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Review

Ecology, Life History, and Management of Tropilaelaps Mites

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Abstract

Parasitic mites are the major threat to the Western honey bee, *Apis mellifera* L. For much of the world, *Varroa destructor* Anderson & Trueman single-handedly inflicts unsurmountable problems to *A. mellifera* beekeeping. However, *A. mellifera* in Asia is also faced with another genus of destructive parasitic mite, *Tropilaelaps*. The life history of these two parasitic mites is very similar, and both have the same food requirements (i.e., hemolymph of developing brood). Hence, parasitism by *Tropilaelaps* spp., especially *Tropilaelaps mercedesae* and *Tropilaelaps clareae*, also results in death of immature brood or wing deformities in infested adult bees. The possible introduction of Tropilaelaps mites outside their current range heightens existing dilemmas brought by Varroa mites. In this review, we provide historic, as well as current information on the taxonomic status, life history, distribution and host range, diagnosis, and control of Tropilaelaps mites. Because the biology of Tropilaelaps mites is not well known, we also suggest areas of research that demand immediate attention. Any biological information about Tropilaelaps mites will provide useful information for the development of control measures against them.

Key words: *Tropilaelaps mercedesae*, *Tropilaelaps clareae*, *Varroa destructor*, intergeneric competition, *Apis mellifera*

The impact of nonnative species on our ecosystem and economy is very costly because they can inflict extensive damage on native species. Although some alien species thrive and establish themselves in new locations, they are poorly adapted against native pests, parasites, or diseases. A good example is the plight of the Western honey bee, *Apis mellifera* L., in fighting against several serious exotic parasites, pests, and pathogens. *Varroa destructor* Anderson & Trueman, which is indigenous to Asia, and the Deformed wing virus (DWV) it vectors, are major threats to *A. mellifera* colonies worldwide (Wilfert et al. 2016). On the other hand, the introduction of *A. mellifera* to Asia has resulted in successful host shifts not only by the mite genus *Varroa*, but also by a more serious mite genus, *Tropilaelaps*. While *A. mellifera* and the native Eastern honey bee (*Apis cerana* Fabr.) share Varroa mites, *A. mellifera* and the native giant honey bees (*Apis breviligula* Maa, *Apis dorsata* Fabr., and *Apis laboriosa* Smith) share Tropilaelaps mites. Therefore, these unmanaged Asian honey bees serve as reservoirs for Varroa and Tropilaelaps mites to infest domesticated *A. mellifera* colonies, and vice versa. For example, Tropilaelaps mites in Hisar, India, are capable of a reproductive continuum, as they reproduce from January to March in *A. mellifera*, and from March to May in *A. dorsata* (Aggarwal 1988).

Varroa and Tropilaelaps mites have coexisted in *A. mellifera* colonies in Asia for >50 yr (Delfinado 1963). However, Tropilaelaps mites are considered to be the more dominating and reproductively successful parasites of *A. mellifera* than Varroa mites (Burgett et al. 1983, Buawangpong et al. 2015). In 2007, a molecular examination of Tropilaelaps mites collected from different honey bee hosts from several Asian countries revealed two new *Tropilaelaps* species (*Tropilaelaps mercedesae* and *Tropilaelaps thaii*) distinctly separate from *Tropilaelaps clareae* and *Tropilaelaps koenigerum* (Anderson and Morgan 2007). Among these four species, *T. mercedesae* and *T. clareae* are the most serious Tropilaelaps mites of *A. mellifera*. However, *T. mercedesae* exhibits a wider distribution than *T. clareae*. The life history of Tropilaelaps mites and food requirements are similar to that of Varroa mites. As a result, both mite genera can inflict severe damages on *A. mellifera* colonies.

The detection of Tropilaelaps mites in Africa (Kumar et al. 1993a) demonstrates that these mites can survive long distances. However, it is unclear if these mites were successfully eradicated. In addition, the successful establishment of *T. mercedesae* in South Korea, where winter can be harsh and honey bee brood rearing limited, reveals that these mites can thrive in temperate climates like Varroa mites, the small hive beetle (*Aethina tumida* (Murray)), and *Nosema ceranae*. These latter stressors are now globally distributed and cause colony damages to *A. mellifera* (Higes et al. 2013, Neumann et al. 2016). It is therefore likely that Tropilaelaps mites will also become established around the world. In this review, we provide historic and current information on the taxonomic status, life history, distribution and host range, diagnosis, and control of Tropilaelaps mites. Because *T. mercedesae* and *T. clareae* are the two *Tropilaelaps* spp. that are of most economic importance to *A. mellifera*, they are the focus of this review. Unless specified, "Tropilaelaps mites" is used as the common name for both *Tropilaelaps* species. We also referred to *A. cerana indica* F. of India as *A. indica*, and *A. dorsata breviligula* of the Philippines as *A. breviligula* (Lo et al. 2010).

Molecular and Morphological Identification

Mites under the genus *Tropilaelaps* belong to the order Mesostigmata and family Laelapidae. In 2007, the genus was reclassified into four distinct species: *T. clareae*, *T. koenigerum*, *T. mercedesae*, and *T. thaii* (Anderson and Morgan 2007). This breakthrough indicates that earlier studies observing *T. clareae* may refer to *T. mercedesae*. Hence, for simplicity and to avoid confusion, all studies on *T. clareae* conducted in areas east of the Wallace line, including New Guinea, presumably refer to *T. mercedesae*, whereas those west of the Wallace line refer to *T. clareae* (Anderson and Morgan 2007; Table 1). The Wallace line is a faunal boundary line proposed by Alfred Russel Wallace in 1859 wherein species to the west of the line are of Asian origin while those to the east are mainly of Australian descent.

Molecular Identification

Molecular studies had been conducted to understand the systematic biology of Tropilaelaps mites (Tangjingjai et al. 2003, Anderson and Morgan 2007, Luo et al. 2011b). Genetic variation in Tropilaelaps mites can be determined using mitochondrial *CO-I* and nuclear ITS1-5.8S-ITS2 gene sequences. The primers TCF1 (5′-CTATCCTCAATTATTGAAATAGGAAC-3′) and TCR2 (5′-TAGCGGCTGTGAAATAGGCTCG-3′) amplify a single 538 DNA base pair fragment. Patterns of digested PCR-amplified CO-I DNA assign an unknown Tropilaelaps mite to species level. For example, BsrI digests cox1 fragments of *T. mercedesae*, whereas BstYI digests cox1 fragments of *T. clareae*. Target site for the restriction enzyme Bme1580 I is also found within the ITS1-5.8S-ITS2 sequence of *T. mercedesae* (Anderson and Morgan 2007). The entire ITS1-5.8S-ITS2 gene region can also be amplified using an ITS4 primer (5′-TCCTCCGCTTATTGATATGC-3′) and an ITS5 primer (5′-GGAAGTAAAAGTCGTAACAAGG-3′). Within the ITS1-5.8S-ITS2 sequence, the target site for the restriction enzyme Bme 1580 I was located in *T. mercedesae* (Anderson and Morgan 2007). *Tropilaelaps mercedesae* can also be identified using the RAPD primers OPA 17, OPA 11, and OPA 12 (Tangjingjai et al. 2003).

Morphological Identification

Tropilaelaps mites are morphologically similar based on female characteristics. The adults are red-brown in color, and the idiosoma is entirely covered by a dorsal shield. Legs have large ambulacra with claws to attach to the host's body during phoresy (Rath et al. 1991), or to grasp on to conspecific females during precopulation or conspecific males during mating bouts. Legs 1 are long and slender (antennae-like), and appear to perform a sensory function (Delfinado-Baker et al. 1992). Nymphal stages are white in color.

A simple key to differentiate all *Tropilaelaps* species has been summarized by Oldroyd and Wongsiri (2006). The bodies of Tropilaelaps mites are longer than wide, which may facilitate high mobility on combs and between hairs of bees (Delfinado-Baker et al. 1992). However, adult females of *T. mercedesae* are larger (average length = 979 μm; average width = 542 μm) compared with *T. clareae* females (average length = 882 μm; average width = 484 μm). *Tropilaelaps mercedesae* males are 921 μm long and 523 μm wide, whereas *T. clareae* males are 857 μm long and 501 μm wide on average (Anderson and Morgan 2007; Fig. 1). While *T. clareae* always has a bluntly pointed epigynial plate, variations in the apex of the epigynial plates (from bluntly to sharply pointed), as well as the reticulated patterns of both the epigynial and anal plates, exist among *T. mercedesae* haplotypes. The males of both Tropilaelaps mites have similar characteristics: the chelicerae are toothed and movable, and are modified into a spermatodactyl (sperm transfer organ) with coiled apexes; the anal plates are rectangular in shape (Delfinado and Baker 1961, Anderson and Morgan 2007).

Host Range and Distribution

Tropilaelaps mercedesae

Host Range

Tropilaelaps mercedesae is commonly observed infesting *A. mellifera* and *A. dorsata* colonies in mainland Asia (Table 1). Although it is considered to be a serious parasite of *A. mellifera*, this Tropilaelaps mite has not been detected infesting *A. mellifera* colonies in the Philippines' Palawan Islands where *A. dorsata* is also found (Anderson and Morgan 2007). In addition, these Tropilaelaps mites have been collected from colonies of other Asian honey bees, including *A. florea* F. and *A. indica* colonies in India (Kapil and Aggarwal 1987, Abrol and Kakroo 1997), *A. cerana* colonies in Pakistan, Myanmar, and Thailand (Delfinado-Baker 1982), and *A. laboriosa* in Vietnam (Anderson and Morgan 2007). Reproduction by only one female *T. mercedesae* was observed in *A. cerana* brood in Thailand (Anderson and Morgan 2007). Well established populations of Tropilaelaps mites in *A. indica* colonies had been reported in the Jammu region of India (Abrol and Kakroo 1997), an indication of reproductive success of Tropilaelaps mites in these native honey bees. When drone brood is absent, Tropilaelaps mite infestation on adult *A. florea* is generally higher than its indigenous parasite, *Euvarroa sinhai* Delfinado and Baker (Aggarwal 1988). Furthermore, *T. mercedesae* have been observed infesting carpenter bees, *Xylocopa iridipennis*, in India (Abrol and Putatunda 1996). However, the type or degree of infestation remains unclear.

Distribution

The biogeography of Tropilaelaps mites predominately mirrors that of the giant honey bee (Anderson and Morgan 2007). *Tropilaelaps mercedesae* and its indigenous host, *A. dorsata*, are abundant in mainland Asia and Palawan Islands, Philippines (Anderson and Morgan 2007; Table 1). This successful expansion and colonization of *T. mercedesae* in these countries may be due in part to the behavior of *A. dorsata*. Annually, these *A. dorsata* migrate and often aggregate (Woyke et al. 2012). Over 120 *A.*

Table 1. Distribution and host range of *Tropilaelaps mercedesae* and *Tropilaelaps clareae*

Country	Honey bee host	References
A. *Tropilaelaps mercedesae*		
Afghanistan	*A. mellifera*	Woyke 1984
China	*A. dorsata*, *A. mellifera*	Anderson and Morgan 2007
India	*A. indica*, *A. dorsata*, *A. florea*, *A. mellifera*, *X. iridipennis*	Bharadwaj 1968, Kapil and Aggarwal 1987, Abrol and Putatunda 1996, Abrol and Kakroo 1997, Anderson and Morgan 2007
Indonesia, except Sulawesi	*A. dorsata*, *A. mellifera*	Anderson and Morgan 2007
Kenya	*A. mellifera scutellata*	Kumar et al. 1993a
Laos	*A. dorsata*	Anderson and Morgan 2007
Malaysia	*A. dorsata*	Koeniger et al. 2002, Anderson and Morgan 2007
Myanmar (Burma)	*A. cerana*, *A. mellifera*	Delfinado-Baker 1982, Anderson and Morgan 2007
Nepal	*A. dorsata*, *A. laboriosa*	Anderson and Morgan 2007, Delfinado-Baker et al. 1985
Pakistan	*A. cerana*, *A. mellifera*	Delfinado-Baker 1982, Camphor et al. 2005
Philippines, but only Palawan Islands	*A. dorsata*	Anderson and Morgan 2007
Papua New Guinea	*A. mellifera*	Anderson and Morgan 2007
South Korea	*A. mellifera*	Anderson and Morgan 2007
Sri Lanka	*A. dorsata*	Anderson and Morgan 2007
Thailand	*A. cerana*, *A. dorsata*, *A. mellifera*	Anderson and Morgan 2007 Wongsiri et al. 1989
Vietnam	*A. dorsata*, *A. laboriosa*, *A. mellifera*	Stephen 1968, Anderson and Morgan 2007
B. *Tropilaelaps clareae*		
Indonesia, but only Sulawesi Island	*A. d. binghami*	Anderson and Morgan 2007
Philippines, except Palawan Islands	*A. breviligula, A. cerana, A. mellifera*	Delfinado and Baker 1961, Laigo and Morse 1968, Morse and Laigo 1969, Anderson and Morgan 2007

Note: All references before 2007 referred Tropilaelaps mites as *T. clareae*; they have since been designated as *T. mercedesae* based on the study of Anderson and Morgan (2007).

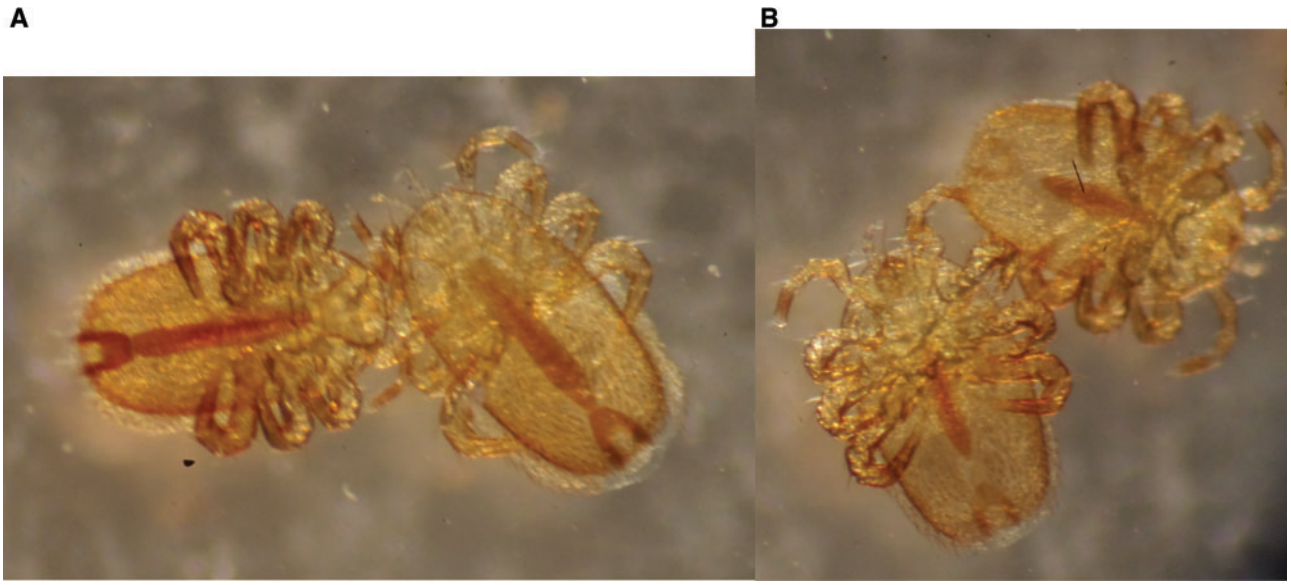

Fig. 1. Venter of *T. mercedesae* adults from Chiang Mai, Thailand. (**A**) Adult females— epigynial plates sharply to bluntly pointed; truncated anal plates, and (**B**) Adult males—epigynial plates sharply pointed; anal plates blunt posteriorly but narrow anteriorly; well separated epigynial and anal plates (Photos by K. Khongphinitbunjong).

dorsata nests may occur on a single tree (Oldroyd et al. 2000), which may promote intercolony transmission of the mite and help sustain *T. mercedesae* populations. This tropilaelaps mite is also well established outside the geographical range of the giant honey bees, infesting *A. mellifera* colonies in Afghanistan, Papua New Guinea, and South Korea (Burgett et al. 1983, Woyke 1984, Delfinado-Baker and Aggarwal 1987, Kumar et al. 1993b, Anderson 1994, Matheson 1996, Otis and Kralj 2001). Although it was detected in Kenya (Kumar et al. 1993a), no established population of mites has been reported. Of the 26 haplotypes of *T. mercedesae*, 20 were found on *A. dorsata* and 6 on *A. mellifera* (Anderson and Morgan 2007). One of the two haplotypes collected from *A. laboriosa* was also found in *A. dorsata* in Thailand. The mainland haplotype of *T. mercedesae* is common on *A. dorsata* on mainland Asia.

Tropilaelaps clareae

Host Range

First collected from field rats near hives in the Philippines, *T. clareae* was the first *Tropilaelaps* species identified (Delfinado and Baker 1961). This mite species has been recorded from four honey bee species: *A. indica* (Morse and Laigo 1969), *A.d. binghami*, *A. breviligula*, and *A. mellifera* (Anderson and Morgan 2007; Table 1). At present, 16 *T. clareae* haplotypes (four on *A. mellifera* and 12 on *A. dorsata*) have been identified (Anderson and Morgan 2007).

Distribution

Tropilaelaps clareae has a more limited distribution than *T. mercedesae*. The sparse distribution of *T. clareae* is probably due to the isolation of their adapted hosts, *A. d. binghami* and *A. breviligula*. The former is only found on Sulawesi Island, Indonesia (Anderson and Morgan 2007), and its taxonomy is uncertain (Lo et al. 2010), whereas the latter, *A. breviligula*, which is known for its black and white stripes, has recently been considered to be a separate species (Lo et al. 2010). *Apis breviligula* is found all over the Philippines, except in Palawan Islands, where the only giant honey bee present is *A. dorsata*. Unlike *A. dorsata*, *A. breviligula* do not aggregate (Morse and Laigo 1969). This behavior possibly contributes to the limited distribution of *T. clareae*, which also infests *A. mellifera* colonies all over the Philippines except in Palawan Islands (Anderson and Morgan 2007). Recently, coinfestations of Varroa and Tropilaelaps mites in *A. mellifera* colonies in the island have been observed (Cervancia et al. 2016). However, the genetic identity of these Tropilaelaps mites has not been identified.

Life History and Behavior

Like *Varroa spp*., *Tropilaelaps* spp. are ectoparasites that primarily reproduce within capped brood cells; their progeny mature alongside developing honey bee hosts. Much of the known life history of *T. mercedesae* describes parasitism of *A. mellifera*, and occurred when this mite species was classified as *T. clareae*. As a result, the biology of *T. clareae* has been largely unexplored. Therefore, re-examination of the life history of *T. mercedesae* or *T. clareae* parasitizing *A. mellifera*, as well as other sympatric honey bee species, is needed. Furthermore, inconsistent life cycle and natural history observations among studies is common, and can possibly be explained by differences in experimental methods, geographical locations, weather, genotype of the mites, as well as host species or subspecies studied.

Life Cycle

In *A. mellifera*, just like with other host species, the life cycle of Tropilaelaps mites begins when a mature, mated female enters a partially capped brood cell containing a late-stage honey bee larva (Ritter and Schneider-Ritter 1988, Kumar et al. 1993b). Depending on infestation rates, multiple females may enter a single cell, although most cells are invaded by a single female (Ritter and Schneider-Ritter 1988). In its adapted host, *A. mellifera*, Tropilaelaps mites appear to prefer drone brood over that of workers (Woyke 1987a, Ritter and Schneider-Ritter 1988, Pettis et al. 2013). In contrast, no preference between workers and drones was described during parasitism of its native host, *A. dorsata* (Buawangpong et al. 2013). This difference in brood preference is thought to be due to the clumping of drone brood in *A. mellifera*, whereas drone brood is randomly dispersed in *A. dorsata* colonies (Burgett et al. 1990, Dongwon 2016).

In contrast to Varroa mites that must feed on larval hemolymph to activate oogenesis (Frey et al. 2013), feeding on larva is not required for oviposition for Tropilaelaps mites (Woyke 1994b). The mature females lay eggs within 2 d of mating, as they quickly become gravid (Woyke 1994b). Eggs are mostly laid when cells contain prepupae; however, eggs can be observed as early as the spinning larval stage and as late as the 2-d-old pupal stage (Woyke 1987d). Unlike Varroa mites, which lay eggs in 30-h intervals (Ifantidis 1983), *T. mercedesae* appears to lay eggs in quicker succession, possibly every 24 h (Woyke 1987d).

Following eclosion, Tropilaelaps mites go through three instars (larva, protonymph, and deutonymph) before the final adult moult (Lindquist et al. 2009; Fig. 2). The total development time in worker bees is ~6–9 d (Woyke 1987d, Kumar et al. 1993b), although males appear to require ~24 h less to develop (Rath et al. 1991). Eggs and larvae require the shortest incubation time, ~0.4 and 0.6 d, respectively. A longer development time for protonymphs (~2.0 d) and deutonymphs (3.0 d) was observed (Woyke 1987d). Just prior to worker bee emergence, only late-phase deutonymphs are found, with most mites completing their development by host bee emergence. This observation suggests that foundress egg-laying rarely occurs after worker pupae are 1–2 d old (Woyke 1987d, Kumar et al. 1993b).

Mating Behavior

The mating process in *Tropilaelaps* spp. is accomplished by podospermy, which involves the transfer of sperm to paired female extragenital openings using the male chelicerae (Rath et al. 1991, Woyke 1994a). This process is similar to that of *V. destructor* (Rosenkranz et al. 2010). It begins with the male quickly grasping and mounting the female (Rath et al. 1991, Woyke 1994a). If initial mounting occurs dorsally, the male quickly repositions ventrally by sliding around the female while still holding her. Then, the male uses his Leg I to clasp the female between her legs I and II, while his legs III and IV wrap around the posterior portion of her body. The male then moves posteriorly so that his mouthparts, as well his genital orifice, are approximately half way along the female's epigynial plate. The couple remains in this position for ~4 min, with the male vibrating, possibly prior to secretion of the spermatophore. The sperm is then introduced into the gonopore located on either side between coxae III and IV using his chelicerae, which is modified as spermadactyl. Next, the male slides partially down the female, and repositions asymmetrically across her so that his mouthparts are between the base of her legs III and IV, either on her left or right side. Although not observed, it is likely that the spermatophore is then inserted into the female's gonopore, just next to the base of her legs III and IV, which is connected to the sperm sacculus. Between 100 and 522 strokes are performed. The whole process lasts 5–20 min, which likely serves to promote the passage of sperm into the female's reproductive organ. The male then returns to a central position, still while retaining an asymmetric leg position, vibrates, and moves to the opposite flank of the female to repeat the stroking behavior. Afterwards, the male returns to the central ventral position, and detaches. The total mating process takes between 15–23 min on average (Rath et al. 1991, Woyke 1994a).

Reproduction and Sex Ratio

Fecundity

Reports on the fecundity (number of progeny per foundress) of *T. mercedesae* are contradictory. In Thailand, an average reproductive rate of 1.4 progeny was reported in brood cells of *A. mellifera* (Ritter and Schneider-Ritter 1988), which was similar (1.48 progeny) to that

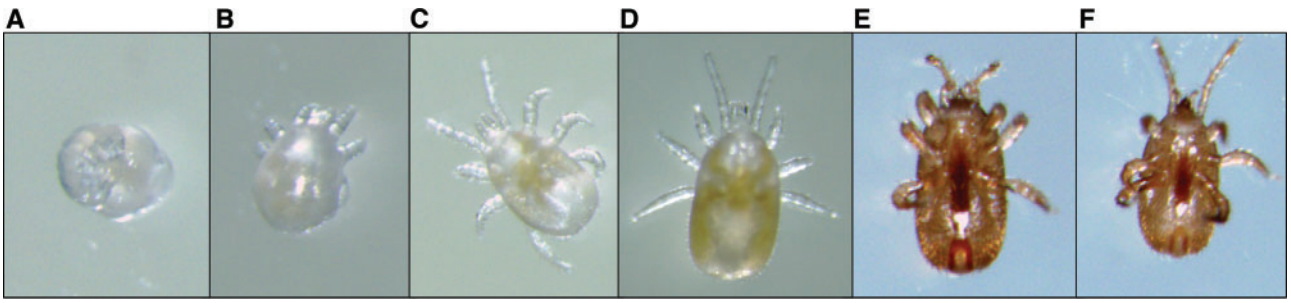

Fig. 2. Developmental stages of *T. mercedesae*: (**A**) Egg, (**B**) Six-legged larva, (**C**) Protonymph, (**D**) Deutonymph, (**E**) Adult female, and (**F**) Adult male (Photos by K. Dongwon).

reported by other authors (Buawangpong et al. 2015). However, a higher fecundity of about two progeny was observed in *A. dorsata* and two stocks of *A. mellifera* (Kavinseksan 2003), as well as under laboratory conditions (1.95 progeny; Rath 1991a). A similar fecundity rate (1.86 progeny) was also observed in brood cells that were deliberately infested with Tropilaelaps mites, which is significantly higher than that observed in naturally infested brood cells (0.79 progeny; Khongphinitbunjong et al. 2013). In Afghanistan and Vietnam, a similar fecundity (1.6–2.1 progeny) was observed in *A. mellifera* colonies (Woyke 1987a). Furthermore, a mite-transfer study in South Korea showed that the number of progeny per infested brood cell increases with increasing number of foundress mites (Dongwon 2016). While one foundress produced 1.6 progeny on average, brood cells inoculated with two (2.4 progeny) or three (2.8 progeny) foundress mites supported higher numbers of progeny. This observation suggests that the fecundity of foundress Tropilaelaps mites is not inhibited when coinfesting the same brood cell.

Nonreproduction

With Varroa mites, an adult female is considered nonreproductive (NR) if no viable progeny is produced. It is thought to be influenced by increased removal of infested brood, a behavior displayed by the Varroa Sensitive Hygienic and Russian honey bees (Harris et al. 2010, de Guzman et al. 2015, Kirrane et al. 2015). Several studies showed that NR Tropilaelaps mites also vary. Using *A. mellifera* colonies, studies conducted in Afghanistan and Vietnam showed that 7–18% of foundress were infertile (Woyke 1987a), whereas in Thailand, about 30% of Tropilaelaps mites did not reproduce (Ritter and Schneider-Ritter 1988). Even higher NR rates were recorded by Kavinseksan (2003) in *A. mellifera* (50%) and *A. dorsata* (65%). *Apis mellifera* in South Korea also supported high NR (50%), which increases (up to 85%) with increasing number of foundress mites inoculated within brood cells (Dongwon 2016). In Thai *A. mellifera*, up to 93% NR was recorded (Khongphinitbunjong et al. 2013). The authors speculated that high NR may indicate increased hygienic behavior toward Tropilaelaps-infested brood. Although adult Tropilaelaps females are able to mate outside brood cells and can also mate several times (Woyke 1994a), the contribution of NR to the overall number of mites in the colony needs to be assessed.

Sex Ratio

Although the sex ratio of Tropilaelaps mites favors females, it varies considerably. In Afghanistan and Vietnam, a sex ratio of 1:2 (male to female offspring) was observed in brood cells of *A. mellifera* (Woyke 1987a), while a ratio of 1:5 was observed under laboratory conditions in Thailand (Rath et al. 1991). In active colonies of *A. dorsata*, the sex ratio (male to female adults) is 1:4 in brood cells and 1:2 on adult bees, whereas 1:5 to 1:8 in brood cells of abandoned combs (Kavinseksan 2003). Examinations of hive debris of *A. mellifera* in Thailand showed a similarly (1:3 to 1:4) skewed ratio of male to female adults (Rath et al. 1991). The sex ratios of Tropilaelaps mites found in hive debris of *A. dorsata* ranged from 1:2 to 1:56 (Rath et al. 1991, Kavinseksan 2003). The reason for this unbalanced sex ratio may be due to the haplodiploid sex determination system of Tropilaelaps mites, wherein males are produced from unfertilized eggs (Rath et al. 1991). Although female and male offspring can be produced from any egg during successive oviposition, daughters are relatively more common as first and second offspring, whereas sons are more common afterwards (Rath et al. 1991). However, the majority of foundress Tropilaelaps (51% in *A. dorsata* and 41–64% in *A. mellifera*) produced only one progeny; only about 1/3 of females produced at least two (Ritter and Schneider-Ritter 1988, Kavinseksan 2003). These observations are indicative of female offspring being laid more frequently. In addition to being lower in numbers, the males are also short lived compared with the females (5 vs. 50 d; Rath et al. 1991). Hence, a skewed sex ratio favoring females is realized, and contradicts the findings of Ritter and Schneider-Ritter (1988) that stated that male and female eggs are laid in relatively equal proportions.

Survival of Adults Outside Capped Brood Cells

Comparative infestation rates between brood and adult bees suggest that *T. mercedesae* spend relatively little time outside of brood cells. Depending on the location and time of the year, brood infestations by Tropilaelaps mites in *A. mellifera* colonies can range from 2–54% as compared with 1–3% infestations on adult bees (Woyke 1984, 1987c, b). Further work investigating brood to adult infestation rates suggests that Tropilaelaps mites remain outside sealed brood for one-tenth the time as Varroa mites (Woyke 1987c). Given that Varroa mites remain outside capped brood cells for 13 d (Schulz 1984), the authors deduced that Tropilaelaps mites spent ~1.3 d out of the cells. This short period allows the mites to have two generations in 25 d (Woyke 1987a). Accompanying work also supported this claim, observing that most female *T. mercedesae* remain outside of brood cells for 1–2 d (Woyke 1987c). However, in South Korea, unusually high phoretic rates of 18–22% have been reported (Dongwon 2016). Adult Tropilaelaps mites can also be seen on comb and other hive parts, where they are notorious for rapid locomotion (Pettis et al. 2013).

Laboratory studies investigating survival of adult female *T. mercedesae* showed similar trends. Koeniger and Muzaffar (1988) observed Tropilaelaps mites to survive for up to 25 h on adult bees of *A. mellifera*, 27 h on *A. cerana*, and 57 h on its native host, *A.*

dorsata. Likewise, maintaining workers at both ambient and broodnest conditions, Rinderer et al. (1994) confirmed that most *T. mercedesae* survive for only 1 d on adult *A. mellifera* workers. However, some individuals survived up to 3 d. Likely reasons for shortened life span on adults bees are because of a lack of morphological adaptations for attachment (Delfinado-Baker et al. 1992), and their inability to feed on adult bees. An examination of the gnathosomal structures of Tropilaelaps mites showed that their chelicerae are tearing organs, and therefore require a host with soft integument to function efficiently (Koeniger and Muzaffar 1988). In general, adult bees have hard integuments, but also have soft membranes around the joints or in between segments such around the neck and wing axillaries. However, possible feeding of Tropilaelaps mites was observed as the mouthparts appeared to be pierced into the soft membrane of the wing axillaries; this was accompanied by a pumping or pulsating motion of the opisthosoma (LIG and KK, personal observation). Conversely, *T. mercedesae* can survive an extended period of time on pupae maintained under laboratory conditions. Koeniger and Muzaffar (1988) observed Tropilaelaps mites to survive for >5 d on pupae as compared with 1 d on adult bees. A longer survival of 4 wk was observed when Tropilaelaps mites were kept with brood combs containing a constant supply of 4-d-old worker larvae (Woyke 1994b). This observation suggests that the Tropilaelaps mites may also feed on precapped stages of larvae. Without food, Tropilaelaps mites can survive for 1–3 d (Koeniger and Muzaffar 1988), which is similar to their survival time (1–2 d) on combs (Woyke 1984).

Phoresy and Dispersal

Like Varroa mites, Tropilaelaps mites can spread naturally within a colony, among colonies of the same apiary, or among apiaries via phoresy by both male and female mites (Rath et al. 1991). It is likely that the mouthparts (chelicerae) or claws (pretarsal ambulacra) are used to grasp host hairs. Several morphological characters of Tropilaelaps mites such as elongated body shape (facilitates movement among the bees and combs) and large ambulacra of the legs with claws (to gain attachment on the host body), support phoresy of a limited duration (Rath et al. 1991). Phoretic Tropilaelaps mites often assume a safe position typically between the thorax and the abdomen (petiole), or the head and thorax of adult bees (Ritter and Schneider-Ritter 1988, Delfinado-Baker et al. 1992, Khongphinitbunjong et al. 2012), to avoid honey bee grooming efforts (Khongphinitbunjong et al. 2012). Because drones do not perform social grooming like worker bees, drifting drones may also play an important role in dispersing mites among colonies (Rath et al. 1991).

Phoretic dispersal is achieved by worker bees robbing colonies of stored food (*A. dorsata* to *A. mellifera*, *A. mellifera* to abandoned *A. dorsata* nest, or *A. mellifera* to *A. mellifera*), and accidental drifting of infested bees (Laigo and Morse 1968, Fries and Camazine 2001). Since Tropilaelaps mites generally mate within brood cells before bee emergence, mated adult females are reliably dispersed, which increases their chance of establishing a new population in another colony or new site. Mites can also jump between host species (or among the Asian honey bees) when uninfested and infested foragers visit the same flowers simultaneously (Burgett et al. 1983, Woyke 1984, Delfinado-Baker and Aggarwal 1987). Illegal shipment of queens and packaged bees also promotes dispersal of Tropilaelaps mites around the world. Other beekeeping practices, such as making colony divisions or transferring brood frames from one colony to another, as well as migratory beekeeping, can spread these ectoparasitic mites. For most beekeeping countries, legislations prohibit or regulate importation of honey bees. However, accidental transportation of honey bees via swarms among cargo (e.g., ships, trucks) provides a means of spreading invasive species over long distances. Although Tropilaelaps mites exhibit short phoresy that may negatively affect their dispersal, vigilance is needed to contain the spread of Tropilaelaps mites around the world.

Population Dynamics

Information on the population dynamics of parasitic mites can be very useful as part of an Integrated Pest Management (IPM) program because beekeepers can properly time application of control measures. However, various factors likely drive mite population dynamics, including host hygienic behavior (Boecking et al. 1992, Delfinado-Baker et al. 1992, Khongphinitbunjong et al. 2012, Khongphinitbunjong et al. 2013), beekeeper-applied miticides (Garg et al. 1984, Burgett and Kitprasert 1990), other management techniques (Woyke 1985), as well as climate.

As parasites requiring brood to complete their life cycle, mite prevalence and intensity of Tropilaelaps mites can be high during periods of active honey bee brood rearing. However, these infestation parameters may also be driven by intergeneric (involving different genera of mites), interspecific (the same genus of mites but different species; also called intrageneric), and intraspecific (the same mite species but may belong to different mite populations) competition.

Apiary-Level Pattern

In countries experiencing temperate climates, prevalence fluctuation of Tropilaelaps mites in *A. mellifera* colonies qualitatively parallel that of Varroa mites in many regions of North America and Europe. This similarity is due to the availability of brood required for mite reproduction in these regions. In South Korea, Tropilaelaps mites were observed only in autumn, with 44% of the 43 apiaries being infested (Jung et al. 2000). Five years later, the proportion of apiaries infested with Tropilaelaps mites decreased to 26% during this time of the year (Lee et al. 2005). On the other hand, Varroa mites were found in 91% of sampled apiaries. Differences in the proportion of apiaries infested with either mite genera may have resulted from limited brood production in autumn and the ability of Varroa mites to survive extended broodless periods (Rosenkranz et al. 2010), unlike *T. mercedesae* which have short phoretic phase (Woyke 1985). In China, high proportions of *A. mellifera* apiaries were also found infested with Tropilaelaps mites in autumn (86%), followed by summer (67%), spring (17%), and winter (15%; Luo et al. 2011a). Apiaries located in southern China were much more likely to be infested (71 vs. 29%) because of extended broodrearing periods than those in the north, which has more temperate weather. It is also likely that migratory beekeepers moving colonies to the north in the spring for pollination and honey production reintroduce the mites each year.

Colony-Level Pattern

In subtropical and tropical regions, *T. mercedesae* prevalence also coincides with honey bee brood rearing. In Pakistan, near its western range limit, *T. mercedesae* can reproduce year-round in brood cells. However, prevalence peaked in May and October when *A. mellifera* brood rearing is high because of regional nectar flows (Camphor et al. 2005). In the Indian region of Jammu, the highest colony-level prevalence was observed from March to May (~32% of colonies) and September to November (~23% of colonies), when high brood

rearing activities of *A. mellifera* occur, and lowest in January (1%) and June to August (~2%), when brood production slows down (Abrol and Kakroo 1997). Similar trends in *A. dorsata* colonies were observed. Furthermore, 77% of 17 Thai *A. dorsata* colonies examined in March were infested by *T. mercedesae* (Burgett et al. 1990), suggesting that colony-level prevalence of *T. mercedesae* is higher in its native host *A. dorsata* compared with *A. mellifera*. Similarly, *T. clareae* was found in 88% of *A. dorsata* colonies, but only about 31% of *A. mellifera* colonies examined in the Philippines (Laigo and Morse 1968).

Brood Cell-Level Pattern

Variation in the prevalence of Tropilaelaps mites within brood cells also exists. In Pakistan, where brood rearing can occur year-round, brood cell prevalence in *A. mellifera* colonies ranged from ~14% during peak nectar flows (May and November) to 4% in winter, and 6% during the extreme heat in July (Camphor et al. 2005). Conversely in Kabul, Afghanistan, which experiences a cold, semi-arid climate, 20% of brood cells were infested in July, but nearly no infestation was detected in October when winter begins (Woyke 1984). Three years later, prevalence of 24% and 37% were observed in May and September, respectively (Woyke 1987a). In subtropical regions where brood rearing occurs year-round such as in northern Vietnam, the highest brood cell prevalence was observed between August and November (~23%), as well as in June (17.4%), compared with only 2% in July and August (Woyke 1987a). Differences in bee genotype may account for differences in brood cell prevalence.

Phenology and Mite Reproduction in Concurrently Infested Colonies

Tropilaelaps spp. share much of its range with *V. destructor*. Hence, concurrent parasitism by both Varroa and Tropilaelaps mites is frequently observed in *A. mellifera* colonies (Burgett et al. 1983; Woyke 1987a,b; Ritter and Schneider-Ritter 1988; Buawangpong et al. 2015), but has also been observed in *A. indica* (Abrol and Kakroo 1997). However, prevalence of Tropilaelaps mites is often greater than that of Varroa mites (Burgett et al. 1983, Abrol and Kakroo 1997, Buawangpong et al. 2015). Although Tropilaelaps mites have been observed in *A. indica*, *A. dorsata*, and *A. mellifera* in Jammu, India, coinfestations by Varroa and Tropilaelaps mites were only recorded in *A. indica* colonies (Abrol and Kakroo 1997). The seasonal population fluctuation of Tropilaelaps mites in *A. indica* followed that of the two other species (highest in March to May, and September to November). However, Varroa mites were only observed from February to May, with the highest infestation observed in April (Abrol and Kakroo 1997). Varroa mites have high drone brood preference over worker brood of *A. cerana* (Rath 1991b). It is possible that *A. indica* may also have periodic drone production like *A. cerana* does. Hence, this limited duration of infestation by Varroa mites in *A. indica* was probably due to the seasonal production of drone brood. In northern Thailand, seasonal differences in prevalence of Tropilaelaps mites were also observed, with a peak prevalence in September (10–15% brood cells infested) and lowest in January (2%) and August (<1%) (Buawangpong et al. 2015). In these colonies, rates of Varroa mite infestation were generally lower than those of Tropilaelaps mites but increased in July to September. In a separate assessment of colonies, the authors also observed that on average, the worker brood infestations of *T. mercedesae* (20%) were significantly higher than that of *V. destructor* (0.7%). Nevertheless, reproduction rates of both mites in these concurrently infested colonies were similar (Tropilaelaps = 1.5; Varroa = 1.7 progeny per foundress; Buawangpong et al. 2015). In South Korea, brood cell prevalence for *T. mercedesae* in *A. mellifera* colonies was 2% as compared with 18% for *V. destructor* (Lee et al. 2005). In the Philippines, *A. mellifera* colonies with higher infestations of *T. clareae* than Varroa mites in April had higher Varroa mites than *T. clareae* infestations in September (Cervancia and Fajardo 2002). A recent survey in the Philippines revealed that Varroa mites were found infesting *A. mellifera* colonies nationwide. However, Tropilaelaps mites (species unknown) were only observed coinfesting *A. mellifera* colonies in the Palawan Islands (Cervancia et al. 2016).

Concurrent infestation of Varroa and Tropilaelaps in the same brood cells is relatively rare in naturally infested *A. mellifera* colonies. In Thailand, <1% coinfestation of cells was observed (Ritter and Schneider-Ritter 1988). In contrast, a higher coinfestation rate of 26% was observed in South Korea (Dongwon 2016). *Tropilaelaps mercedesae* is believed to outcompete Varroa mites when they coinfest a brood cell (Burgett et al. 1983). In South Korea, both mites did not reproduce when artificially inoculated into the same brood cells (Dongwon 2016). In contrast, a study conducted in Thailand that also employed artificial infestation of cells showed that 85% of the deliberately coinfested pupae supported reproduction by both mites (Buawangpong et al. 2015). Furthermore, concurrent parasitism yielded higher reproductive rate by *V. destructor* (2.2 progeny per foundress) than did *T. mercedesae* (1.5 progeny). It is possible that chemicals or volatiles released by resident Tropilaelaps mites, or from the mite-feeding wounds of bee hosts, deter Varroa mites from invading or reproducing (Buawangpong et al. 2015), or vice versa. Roles of pheromones, visual cues, and acoustic signals in regulating invasion by Tropilaelaps mites need to be studied.

Pathology and Epidemiology

Damage at the Individual Level

Tropilaelaps mites have similar life histories and food requirements as Varroa mites. Hence, both mites inflict similar detrimental effects on infested hosts by weakening or killing brood or promoting viral infections in surviving adults (Laigo and Morse 1968, Morse and Laigo 1969, Atwal and Goyal 1971, Burgett et al. 1983, Kitprasert 1984; Fig. 3). Parasitism of *T. mercedesae* also reduces weight and longevity of infested adult bees (Khongphinitbunjong et al. 2016). Additionally, feeding activities of Tropilaelaps mites reduce total protein concentration of infested pupae (Negi and Kumar 2014), which may contribute to the alteration of immune responses and viral infections in parasitized pupae (Khongphinitbunjong et al. 2015). The impact of Tropilaelaps mites on the reproductive fitness of infested drones has not been studied.

Damage at the Colony Level

Without effective control treatment, population growth of Tropilaelaps mites increases rapidly in *A. mellifera* colonies (Rinderer et al. 1994). Infestations of *T. mercedesae* in brood cells can be high (>90%; Burgett et al. 1983, Kitprasert 1984, Ritter and Schneider-Ritter 1988), which can lead to low honey yield (Laigo and Morse 1968, Camphor et al. 2005, Raffique et al. 2012). Due to considerable morphological and physiological deformities inflicted by these parasites on infested bees, the colony becomes susceptible to wax moth infestation because of a declining bee population (Laigo and Morse 1968), or can lead to outright colony

death (Burgett and Akratanakul 1985, Camphor et al. 2005). Significant death of brood can also result in irregular brood patterns (Laigo and Morse 1968; Fig. 4A). In addition, opened or bald brood (Fig. 4B) can also be observed as a result of hygienic activities of worker bees (Ritter and Schneider-Ritter 1988). For *A. breviligula*, queenless colonies with laying workers have higher levels of *T. clareae* infestation than queenright colonies (Laigo and Morse 1968). Serious infestations of *T. clareae* and wax moths may trigger absconding in *A. breviligula* colonies (Laigo and Morse 1968).

Tropilaelaps Mites as Vectors of Pathogens

Many studies show that loss of *A. mellifera* colonies due to Varroa mites is aggravated by the viruses that they vector and from secondary infections of the wounds they inflict (Chen and Siede 2007, Wilfert et al. 2016). At present, the same conjecture cannot be formulated about Tropilaelaps mites because of limited research. So far, honey bees parasitized with *T. mercedesae* have been found to harbor DWV and Black queen cell virus. However, the presence of these two viruses is not related to the number of Tropilaelaps mites infesting the pupae (Khongphinitbunjong et al. 2015). Only DWV has been detected in the Tropilaelaps mites infesting virus-infected hosts (Dainat et al. 2009, Khongphinitbunjong et al. 2015). Higher levels and incidence of DWV have been observed in pupae infested with *T. mercedesae* compared with uninfested bees (Forsgren et al. 2009; Khongphinitbunjong et al. 2015,2016). *Tropilaelaps mercedesae* have tested positive for the antisense RNA of DWV (an indicative of viral replication) and thus, these mites appear to serve as biological vectors of DWV (Dainat et al. 2009, Forsgren et al. 2009). Nevertheless, some *T. mercedesae* collected from DWV-positive hosts are found negative for DWV (Forsgren et al. 2009, Khongphinitbunjong et al. 2015). Perhaps, the major negative impact of Tropilaelaps mite infestation is caused by the feeding of the mite itself (Khongphinitbunjong et al. 2015). While Varroa mites create one large wound for communal feeding (Kanbar and Engels 2005), Tropilaelaps mites inflict multiple, small wounds on developing host bees (Fig. 5).

Fig. 3. An *A. mellifera* worker bee with deformed wings caused by *T. mercedesae* (arrow) in Chiang Mai, Thailand (Photo by N. Soakaew).

Detection and Control

Diagnosis and Detection

Like Varroa mites, Tropilaelaps mites are ectoparasites that are associated with both brood and adult honey bees. Hence, methods of determining infestation or detecting their presence in colonies are very similar (Anderson and Roberts 2013, Dietemann et al. 2013).

Examining Brood Cells

Drone or worker brood can be examined by opening about 100–200 capped brood cells (de Guzman et al. 2007). Accurate assessment of mite reproduction and mite intensity (number of mites per infested brood) can be best performed by examining frozen, cut sections of capped brood because of the rapid movement of adult Tropilaelaps mites on combs.

Examining Adult Bees

Powdered Sugar

A sample of about 300 bees can be scooped into a jar or sealable plastic bag containing about two tablespoons of powdered sugar from the brood nest; it is best to use brood frames with emerging bees or with larvae that are about to be sealed. The container should be shaken gently for 1–2 min to evenly coat the bees and to dislodge mites. The bees are then dumped out over an 8-mesh screen to allow

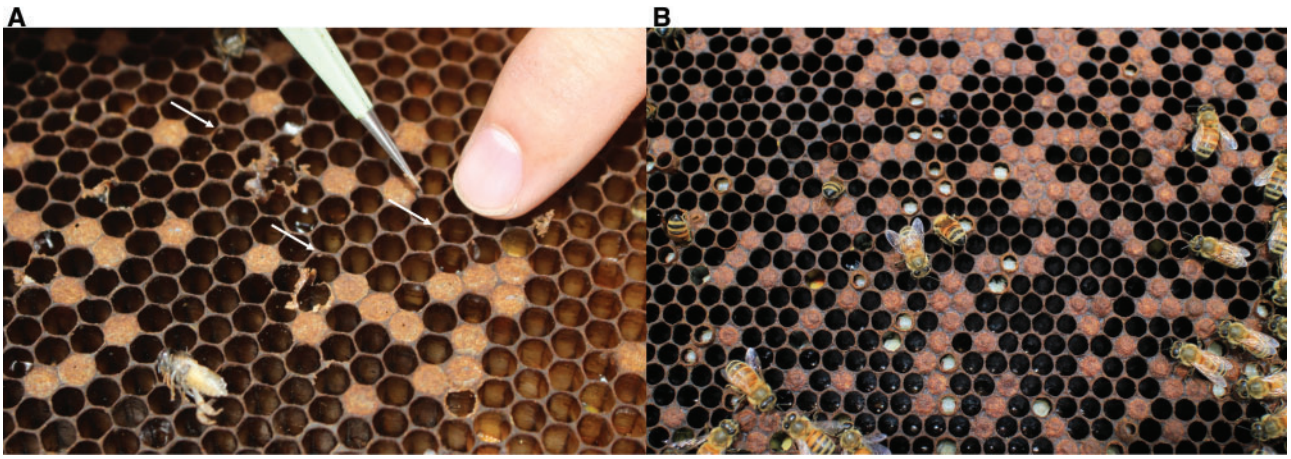

Fig. 4. (**A**) Spotty brood pattern of *Tropilaelaps*-infested brood of *A. mellifera* in Palawan, Philippines, and adult *Tropilaelaps* mites (arrows) on combs (Photo by L. de Guzman). (**B**) Opened brood from an *A. mellifera* colony infested with *T. mercedesae* in Chiang Mai, Thailand (Photo by K. Khongphinitbunjong).

Fig. 5. A. Two gravid adult females and one protonymph (arrow) of *T. mercedesae* feeding on a prepupa of *A. mellifera* in Andong, South Korea. Multiple brown to black spots are feeding injuries inflicted by the mites (Photo by K. Dongwon).

mites to fall onto light-colored paper or a tray. A light water mist sprayed over the paper or tray will dissolve the powdered sugar and thus, facilitate finding and counting of mites.

Soapy Water or Alcohol Wash

The use of dishwashing detergent is recommended because it is environmentally safer than ethanol (Rinderer et al. 2004). Using a mason jar, about 300 bees can be collected, covered in soapy water, and shaken vigorously for about 1 min to dislodge mites. The bees should then be poured into a pan where an 8-mesh screen catches the bees but allow the mites to pass through.

Bump Method

Banging combs on a paper-covered table helps dislodge Tropilaelaps mites (Laigo and Morse 1968). Recently, this method is recommended for early detection of Tropilaelaps mite infestations by bumping a frame of capped brood four times over a white metal pan to collect fallen mites (Pettis et al. 2013). Here, we propose several modifications to the method of Pettis et al. (2013): 1) a brood frame containing older pupae (purple-eyed or older) should be used since younger capped brood are easily damaged by bumping brood frames; 2) bumping the brood frame onto a sheet of light-colored paper or pan with a small amount of powdered sugar will prevent Tropilaelaps mites from escaping, and spraying a small amount of water thereafter facilitates locating and counting mites; and 3) scratching cell cappings with a capping scratcher before bumping brood frames will release mites within the brood cells. This latter technique will facilitate detection of Tropilaelaps mites, especially when infestation is low.

Mite Drop

Tropilaelaps mites that drop naturally can also be monitored for at least 24 h using sticky traps placed on the bottom board protected by 8-mesh screen. Hive debris can be collected using white paper inserts smeared with petroleum jelly and vegetable oil (1:1), or any commercially available sticky materials such as tanglefoot. Paper inserts can be examined under a microscope or with an illuminated magnifying glass.

Control and Management

Chemical Control

Acaricides

Chemical treatment is the most popular method for parasitic mite control because products are readily available and easy to use. However, pesticide use poses a risk for bee product contamination, accumulation of chemical residues in bee equipment, and the development of resistance to the chemical products by parasitic mites. Although there are no products specifically approved for the control of Tropilaelaps mites, chemicals used for Varroa control are also effective. Apistan (fluvalinate), Checkmite+ (coumaphos), and Bayvarol (flumethrin) have been used to treat *A. mellifera* colonies against Tropilaelaps mites in some regions of Asia (Lubinevski et al. 1988, Burgett and Kitprasert 1990, Camphor et al. 2005, Kongpitak et al. 2008). Applied as strips, both Apistan and Checkmite+ negatively affect the reproductive fitness of drones or the performance of queens (Rinderer et al. 1999, Haarmann et al. 2002, Burley et al. 2008). Strips of filter papers soaked in 15% potassium nitrate and 12.5% of amitraz solution are also used as a hive fumigant to suppress Tropilaelaps mites (Anderson and Roberts 2013). Four applications of 200 mg of precipitated sulfur per frame at 7-d intervals have also been recommended to control Tropilaelaps mites in India (Garg and Sharma 1988).

Organic Acids and Essential Oils

Formic acid, thymol, and a combination of thymol and oxalic acid showed highest efficacy against Tropilaelaps mites (Garg et al. 1984, Hoppe et al. 1989, Mahmood et al. 2011, Mahmood et al. 2012, Raffique et al. 2012). However, >2 ml of 60% formic acid applied onto a sponge per Langstroth comb can cause damage to bees (Ritter and Akratanakul, 2006). Thymol mixed with D-limonene, applied as a smoke or fumigant, reduced Tropilaelaps mite populations in colonies in South Korea (Choi et al. 2012). Tobacco smoke (tobacco placed inside the smoker) also caused mites to drop off bees (Anderson and Roberts 2013). Recently, lemon grass oil delivered through porous ceramics to control evaporation rates has been successfully used as a hive fumigant by lowering Tropilaelaps mite population in Thailand (Booppha et al. 2010). Although generally safe, organic acids have negative effects on honey bees. For example, formic acid is known to affect drone production (de Guzman et al. 1999), while thymol and oxalic acids reduce worker brood production (Higes et al. 1999, Floris et al. 2004).

All chemical treatments have to be suspended at least 8 wk before the honey flow season starts to avoid chemical contamination. Precautionary measures are needed when handling these chemicals.

Apicultural Practices

A variety of beekeeping practices can also be employed as an IPM program to drastically reduce chemical exposure of honey bee colonies while simultaneously reducing mite populations.

Interruption of Brood Rearing

Interruption of brood rearing results in an absence of suitable larval hosts, which forces Tropilaelaps mites to stay on adult bees. Since Tropilaelaps mites cannot survive on adult bees for a long period of time, this technique leads to the death of most mites in the colonies. Queens can be caged for 9 d and all capped brood destroyed (Woyke 1984, 1985). If brood is not destroyed, they can be placed in other colonies that are either queenless or have caged queens. Queens can also be caged for >21 d until all brood has emerged (Woyke 1993). Queen-caging prevents egg-laying, while the removal of uncapped brood deprives the mites from infesting suitable hosts. Two variations of this technique were offered by Dung et al. (1997): 1) the colony is devoid of all stages of brood while the queen is allowed to lay eggs; thereafter, the first two frames with capped brood are destroyed; 2) all brood (capped and uncapped) frames are kept in the colony, but the queen is removed and replaced with a recently capped queen cell; this allows for the emergence of all brood before the new queen can mate and oviposit. Thereafter, the first two frames with capped brood produced by the newly mated queen are destroyed. Broodlessness in colonies can also be achieved by removing all brood frames or starting colonies using broodless nuclei (Woyke 1984, 1985). These methods are not only labor-intensive but also destructive; therefore, they are considered impractical for beekeepers. Brood combs removed from colonies, together with the bees covering the frames, should be placed in an empty box next to the parent colony for emergence; the two can be united after 3 wk (Woyke 1993).

To avoid destruction of brood while at the same time allowing continuous brood production, the same outcomes can probably be achieved by using a Cloake board placed between two hive boxes (de Guzman et al. 2015). This consists of a queen excluder mounted to a wooden frame with grooves that allow for a removable sheet of thin metal (Cobey 2005). The metal sheet is installed to separate the upper (containing emerging brood frames only) from the lower box (containing the queen and precapped brood frames), and also serves as a temporary floor with an upper entrance. The lack of suitable hosts in the upper box will lead to starvation and death of Tropilaelaps mites that emerged with the bees. After 1 wk, bees in both boxes can be reunited by removing the metal sheet. The queen excluder prevents the queen from laying eggs in the upper box. This process can be repeated when capped brood in the lower box is about to emerge.

Natural Biological Processes

Honey bee colonies may undergo different processes such as migrating, swarming, or absconding. Brood production is interrupted during each of these events, disrupting Tropilaelaps mite reproduction.

Migrating, Swarming, or Absconding

For the giant honey bees, the broodless period is associated with the bees' seasonal migration (Kavinseksan et al. 2016). When these bees migrate to another site, the bees must build a new comb before the queen starts laying eggs. This extended broodless period from comb-building to having larval stages suitable for mite infestation may lead to death of most, if not all, phoretic Tropilaelaps mites since they cannot live extended periods on adult bees (Woyke 1984, Koeniger and Muzaffar 1988, Rinderer et al. 1994). This may explain why Kavinseksan (2003) detected no Tropilaelaps mites in newly established swarms of *A. dorsata* in Thailand. On the other hand, Woyke et al. (2004) observed that both *A. dorsata* in India and *A. laboriosa* in Nepal left sealed brood untouched in deserted combs even when the brood was dead due to mite parasitism or brood diseases. In Thailand, out of the 986 sealed brood examined (from 13 deserted combs), 133 (13.5%) were infested with Tropilaelaps mites (Kavinseksan 2003). The infestation levels of the 13 deserted combs of *A. dorsata* varied from 0 to 74%. Therefore, this behavior likely prevents the spread of Tropilaelaps mites or brood diseases in giant honey bees (Woyke et al. 2004). Similarly, swarming and absconding activities support broodless periods in *A. mellifera* colonies. Starting new colonies with package bees and frames with wax or plastic foundations also provides broodless stage in *A. mellifera* colonies.

Nesting Behavior

Nests of the giant honey bees can act as reservoirs of Tropilaelaps mites that can infest *A. mellifera* colonies, and vice versa (Kavinseksan et al. 2016). However, the nesting behavior of giant honey bees (original host) and their response to infested brood and phoretic mites can help regulate Tropilaelaps mite population. *Apis dorsata* is thought to remove mite-infested brood (Burgett et al. 1990) and phoretic Tropilaelaps mites (Rath et al. 1991, Büchler et al. 1992, Koeniger et al. 2002, Khongphinitbunjong et al. 2012). Since giant honey bee nests are built in the open, mites that fall off due to hygienic and grooming activities cannot return and reinfest colonies (Kavinseksan et al. 2016). In contrast, hives of cavity nesting *A. mellifera* have bottom boards where live mites fall due to hygienic and grooming activities by worker bees, but can hitchhike on passing bees to return to the broodnest. The use of screen bottom board can therefore prevent reentry of mites into *A. mellifera* colonies.

Environment

Climate

In temperate countries, little or no brood production in *A. mellifera* colonies occurs during winter months. *Apis mellifera* colonies overwintered in cold areas of Afghanistan were free of Tropilaelaps mites (Woyke 1984). However, *A. mellifera* colonies produce patches of brood during winter in South Korea, and therefore likely explain why populations of the species can be found in that country. *Apis dorsata* nests are usually covered with several layers of bee curtains to maintain nest temperature, which may also promote the production of small amounts of brood during winter. It is not known if giant honey bees in the Himalayas produce brood during winter months.

Mite-Resistant Honey Bees

Breeding for resistance to parasitic mites has proved to be successful both in the United States and Europe (Büchler et al. 2010, Rinderer et al. 2010). Because Tropilaelaps mites have life histories very similar to Varroa mites, breeding honey bees resistant to Tropilaelaps mites appears to also be feasible. Several studies in Thailand had demonstrated behavioral responses of *A. mellifera* toward adult Tropilaelaps or Tropilaelaps-infested brood that might serve as the basis of systematic breeding programs (Rath et al. 1991; Boecking et al. 1992; Büchler et al. 1992; Kavinseksan 2003; Khongphinitbunjong et al. 2012, 2013).

Hygienic Behavior

Bald brood, the condition where the wax cappings of pupae has been removed by worker bees, is thought by beekeepers to indicate heavy mite infestation levels in *A. mellifera* colonies (Pettis et al. 2013). At these levels, adult Tropilaelaps mites can be observed running on the surface of the combs; therefore, this hygienic behavior may interrupt mite reproduction.

The removal of mite-infested brood is a mechanism of resistance for Varroa-resistant stocks such as Varroa Sensitive Hygienic trait and Russian honey bees (Harris et al. 2010, de Guzman et al. 2015, Kirrane et al. 2015). The removal of infested brood interrupts egg-laying by the infesting mites, thereby limiting the total number of progeny produced or the number of progeny that reach adulthood. This trait also forces adult mites to become phoretic by exposing them to bees' grooming activities. This behavior has also been observed in Thai *A. mellifera* that remove about half of the brood cells that were artificially infested with Tropilaelaps mites, and even more (67%) if brood cells were infested with both Varroa and Tropilaelaps mites (Boecking et al. 1992). Brood hygiene may also explain the scattered brood pattern and the presence of opened and partly eaten brood in *A. mellifera* colonies having 2–54% Tropilaelaps mite infestation (Woyke 1984). This increased removal of brood infested by both mite genera may be due to the unusually high number of mites (adults plus progeny) because of mixed infestation within the cells. Also, a higher response to concurrently infested brood may be due to fast-moving Tropilaelaps mites within cells, or bleeding hemolymph from the many wounds inflicted on the developing host. Varroa is known to inflict one or two large wounds only per infested host (Kanbar and Engels 2004), while feeding of Tropilaelaps mites causes multiple small wounds (Fig. 5). This high removal of brood coinfested with Tropilaelaps and Varroa mites may explain why coinfestation of these mites in the same brood cell of *A. mellifera* is rare (Boecking et al. 1992, Buawangpong et al. 2015). Similar to Varroa mites (Rinderer et al. 2010, Kirrane et al. 2011), a high proportion of brood with nonreproductive Tropilaelaps mites may indicate increased hygienic behavior (Khongphinitbunjong et al. 2013).

Grooming Behavior

Grooming activity is thought to limit the number of phoretic attachment sites and reduce the number of mites undergoing dispersal (Delfinado-Baker et al. 1992). On its adapted host, *A. dorsata*, most phoretic Tropilaelaps mites are found near the wing base and petiole regions of adult bees (Khongphinitbunjong et al. 2012). Although the propodeum provides good protection against bee grooming, twisting of the body of *A. dorsata* irritates Tropilaelaps mites and forces them to go to more exposed sites (Büchler et al. 1992, Khongphinitbunjong et al. 2012). About 20–34% of fallen mites were injured in cages with *A. dorsata* (Koeniger and Muzaffar 1988, Khongphinitbunjong et al. 2012). However, aside from biting, mite displacement can also be caused by body shaking and wing beating in this honey bee species (Khongphinitbunjong et al. 2012). Allogrooming is not important for *A. dorsata* (Büchler et al. 1992), or *A. cerana* and *A. mellifera* (Khongphinitbunjong et al. 2012).

The removal of Varroa mites from adult bees can reduce Varroa mite population in *A. mellifera* colonies (Guzman-Novoa et al. 2012, Rinderer et al. 2013, de Guzman et al. 2015). In Asia, *A. mellifera* has only been exposed to Varroa and Tropilaelaps mites for >50 yr (Delfinado 1963). Nevertheless, it displays autogrooming against Tropilaelaps mites, but at lower levels than its adapted host *A. dorsata* (Khongphinitbunjong et al. 2012). Russian honey bees imported from the United States are more efficient in grooming Tropilaelaps mites than Thai *A. mellifera* (Kavinseksan 2003, 2012). Grooming by Thai *A. mellifera* was also found to be inferior to *A. cerana* and *A. dorsata*, as only about 50% of the mites were removed after 12 h; only 1/5 of the mites that fell and observed were injured (Khongphinitbunjong et al. 2012). Based on these observations, a selection program may result in a stock of *A. mellifera* resistant to Tropilaelaps mites.

Conclusion and Outlook

If Varroa mites can singly inflict unsurmountable problems to worldwide *A. mellifera* beekeeping, the possible introduction of Tropilaelaps mites outside its current range heightens existing dilemmas. At present, all aspects of research about *Tropilaelaps* are incomplete. Adequate knowledge on the biology and roles of both parasite and host is crucial in the development of an IPM program for these serious ectoparasitic mites. Immediate attention to the following research areas is encouraged:

1. *Apis mellifera* harbors many parasitic mite species, including internal and external *Acarapis*, *Varroa*, and *Tropilaelaps* species. Determining if interactions among these coinfesting mite genera or between two mite genera, especially Varroa and Tropilaelaps mites, is additive or synergistic is essential.
2. The transmission of pathogens in colonies experiencing mixed genera infestation may be higher than in colonies infested with parasitic mites from only one genus. The ability of different mite genera to transmit pathogens needs to be assessed.
3. Concurrent infestation of Varroa and Tropilaelaps mites in the same brood cell is rare. The cues that allow either mite genus to detect already infested brood can be an avenue for future research. Finding the chemical signals that deter invasion of either genus of mites may lead to potential management strategies.
4. The economic injury level and economic threshold of Tropilaelaps mites should be established to promote beekeeper IPM.
5. Physiological stresses brought about by concurrent parasitism may result in survival or performance variation among honey bee species or stocks of *A. mellifera*. Different honey bee species may have different susceptibilities to different mite genera or species, and different mite genera or species may have different reproductive rates on different honey bee species or different stocks of *A. mellifera*. Verification of these hypotheses may help understand why one mite genus is more dominant and virulent than others. Identifying the role of mite resistance is essential.
6. The majority of Tropilaelaps mites infesting a colony are protected inside capped brood cells, while a large proportion of Varroa mites are phoretic on adult bees. Thus, recommendations developed to control Varroa mites may not work effectively for Tropilaelaps mites. Optimum timing of treatments should be studied that take into consideration the short phoretic phase of Tropilaelaps mites.
7. Adult Tropilaelaps mites have a short phoretic period and are highly mobile on combs. Hence, sampling methods that accurately estimate tropilaelaps mite population in the colonies should be established.

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