of the small size of the mites which cannot be observed with the naked eye, beekeepers cannot detect the mites at the initial stage of a mite infestation. When the colony progressively deteriorates, beekeepers notice the stress signs of the colonies such as declining populations and weak worker bees with deformed wings and metasoma (Sammataro 1995). These might be attributed to other causes that are more visibly conspicuous such as endemic *Varroa* or *Tropilaelaps* mites. Methods for the diagnosis of tracheal mites are also tedious, time-consuming and require experience to perform (Ragsdale and Furgala 1987; Fichter 1988; Ragsdale and Kjer 1989; Shimanuki and Knox 1991; Grant et al. 1993). Hence, reports of *A. woodi* in Asia might have been overlooked because the maladies can superficially resemble symptoms that are caused by other agents. This hypothesis is more or less comparable to the explanations for the lack of finding *A. woodi* in Europe before the early twentieth century (Eickwort 1988; Sammataro et al. 2000).

The second hypothesis is that, because *A. woodi* can increase its population size dramatically during the winter in the temperate areas of America and Europe, where most of the worker bees stay close together for a period of time, it causes the most damage (Eischen 1987; Otis and Scott-Dupree 1992; Sammataro et al. 1994). This situation presents a potential problem for the tracheal mite when it parasitises bees that are kept in a tropical climate, since the temperature during the “winter” in the tropics is not cold enough to inhibit the bees from foraging or performing other tasks. The “lack of winter” may be the reason why *A. woodi* is not established and causing difficulties for Asian beekeepers. Though, there is no direct evidence to suggest that seasonal change and ambient temperature have direct or indirect effects on the reproduction ability of the mites in the tropics.

There are other mites congeneric with *A. woodi* that live exclusively externally on the surface of the thorax and wing base of *A. mellifera* and *A. cerana* in Asia (Delfinado-Baker et al. 1989; De Guzman et al. 2001). *A. dorsalis* and *A. externus* are thought to be closely related to *A. woodi*. Thus far, there are no reports on the damage caused by these two mites on honeybee colonies (Bailey and Ball 1991; Sammataro et al. 2000).

## 16.6 Non-Parasitic Mites Associated with Asian Honeybees

Parasitic mites, described in the earlier sections, of this chapter represent only a minor fraction of the diversity of Acari associations with honeybees. Most Acari found in the nests of honeybees usually have a saprophagous lifestyle (Eickwort 1990) and feed on fungus-infected debris in the hives, dead bees and sometimes pollen (kleptophages). Three main orders of non-parasitic mites are commonly found in honeybee colonies: “Astigmata”, Prostigmata and Mesostigmata. Mites of the order “Astigmata”, currently placed in the order Oribatida (Krantz and Walter 2009), are the most abundant in the colonies of honeybees (Eickwort 1990). Two subfamilies of the family Acaridae, particularly Forcelliniinae and Horstiinae, are frequently found (O’Connor 1982, 1988; Delfinado-Baker and Baker 1987). Although primarily a myrmecophilous species, *Forcellinia faini* (Forcelliniinae), can be found on the hive floors of *A. cerana* colonies in Thailand (Fain and Gerson 1990). Among the prostigmatid mites, except for the parasitic tarsonemid mite on honeybee, *A. woodi*, members of this family are fungivorous and occur facultatively in honeybee colonies (Lindquist 1986). Generally, prostigmatid mites associated with social insects are known to have relatively short life-cycles and are commonly phoretic (Lindquist 1986; Eickwort 1990). The fore-tarsal claws of these mites are usually enlarged to hold onto the setae of their hosts. Sumangala and Haq (2002) reported that *Pseudoacarapis indoapis* (Tarsonemidae) is found in *A. cerana* colonies in India feeding on fungal debris and stored pollen.

Mites in the order Mesostigmata are primarily free-living predators, but many lineages have evolved parasitic lifestyles with other arthropods, e.g. *Varroa* mites (Hunter and Rosario 1988). Many mesostigmatid mites found in honeybees are free-living and feed on other saprophagous mites, insects, fungi and pollen. *Neocyphophlaelaps indica* (Family Ameroseiidae) is a common facultative kleptophage of *A. cerana*, *A. florea* and *A. dorsata* in Asia (Delfinado-Baker et al. 1989; Needham et al. 2001). The primary habitat of *N. indica* is on subtropical and tropical tree flowers where it feeds on pollen; however, during a foraging trip of a worker bee, this mite can “hitch-hike” on the mesosoma or metasoma to be brought back to the colonies, where the mite then feeds on stored pollen (Delfinado-Baker et al. 1989; Haq et al. 2001). Another Ameroseiidae species is also reported to be found associated with *A. cerana*, i.e. genus *Afrocyphophlaelaps* (Delfinado-Baker et al. 1989).

Works on the diversity and life history of the non-parasitic Asian honeybee mites are progressing more slowly than the corresponding parasitic groups. This may result from the non-commercial importance of the non-parasitic mites so that they receive less attention from bee researchers. Further investigations into population diversity of Asian honeybees will undoubtedly result in the discovery of additional unknown non-parasitic mites associated with honeybees in Asia.

## 16.7 Conclusion

As much as we know about the life history and biology of honeybee mites, we still have little information regarding variations in the genetics, behaviour and pathology of mites from different locations. The past decade has provided beekeepers and researchers with a fruitful “glimpse” into the complexity and diversity of the Asian honeybee mites. We are starting to learn about the genetic and reproductive variations of the Asian mites observed in different geographical regions that have impact on beekeeping industries in both western and eastern regions of the world. Future genetic and experimental work focusing on the population level of the mites can be of immense importance to the discovery of new genetic-types of mites and their corresponding levels of pathogenicity on their native host populations and on *A. mellifera*. Besides, studies of the Asian honeybee populations can reveal significant information regarding where to probe for genetically distinct types of mite populations. Microbes, particularly viruses associated with the mites, are also another subject of interest that will expand our knowledge for understanding the interactions among the hosts, parasites and pathogens. Biogeographical studies of the patterns of co-evolution between the honeybee and mite populations could well benefit from including the pathogen perspective to elucidate a clearer understanding of these complex honeybee–mite associations in Asia.

## Appendix

A key to the female parasitic mesostigmatid mites of Asian honeybees (modified from Oldroyd and Wongsiri 2006)

Morphological characters	Mite species
(1) (a) Body elongated (considerably longer than wide)	Genus <i>Tropilaelaps</i> (2)
(b) Body broadly elliptical, as wide or wider than long; small reversed triangular-shaped anal shield	Genus <i>Varroa</i> (5)
(c) Body broadly pear-shaped or triangular, approximately same width and length; anal shield more or less rectangulate, about 1/3–1/4 as long as body length	Genus <i>Euvarroa</i> (8)
(2) (a) Anal plate rectangular	(3)
(b) Anal plate pear-shaped	(4)
(3) (a) Apex of epigynial plate varies, from bluntly pointed to sharply pointed; female body size: length $978.8 \pm 31.5 \mu\text{m}$ and width $542.5 \pm 23.6 \mu\text{m}$ ; male body size: length $920.9 \pm 19.5 \mu\text{m}$ and width $523.2 \pm 19.2 \mu\text{m}$	<i>Tropilaelaps mercedesae</i> <sup>a</sup> (parasite of <i>A. dorsata</i> and <i>A. laboriosa</i> , and <i>A. mellifera</i> on Mainland Asia, Indonesia (except for Sulawesi) and Papua New Guinea)
(b) Apex of the epigynial plate always bluntly pointed; female body size: length $881.9 \pm 24.1 \mu\text{m}$ and width $484.4 \pm 14.5 \mu\text{m}$ ; male body size: length $856.6 \pm 19.2 \mu\text{m}$ and width $500.9 \pm 9.8 \mu\text{m}$	<i>Tropilaelaps clareae</i> <sup>a</sup> (parasite of <i>A. brevilligua</i> and <i>A. dorsata binghami</i> , and <i>A. mellifera</i> on the Philippines and Sulawesi)
(4) (a) Subapical tooth on moveable chela present	<i>Tropilaelaps koenigerum</i> (found primarily parasitising <i>A. dorsata</i> and <i>A. laboriosa</i> )
(b) Subapical tooth on moveable chela absent	<i>Tropilaelaps thaii</i> (parasite of <i>A. laboriosa</i> )
(5) (a) Peritremes long looping up from ventral side, extending beyond the lateral margin and thus sometimes visible from dorsal surface	<i>Varroa rindereri</i> (primarily found parasitising <i>A. koschevnikovi</i> )
(b) Peritremes not extending beyond lateral margin and not visible from dorsal surface	(6)
(6) (a) Setae of the lateral margin long and slender	<i>Varroa underwoodi</i> (primarily found parasitising <i>A. dorsata</i> , <i>A. laboriosa</i> and <i>A. brevilligula</i> )
(b) Setae shorter and stout	(7)
(7) (a) Body size ratio (width to length) 1.2–1.3:1	<i>Varroa jacobsoni</i> <sup>b</sup> (parasitise on Mainland <i>A. cerana</i> and <i>A. mellifera</i> worldwide)
(b) Body size ratio $\geq 1.4:1$	<i>Varroa destructor</i> <sup>b</sup> (parasitise on Sundaland <i>A. cerana</i> , including <i>A. nigrocincta</i> on Sulawesi)

(continued)

Morphological characters	Mite species
(8) (a) Body pear-shaped with 39–40 µm long lanceolate setae on rounded posterior margin	<i>Euvarroa sinhai</i> (primarily found parasitising on <i>A. florea</i> )
(b) Body triangular with 47–54 µm long lanceolate setae on wide posterior margin	<i>Euvarroa wongsirii</i> (primarily found parasitising <i>A. andreniformis</i> )

<sup>a</sup>Measurements of *T. mercedesae* and *T. clareae* body size (length and width of the dorsal plate) are taken from Anderson and Morgan (2007). Readers should not depend on the body size of these mites exclusively to use as diagnostic characters of species. DNA sequencing and/or RFLPs profiles of the mtDNA COI and nuclear ITS1-5.8S-ITS2 gene sequences (Anderson and Morgan 2007) are appropriate markers for differentiating the species

<sup>b</sup>Body size ratio is not a reliable characteristic to differentiate between *V. jacobsoni* and *V. destructor*. Molecular diagnostics – DNA sequencing and/or RFLPs – of the mtDNA COI gene should be used to confirm the identification of the species (Anderson and Trueman 2000; Warrit et al. 2004, 2006)

## References

- Abrol DP (2000) Beekeeping with *Apis cerana* in Jammu and Kashmir: present status and future prospects. *Bee World* 81:149–152
- Abrol DP, Putatunda BN (1995) Discovery of the ectoparasitic mite *Tropilaelaps koenigerum* Delfinado-Baker and Baker (Acari: Laelapidae) on *Apis dorsata* F, *A. mellifera* and *A. cerana* F in Jammu and Kashmir, India. *Curr Sci* 68:10
- Adlakha RL (1976) Acarine disease of adult honey bees in India. *Am Bee J* 116(324):344
- Aggarwal K (1988) Incidence of *Tropilaelaps clareae* on three *Apis* species in Hisar (India). In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE (eds) Africanized honey bees and bee mites. Ellis Horwood, Chichester, pp 396–403
- Aggarwal K, Kapil RP (1988) Observations on the effect of queen cell construction on *Euvarroa sinhai* infestation in drone brood of *Apis florea*. In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE (eds) Africanized honey bees and bee mites. Ellis Horwood, Chichester, pp 404–408
- Akratanakul P, Burgett M (1976) *Euvarroa sinhai* Delfinado and Baker (Acarina: Mesostigmata): a parasitic mite of *Apis florea*. *J Apic Res* 15:11–13
- Anderson DL (1994) Non-reproduction of *Varroa jacobsoni* in *Apis mellifera* colonies in Papua New Guinea and Indonesia. *Apidologie* 25:412–421
- Anderson DL (2004) Implication of the recent findings on parasitic mites for *Apis mellifera* beekeeping in Asia. In: Camaya EN, Cervancia CR (eds) Bees for new Asia. Proceedings of 7th Asian Apiculture Association Conference, Los Banos, pp 19–21
- Anderson DL, Fuchs S (1998) Two genetically distinct populations of *Varroa jacobsoni* with contrasting reproductive abilities on *Apis mellifera*. *J Apic Res* 37:69–78
- Anderson DL, Morgan MJ (2007) Genetic and morphological variation of bee-parasitic *Tropilaelaps* mites (Acari: Laelapidae): new and re-defined species. *Exp Appl Acarol* 43:1–24
- Anderson DL, Sukarsih D (1996) Changed *Varroa jacobsoni* reproduction in *Apis mellifera* colonies in Java. *Apidologie* 27:461–466
- Anderson DL, Trueman JWH (2000) *Varroa jacobsoni* (Acari: Varroidae) is more than one species. *Exp Appl Acarol* 24:165–189
- Arias MC, Sheppard WS (2005) Phylogenetic relationships of honey bees (Hymenoptera: Apinae: Apini) inferred from nuclear and mitochondrial DNA sequence data. *Mol Phylogenet Evol* 37:25–35
- Bailey L, Ball BV (1991) Honey bee pathology, 2nd edn. Academic, San Diego

- Baker RA, Hick A, Chmielewski W (2005) Aspects of the history and biogeography of the bee mites *Tropilaelaps clareae* and *T. koenigerum*. *J Apic Sci* 49:13–19
- Bharadwaj RK (1968) A new record of the mite *Tropilaelaps clareae* from *Apis dorsata* colonies. *Bee World* 49:115
- Boecking O, Spivak M (1999) Behavioral defenses of honey bees against *Varroa jacobsoni* Oud. *Apidologie* 30:141–158
- Boot WJN, Tan NQ, Dien PC, Vanhuan L, Vandung N, Long LT, Beetsma J (1997) Reproductive success of *Varroa jacobsoni* in brood of its original host, *Apis cerana*, in comparison to that of its new host, *A. mellifera* (Hymenoptera: Apidae). *Bull Entomol Res* 87:199–226
- Büchler R, Drescher W, Tornier I (1992) Grooming behaviour of *Apis cerana*, *A. mellifera* and *A. dorsata* and its effect on the parasitic mite *Varroa jacobsoni* and *Tropilaelaps clareae*. *Exp Appl Acarol* 16:313–319
- Burgett M, Akwatanakul P (1985) *Tropilaelaps clareae*, a little known honey bee brood mite. *Am Bee J* 125:112–114
- Burgett M, Akwatanakul P, Morse RA (1983) *Tropilaelaps clareae*: a parasite of honey bees in south-east Asia. *Bee World* 64:25–28
- Burgett M, Rossingol PA, Kitprasert C (1990) A model of dispersion and regulation of brood mite *Tropilaelaps clareae* parasitism in the giant honeybee *Apis dorsata*. *Can J Zool* 68:1423–1427
- Camazine S (1986) Differential reproduction of the mite, *Varroa jacobsoni* (Mesostigmata: Varroidae), on Africanized and European honey bees (Hymenoptera: Apidae). *Ann Entomol Soc Am* 79:801–803
- Clark KJ (1985) Mites (Acari) associated with the honey bee, *Apis mellifera* L. (Hymenoptera: Apidae), with emphasis on British Columbia. Thesis, Simon Fraser University, Burnaby
- Colin ME, Vandame R, Jourdan P, Di Pasquale S (1997) Fluvalinate resistance of *Varroa jacobsoni* (Acari: Varroidae) in Mediterranean apiaries of France. *Apidologie* 28:375–384
- Cook VA (1987) The spread of *Varroa jacobsoni* and *Tropilaelaps clareae*. *Bee World* 68:163–164
- Crane E (1988) Africanized bee, and mites parasitic on bees, in relation to world beekeeping. In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE (eds) Africanized honey bees and bee mites. Ellis Horwood, Chichester, pp 1–9
- Dainat B, Ken T, Berthoud H, Neumann P (2009) The ectoparasitic mite *Tropilaelaps mercedesae* (Acari: Laelapidae) as a vector of honeybee viruses. *Insectes Soc* 56:40–43
- de Guzman LI, Delfinado-Baker M (1996) A new species of *Varroa* (Acari: Varroidae) associated with *Apis koschevnikovi* (Apidae: Hymenoptera) in Borneo. *Int J Acarol* 22:23–27
- de Guzman LI, Rinderer TE (1999) Identification and comparison of *Varroa* species infesting honey bees. *Apidologie* 30:85–95
- de Guzman LI, Rinderer TE, Stelzer JA (1997) DNA evidence of the origin of *Varroa jacobsoni* Oudemans in the Americas. *Biochem Genet* 34:327–335
- de Guzman LI, Rinderer TE, Stelzer JA, Anderson D (1998) Congruence of RAPD and mitochondrial DNA markers in assessing *Varroa jacobsoni* genotypes. *J Apic Res* 37:49–51
- de Guzman LI, Burgett M, Rinderer TE (2001) Biology and life history of *Acarapis dorsalis* and *Acarapis externus*. In: Webster TC, Delaplane KS (eds) Mites of the honey bee. Dadant, Hamilton, IL, pp 17–27
- De Jong D (1997) Mites: *Varroa* and other parasites of brood. In: Morse RM, Flottum PK (eds) Honey bee pests, predators, and diseases, 3rd edn. Root, Medina, Ohio, pp 281–327
- De Jong D, Soares AEE (1997) An isolated population of Italian bees that has survived *Varroa jacobsoni* Oud infestation without treatment for over 12 years. *Am Bee J* 137:742–747
- De Jong D, Morse RA, Eickwort GC (1982) Mite pests of honey bees. *Ann Rev Entomol* 27:229–252
- Delfinado M, Baker EW (1961) *Tropilaelaps*, a new genus of mite from the Philippines (Laelapidae s. lat.). *Fieldiana Zool* 44:53–56
- Delfinado M, Baker EW (1974) Varroidae, a new family of mites on honeybees (Mesostigmata: Acarini). *J Wash Acad Sci* 64:4–10

- Delfinado-Baker M (1982) New records for *Tropilaelaps clareae* from colonies of *Apis cerana indica*. *Am Bee J* 122:382
- Delfinado-Baker M (1988) Variability and biotypes of *Varroa jacobsoni* Oudemans. *Am Bee J* 128:567–568
- Delfinado-Baker M, Aggarwal K (1987a) A new *Varroa* (Acari: Varroidae) from the nest of *Apis cerana* (Apidae). *Int J Acarol* 13:233–237
- Delfinado-Baker M, Aggarwal K (1987b) Infestation of *Tropilaelaps clareae* and *Varroa jacobsoni* in *Apis mellifera ligustica* colonies in Papua New Guinea. *Am Bee J* 127:443
- Delfinado-Baker M, Baker EW (1982) A new species of *Tropilaelaps* parasitic on honey bees. *Am Bee J* 122:416–417
- Delfinado-Baker M, Baker EW (1987) Notes on mites new to beehives in Puerto Rico and North America. *Am Bee J* 127:365–366
- Delfinado-Baker M, Houck MA (1989) Geographical variation in *Varroa jacobsoni* (Acari, Varroidae): application of multivariate morphometric techniques. *Apidologie* 20:345–358
- Delfinado-Baker M, Underwood BA, Baker EW (1985) The occurrence of *Tropilaelaps* mites in brood nests of *Apis dorsata* and *A. laboriosa* in Nepal, with descriptions of the nymphal stages. *Am Bee J* 122:416–417
- Delfinado-Baker M, Baker EW, Phoon ACG (1989) Mites (Acari) associated with bees (Apidae) in Asia, with description of a new species. *Am Bee J* 129:609–613
- Dhaliwal HS, Sharma PL (1974) Foraging range of the Indian honeybee. *J Apic Res* 13:137–141
- Donzè G, Guerin PM (1994) Behavioral attributes and parental care of *Varroa* mites parasitizing honeybee brood. *Behav Ecol Sociobiol* 34:305–319
- Donzè G, Guerin PM (1997) Time-activity budgets and space structuring by the different life stages of *Varroa jacobsoni* in capped brood of the honey bee, *Apis mellifera*. *J Insect Behav* 10:371–393
- Eguaras E, Marcangeli K, Oppendisano N, Fernandez N (1995) Mortality and reproduction of *Varroa jacobsoni* in resistant colonies of honey bees (*Apis mellifera*) in Argentina. *Bee Sci* 3:174–178
- Eickwort GC (1988) The origin of mites associated with honey bees. In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE (eds) Africanized honey bees and bee mites. Ellis Horwood, Chichester, pp 327–384
- Eickwort GC (1990) Associations of mites with social insects. *Annu Rev Entomol* 35:469–488
- Eickwort GC (1994) Evolution and life-history patterns of mites associated with bees. In: Houck MA (ed) Mites: ecological and evolutionary analysis of life history patterns. Chapman & Hall, New York, pp 218–251
- Eischen FA (1987) Overwintering performance of honey bee colonies heavily infested with *Acarapis woodi* (Rennie). *Apidologie* 18:293–304
- Eischen FA (1998a) *Varroa* control problems: some answers. *Am Bee J* 138:107–108
- Eischen FA (1998b) *Varroa*'s response to fluvalinate in the Western US. *Am Bee J* 138:293
- Elzen PJ, Eischen FA, Baxter JR, Pettis J, Elzen GW, Wilson WT (1998) Fluvalinate resistance in *Varroa jacobsoni* from several geographic locations. *Am Bee J* 138:674–676
- Fain A, Gerson U (1990) Notes on two astigmatid mites (Acari) living in beehives in Thailand. *Acarologia* 31:381–384
- Fichter BL (1988) ELISA detection of *Acarapis woodi*. In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE (eds) Africanized honey bees and bee mites. Ellis Horwood, Chichester, pp 526–529
- Forsgren E, de Miranda JR, Isaksson M, Wei S, Fries I (2009) Deformed wing virus associated with *Tropilaelaps mercedesae* infesting European honey bee (*Apis mellifera*). *Exp Appl Acarol* 47:87–97
- Fries I, Camazine S (2001) Implications of horizontal and vertical pathogen transmission for honey bee epidemiology. *Apidologie* 32:199–214
- Fries I, Hauzhen W, Wei S, Jin CS (1996) Grooming behavior and damaged mites (*Varroa jacobsoni*) in *Apis cerana* and *Apis mellifera ligustica*. *Apidologie* 27:3–11
- Garrido C, Rosenkranz P, Paxton RJ, Gonçalves L (2003) Temporal changes in *Varroa destructor* fertility and haplotype in Brazil. *Apidologie* 34:535–541

- Gerson U, Mozes-Koch R, Cohen E (1991) Enzyme levels used to monitor pesticide in *Varroa jacobsoni*. *J Apic Res* 30:17–20
- Grant GM, Di N, Olsen PE, Rice WA (1993) The ELISA detection of tracheal mites in whole honey bee samples. *Am Bee J* 133:652–655
- Griffith DA, Bowman CE (1981) World distribution of the mites *Varroa jacobsoni*, a parasite of honeybee. *Bee World* 62:154–163
- Griffiths DA (1988) Functional morphology of the mouthparts of *Varroa jacobsoni* and *Tropilaelaps clareae* as a basis for the interpretation of their life-styles. In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE (eds) Africanized honey bees and bee mites. Ellis Horwood, Chichester, pp 479–486
- HDOA: Hawaii Department of Agriculture (2010) Hawaii. <http://hawaii.gov/hdoa/pi/ppc/varroa-bee-mite-page/?searchterm=varroa>. Accessed 23 May 2010
- Haq MA, Halliday RB, Walter DE, Proctor HC, Norton RA (2001) Life cycle and behavior of the coconut mite *Neocypsholaelaps stridulans*. *Acarology*. In: Proceedings of 10th international congress, CSIRO, Melbourne, pp 361–365
- Hirschfelder H, Sachs H (1952) Recent research on the acarine mite. *Bee World* 33:201–209
- Hunter PE, Rosario RMT (1988) Associations of Mesostigmata with other arthropods. *Annu Rev Entomol* 33:393–417
- Kapil RP, Aggarwal K (1987) Some observations on the concurrent parasitization of *Apis florea* by *Tropilaelaps clareae* and *Eugarroa sinhai*. *Exp Appl Acarol* 3:267–269
- Kapil RP, Aggarwal K (1989) Observations on reproduction and seasonal population trends of *Eugarroa sinhai* (Mesostigmata: Varroidae) in India. In: Channabasavanna GP, Viraktamath CA (eds) Progress in acarology. Oxford and IBH, New Delhi, pp 277–281
- Kavinseksan B, Wongsiri S, de Guzman LI, Rinderer TE (2003) Absence of *Tropilaelaps* infestation from recent swarms of *Apis dorsata* in Thailand. *J Apic Res* 42:49–50
- Koeniger G, Koeniger N, Anderson A, Lekprayoon C, Tingek S (2002) Mites from debris and sealed brood cells of *Apis dorsata* colonies in Sabah (Borneo) Malaysia, including a new haplotypes of *Varroa jacobsoni*. *Apidologie* 33:15–24
- Koeniger N, Muzaffar N (1988) Lifespan of the parasitic honeybee mite *Tropilaelaps clareae* on *Apis cerana*, *Apis dorsata*, and *Apis mellifera*. *J Apic Res* 27:207–212
- Koeniger N, Koeniger G, de Guzman LI, Lekprayoon C (1993) Survival of *Eugarroa sinhai* Delfinado and Baker (Acari, Varroidae) on workers of *Apis cerana* Fabr., and *Apis mellifera* L. in cages. *Apidologie* 24:403–410
- Krantz GW, Walter DE (2009) A manual of acarology. Texas Tech University Press, Lubbock, TX
- Kraus B, Hunt G (1995) Differentiation of *Varroa jacobsoni* Oud populations by random amplification of polymorphic DNA (RAPD). *Apidologie* 26:283–290
- Kumar NR, Kumar R, Mbaya I, Mwangi RW (1993) *Tropilaelaps clareae* found on *Apis mellifera* in Africa. *Bee World* 74:101–102
- Laigo FM, Morse RA (1968) The mite *Tropilaelaps clareae* in *Apis dorsata* colonies in the Philippines. *Bee World* 49:116–118
- Le Conte Y, Arnold G, Trouiller J, Masson C, Chappe B (1989) Attraction of the parasitic mite *Varroa* on the drone larvae of honey bees by simple aliphatic esters. *Science* 245:638–639
- Lekprayoon C, Tangkanasing P (1991) *Varroa wongsirii*, a new species of bee mite from Thailand. *Int J Acarol* 17:255–258
- Lekprayoon C, Tangkanasing P (1993) Comparative morphology of *Eugarroa sinhai* and *Eugarroa wongsirii*: parasites of *Apis florea* and *Apis andreniformis*. In: Conner LJ, Rinderer TE, Sylvester AH, Wongsiri S (eds) Asian apiculture. Wicwas, Cheshire, pp 427–433
- Lindquist EE (1986) The world genera of Tarsonemidae (Acari: Heterostigmata): A morphological, phylogenetic, and systematic revision, with a reclassification of family-group taxa in the Heterostigmata. *Mem Entomol Soc Can* 136:1–517
- Lipsitch M, Herre EA, Nowak MA (1995a) Host population structure and the evolution of virulence: a “law of diminishing returns”. *Evolution* 49:743–748

- Lipsitch M, Nowak MA, Ebert D, May RM (1995b) The population dynamics of vertically and horizontally transmitted parasites. *Proc R Soc Lond Ser B* 260:321–327
- Lo N, Gloag RS, Anderson D, Oldroyd BP (2010) A molecular phylogeny of the genus *Apis* suggests that the giant honey bee of the Philippines, *A. breviligula* Maa, and the Plains honey bee of southern India, *A. indica* Fabricius, are valid species. *Syst Entomol* 35:226–233
- Lodesani M, Colombo M, Spreafico M (1995) Ineffectiveness of Apistan treatment against the mite *Varroa jacobsoni* Oud. in several districts of Lombardy (Italy). *Apidologie* 26:67–72
- Matheson A (1996) World bee health update 1996. *Bee World* 77:45–51
- Matheson A (1997) Country records for honey bee diseases, parasites and pests. In: Morse RM, Flottum PK (eds) *Honey bee pests, predators, and diseases*, 3rd edn. Root, Medina, OH, pp 587–602
- Moretto G, Gonçalves LS, De Jong DD, Bichuette MZ (1991) The effects of climate and bee race on *Varroa jacobsoni* Oud in several districts of Lombardy (Italy). *Apidologie* 26:67–72
- Morin CE, Otis GW (1993) Observations on the morphology and biology of *Eugarroa wongsirii* (Mesostigmata: Varroidae), a parasite of *Apis andreniformis* (Hymenoptera: Apidae). *Int J Acarol* 19:167–172
- Moritz RFA, Haenel H (1984) Restricted development of the parasitic mite *Varroa jacobsoni* Oud in the Cape honey bee *Apis mellifera capensis* Esch. *Z Angew Entomol* 97:91–95
- Morse RA, Nowogrodzki R (eds) (1990) *Honey bee pests, predators, and diseases*, 2nd edn. Cornell University Press, Ithaca
- Mossadegh MS (1990) Development of *Eugarroa sinhai* (Acari: Mesostigmata), a parasitic mite of *Apis florea*, on *A. mellifera* worker brood. *Exp Appl Acarol* 9:73–78
- Mossadegh MS, Birjandi AK (1986) *Eugarroa sinhai* Delfinado and Baker (Acarina: Mesostigmata): a parasitic mite on *Apis florea* in Iran. *Am Bee J* 126:684–685
- Mussen EC (2001) Introduction, spread and economic impact of tracheal mites in North America. In: Webster TC, Delaplane KS (eds) *Mites of the honey bee*. Dadant, Hamilton, IL, pp 43–56
- Navajas M, Anderson DL, de Guzman LI, Huang ZY, Clement J, Zhou T, Le Conte YL (2010) New Asian types of *Varroa destructor*: a potential new threat for world apiculture. *Apidologie* 41:181–193
- Needham GR, Gerson U, Sammataro D (2001) Mite biology. In: Webster TC, Delaplane KS (eds) *Mites of the honey bee*. Dadant, Hamilton, IL, pp 1–16
- O'Connor BM (1982) Evolutionary ecology of astigmatid mites. *Annu Rev Entomol* 27:385–409
- O'Connor BM (1988) Coevolution in astigmatid mite-bee associations. In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE (eds) *Africanized honey bees and bee mites*. Ellis Horwood, Chichester, pp 339–346
- Oldroyd BP (1999) Coevolution while you wait: *Varroa jacobsoni*, a new parasite of western honeybees. *Trends Ecol Evol* 14:312–315
- Oldroyd BP, Wongsiri S (2006) *Asian honey bees*. Harvard University Press, Cambridge
- Otis GW (1996) Distributions of recently recognized species of honey bees (Hymenoptera: Apidae; *Apis*) in Asia. *J Kans Entomol Soc* 69:311–333
- Otis GW, Kralj J (2001) Parasitic mites not present in North America. In: Webster TC, Delaplane KS (eds) *Mites of the honey bee*. Dadant, Hamilton, IL, pp 251–272
- Otis GW, Scott-Dupree CD (1992) Effects of *Acarapis woodi* on overwintering colonies of honeybees (Hymenoptera: Apidae) in New York. *J Econ Entomol* 85:40–46
- Oudemans AC (1904) Note VIII. On a new genus and species of parasitic Acari. *Notes Leyden Mus* 24:216–222
- Peng CYS, Fang YZ, Xu SY, Ge LS (1987) The resistance mechanism of the Asian honey bee *Apis cerana* Fabr. to an ectoparasitic mite, *Varroa jacobsoni* Oudemans. *J Invertebr Pathol* 49:54–60
- Pettis JS, Wilson WT (1996) Life history of the honey bee tracheal mite (Acari: Tarsonemidae). *Ann Entomol Soc Am* 89:368–374
- Phelan LP, Smith AW, Needham GR (1991) Mediation of host selection by cuticular hydrocarbons in the honey bee tracheal mite *Acarapis woodi* (Rennie). *J Chem Ecol* 17:463–473

- Raffiudin R, Crozier RH (2007) Phylogenetic analysis of honey bee behavioral evolution. *Mol Phylogenet Evol* 43:543–552
- Ragsdale D, Furgala B (1987) A serological approach to the detection of *Acarapis woodi* parasitism in honey bees using an enzyme-linked immunosorbent assay. *Apidologie* 18:1–10
- Ragsdale D, Kjer KM (1989) Diagnosis of tracheal mite (*Acarapis woodi* Rennie) parasitism of honey bees using a monoclonal based enzyme-linked immunosorbent assay. *Am Bee J* 129:550–553
- Rath W (1999) Co-adaptation of *Apis cerana* Fabr. and *Varroa jacobsoni* Oud. *Apidologie* 30:97–110
- Rath W, Delfinado-Baker M, Drescher W (1991) Observations on the mating behavior and sex ratio phoresy and dispersal of *Tropilaelaps clareae* Acari Laelapidae. *Int J Acarol* 17:201–208
- Rinderer TE, Oldroyd BP, Lekprayoon C, Wongsiri S, Boonthai C, Thapa R (1994) Extended survival of the parasitic mite *Tropilaelaps clareae* on adult workers of *Apis mellifera* and *Apis dorsata*. *J Apic Res* 33:171–174
- Ritter W, Michel P, Bartholdi M, Schwendemann A (1990) Development of tolerance to *Varroa jacobsoni* in bee colonies in Tunisia. In: Ritter W (ed) Proceedings of international symposium on recent research in bee pathology, Apimondia, pp 54–59
- Royce LA, Rossignal PA (1989) Honey bee mortality due to tracheal mite parasitism. *Parasitology* 100:147–151
- Ruttner F (1988) Biogeography and taxonomy of honeybees. Springer, Berlin
- Sammataro D (1995) Studies on the control, behavior, and molecular markers of the tracheal mites (*Acarapis woodi* (Rennie)) of honey bees (Hymenoptera: Apidae). Thesis, Ohio State University, Ohio
- Sammataro D (2004) *Tropilaelaps* infestation of honey bees (*Tropilaelaps clareae*, *T. koenigerum*). In: Office International des Epizooties (OIE) Manual of diagnostic tests and vaccines for terrestrial animals, 5th edn, vol 2. OIE, Paris, pp 992–995
- Sammataro D, Needham GR (1996) Host-seeking behavior of tracheal mites (Acari: Tarsonemidae) on honey bees (Hymenoptera: Apidae). *Exp Appl Acarol* 20:121–136
- Sammataro D, Cobey S, Smith BH, Needham GR (1994) Controlling tracheal mites (Acari: Tarsonemidae) in honey bees (Hymenoptera: Apidae) with vegetable oil. *J Econ Entomol* 87:910–916
- Sammataro D, Gerson U, Needham G (2000) Parasitic mites of honey bees: life history, implications, and impact. *Annu Rev Entomol* 45:519–548
- Sasagawa H, Matsuyama S, Peng CYS (1999) Recognition of parasite, hygienic allo-grooming behavior induced by parasitic *Varroa* mites in the Japanese honey bee, *Apis mellifera japonica*. In: Proceedings of 13th international congress, IUSSI, Adelaide, pp 415
- Shimanuki H, Knox D (1991) Diagnosis of honey bee disease. USDA Agricultural Handbook Ah-690
- Sihag RC (1988) Incidence of *Varroa*, *Euvarroa* and *Tropilaelaps* mites in the colonies of honey bees *Apis mellifera* L. in Haryana (India). *Am Bee J* 128:212–213
- Smith DR, Hagen RH (1996) The biogeography of *Apis cerana* as revealed by mitochondrial DNA sequence data. *J Kans Entomol Soc* 69:294–310
- Smith DR, Villafuerte L, Otis G, Palmer MR (2000) Biogeography of *Apis cerana* F. and *A. nigrocincta* Smith: Insights from mtDNA studies. *Apidologie* 31:265–279
- Sumangala K, Haq MA (2002) Ecobiology of *Pseudacarapis indoapis* Lindquist (Acari: Tarsonemidae) 2: ontogeny and breeding behavior. *J Entomol Res* 26:83–88
- Tangkanasing P, Wongsiri S, Vongsamanode S (1988) Integrated control of *Varroa jacobsoni* and *Tropilaelaps clareae* in bee hives. In: Needham GR, Page RE Jr, Delfinado-Baker M, Bowman CE (eds) Africanized honey bees and bee mites. Ellis Horwood, Chichester, pp 409–412
- Tangjingjai W, Verakasala P, Sittipraneed S, Klinbunga S, Lekprayoon C (2003) Genetic differences between *Tropilaelaps clareae* and *Tropilaelaps koenigerum* in Thailand based on ITS and RAPD analyses. *Apidologie* 34:514–524
- Tewarson NC, Singh A, Engles W (1992) Reproduction of *Varroa jacobsoni* in colonies of *Apis cerana indica* under natural and experimental conditions. *Apidologie* 23:161–171

- Waite R (2003) Exotic pest legislation. *Br Beekeep Assoc* 143:7
- Warrit N, Hagen TAR, Smith DR, Cakmak I (2004) A survey of *Varroa destructor* strains on *Apis mellifera* in Turkey. *J Apic Res* 43:190–191
- Warrit N, Smith DR, Lekprayoon C (2006) Genetic subpopulations of *Varroa* mites and their *Apis cerana* hosts in Thailand. *Apidologie* 37:19–30
- Webster TC, Delaplane KS (2001) *Mites of the honey bee*. Dadant, Hamilton, IL
- Wilde J (2000) Is it possible to introduce *Tropilaelaps clareae* together with imported honey bee queens to Europe? *Pszczeln Zesz Nauk* 44:155–162
- Wilson WT, Pettis JS, Henderson CE, Morse RA (1997) Tracheal mites. In: Morse RM, Flottum PK (eds) *Honey bee pests, predators, and diseases*, 3rd edn. Root, Medina, OH, pp 255–277
- Woyke J (1984) Survival and prophylactic control of *Tropilaelaps clareae* infesting *Apis mellifera* colonies in Afghanistan. *Apidologie* 15:421–434
- Woyke J (2005) Aktualne wiadomości o biologii i zwalczaniu roztocza *Tropilaelaps clareae*. *Pasieka* 3:43–47
- Yoder JA, Sammataro D, Peterson JA, Needham GR, Bruce WA (1999) Water requirements of adult females of the honey bee parasitic mite, *Varroa jacobsoni* (Acari: Varroidae) and implications for control. *Int J Acarol* 25:329–335
- Zhang ZQ (2000) Notes on *Varroa destructor* (Acari: Varroidae) parasitic on honeybees in New Zealand. *Syst Appl Acarol Spec Publ* 5:9–14