Variation in the parasitic bee mite

Varroa jacobsoni Oud.

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(Invited paper)

Abstract – Initial searches found little evidence of genotypic or phenotypic variance in the parasitic bee mite Varroa jacobsoni, despite numerous reports of significant variation in the mite’s reproductive behaviour on its adopted host Apis mellifera. However, in a recent search that employed DNA sequencing techniques and large numbers of V. jacobsoni collected from the mites’ native host A. cerana throughout Asia, a remarkable amount of genetic variation was observed. Subsequent analysis of this variation, coupled with follow-up morphological and ecology-based studies, showed that V. jacobsoni was a species complex. Other work carried out as part of that study also showed that only two out of 18 genetically different mites within the complex have switched host to A. mellifera and become a pest of this bee worldwide. These two mites are not V. jacobsoni as has been assumed, but they belong to a group of mites that naturally infest specific populations of A. cerana on mainland Asia. These mites will soon be renamed as a new species. This and other reports of variation in V. jacobsoni are reviewed and discussed.

Varroa jacobsoni / morphological variation / reproductive variation / genetic variation / Apis mellifera / A. cerana

1. INTRODUCTION

The mesostigmatid mite, Varroa jacobsoni Oudemans, was first described as an ectoparasite of the Eastern honey bee, Apis cerana Fabricius in Java in 1904 [38], although it was subsequently found to parasitise A. cerana throughout Asia [28]. The mite later came to the attention of bee researchers when it shifted host to the Western honey bee, A. mellifera Linnaeus, following that bee’s introduction to Asia by man [11, 45]. This opportunistic host-shift led to the mite spreading from Asia to become an almost cosmopolitan pest of A. mellifera, although it has not yet been reported in Australia, New Zealand, Hawaii and parts of Africa [13, 34].

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Details of how *V. jacobsoni* shifted from *A. cerana* to *A. mellifera* are not clear. Some authors [36, 37] have proposed that the shift occurred when *A. mellifera* colonies were transported to Eastern Russia in the first half of this century. This could have allowed *A. mellifera* to come into contact with *Varroa*-infested *A. cerana*, which, until then, had been speciating allopatrically. Regardless of how the shift occurred, however, it is now generally assumed that *Varroa* mites that were natural parasites of mainland Asian populations of *A. cerana* were the first to come into contact with *A. mellifera*. This presumption is supported by early reports of *V. jacobsoni* infesting *A. mellifera*, and from early records of *V. jacobsoni* specimens in the Acarological Collection at Oregon State University, Corvallis, OR, USA, that were collected from *A. mellifera* in China [1].

Following the shift of *V. jacobsoni* to *A. mellifera*, significant efforts were directed at developing appropriate control methods for the mite [40, 41], at understanding the mites’ life-cycle and behaviour [8, 23] and with developing simulations of *V. jacobsoni* population dynamics [9, 33]. Very little attention was initially paid to variation in *V. jacobsoni*. It was not until the 1980s that some studies were directed at morphological variation among *V. jacobsoni* populations [21, 22, 25]. Searches for genetic variation soon followed [7, 14, 16, 27, 30], following numerous reports of significant reproductive variation among different mite populations infesting *A. mellifera* [2–4, 10, 17, 18, 20, 35, 42, 43, 46].

Initial searches for genetic variation in *V. jacobsoni* revealed only limited phenotypic differences between female *V. jacobsoni* collected from the USSR, Japan and Germany [25]. Subsequent searches among large numbers of mites collected from widespread colonies of *A. cerana* and *A. mellifera* also showed a lack of variation in phenotypic characters among female *V. jacobsoni*, except in their body size [21, 22]. The genetic identity of the mites used in those studies was not certain.

Nevertheless, the results clearly demonstrated that female mites infesting *A. cerana* were significantly smaller than those infesting *A. mellifera*, even though there was some overlap in the body size of mites from the two populations. Without a genetic basis, mites in the two groups were regarded as distinct ‘biotypes’. It is now clear that the mites used in those studies belonged to quite different genetic groups. A recent study

2. MORPHOLOGICAL VARIATION IN VARROA JACOBSONI

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Variation in the bee mite *Varroa jacobsoni* DNA (RAPD) technique. It indicated that *V. jacobsoni* infesting *A. cerana* in Malaysian Borneo were genetically distinct from *V. jacobsoni* infesting *A. mellifera* in the US and Germany [30]. Another study [4], which compared mitochondrial DNA (mtDNA) gene sequences, also showed that *V. jacobsoni* from *A. cerana* colonies of Javanese origin, which also lacked the ability to reproduce on *A. mellifera*, were genetically distinct from *V. jacobsoni* that were infesting and reproducing in *A. mellifera* colonies in Germany.

An extensive search for genetic variation among *V. jacobsoni* infesting *A. cerana* has only recently been completed [5, 6]. The level of variation detected was astonishing and, as these results will radically change the way *Varroa* is viewed in the future, they will now be elaborated on in some detail.

The study compared mitochondrial DNA (mtDNA) cytochrome oxidase I (CO-I) coding gene sequences obtained from adult female *V. jacobsoni* collected from populations of *A. cerana* distributed throughout Asia. Similar DNA sequences obtained from *V. rindereri* De Guzman and Delfinado and from *V. underwoodi* Delfinado-Baker and Aggarwal were also used in the study as a gauge of genetic distances between species.

In all, 18 genetically distinct types of mites (called haplotypes) were found. Each was assigned a name from the country or island in which it was discovered. For example, a ‘Korea haplotype’ was found on *A. cerana* in Korea, while a ‘Java haplotype’ was found on *A. cerana* in Java. Only one mite haplotype was found in any one country or isolated island, the exception being on the northern Philippine island of Luzon, where two distinct haplotypes were detected.

Computer-assisted analyses, using the parsimony and likelihood methods, placed the 18 haplotypes into two well-separated groups. Statistical support (bootstrap analyses) was extremely strong for the two groups, but relationships that had been indicated using parsimony and likelihood

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3. REPRODUCTIVE VARIATION IN *V. JACOBSONI* INFESTING *A. MELLIFERA*

Even though female *V. jacobsoni* from widespread populations show great consistency in the way they reproduce on their native host *A. cerana* by reproducing solely on drone (male) brood and hence causing minimal harm to colonies [28, 29, 39], their reproduction on their adopted host *A. mellifera* is not as uniform. Generally, in Europe, the Middle East, Asia and parts of the Americas, female *V. jacobsoni* readily reproduce on both the drone and worker brood of *A. mellifera*, and most bee colonies do not survive mite infestations unless effective mite control methods are implemented [19, 32]. However, in tropical and subtropical America where *A. mellifera* shows a tolerance to *V. jacobsoni* [17, 18, 20, 26, 31, 35, 42, 44, 46], fewer female *V. jacobsoni* reproduce on *A. mellifera* than is observed in Europe and the Middle East [42, 46], and mite offspring mortality rates are higher than in the UK [31]. The greatest variation in *V. jacobsoni* reproduction on *A. mellifera*, however, has been reported for female *V. jacobsoni* of Javanese origin; these are mites from which the species *V. jacobsoni* was first described in 1904. These mites fail to produce eggs or offspring when they enter *A. mellifera* drone or worker brood cells in different parts of Indonesia following their spread from nearby colonies of *A. cerana* [2–4].

4. GENETIC VARIATION IN *V. JACOBSONI* INFESTING *A. CERANA* IN ASIA

The earliest search for variation in *V. jacobsoni* on *A. cerana* employed the use of the random amplification of polymorphic DNA (RAPD) technique. It indicated that *V. jacobsoni* infesting *A. cerana* in Malaysian Borneo were genetically distinct from *V. jacobsoni* infesting *A. mellifera* in the US and Germany [30]. Another study [4], which compared mitochondrial DNA (mtDNA) gene sequences, also showed that *V. jacobsoni* from *A. cerana* colonies of Javanese origin, which also lacked the ability to reproduce on *A. mellifera*, were genetically distinct from *V. jacobsoni* that were infesting and reproducing in *A. mellifera* colonies in Germany.

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methods between three haplotypes from the Philippines (a Mindanao, Luzon 1 and Luzon 2 haplotype), and between these and one of the two main groups, were not supported statistically. Hence, the overall analysis resolved the 18 different haplotypes into two groups plus three other distinct haplotypes from the Philippines. One of the two main groups comprised mites from the Malaysia-Indonesia region. Included were the Malaysia, Sumatra, Borneo, Java, Bali, Lombok, Sumbawa, Flores and Ambon haplotypes. The other main group comprised mites from mainland Asia. It included the Japan/Thailand (found on *A. cerana* in both Japan and Thailand), Korea, China, Vietnam, Nepal and Sri Lanka haplotypes. The Sri Lanka haplotypes may yet be shown to be distinct from the mainland Asia group. A computer-generated tree drawn as an unrooted phylogram to emphasise key topological features between these haplotypes is shown in Figure 1.

The mean genetic distance (pairwise distance) between haplotypes in the Malaysia-Indonesia group and between haplotypes in the mainland Asia group was less than 2%, which was small enough to represent population-level variation. The mean genetic distance between these two groups was 6.2%, which was large enough to indicate species-level separation, as the distance between the Malaysia-Indonesia group to the distinct species *V. rindereri* was 6.4%, while the distance from the mainland Asia group to *V. rindereri* was 8.2%. Corresponding distances from the Malaysia-Indonesia group and the mainland Asia group to the only other known species of *Varroa*, *V. underwoodi*, were 9.0 and 9.1% respectively.

**Figure 1.** A bootstrap consensus tree drawn as an unrooted phylogram from data collected by Anderson and Trueman [6]. The purpose of this tree is to emphasise key topological features between genetically different mites within the *V. jacobsoni* species complex. The tree shows only those groups with > 50% bootstrap support.
Variation in the bee mite *Varroa jacobsoni* was found to be totally reliant on the local *A. cerana javana* for its survival, as it lacked the ability to lay eggs or produce offspring on *A. mellifera* brood. Hence, the Korea and Java haplotypes were shown to be genetically isolated from one another when existing sympatrically in the natural environment in Java.

Overall, these studies demonstrated that *V. jacobsoni* is more than one species. In a new classification that will soon appear in *Experimental and Applied Acarology* [6], *V. jacobsoni* will be redefined as encompassing mites of the Malaysia-Indonesia group given above, as this group contains the Java mite which was first described as *V. jacobsoni* in 1904 [38]. A new species name will be assigned to mites of the mainland Asia group, while further research is needed to determine the taxonomic positions of the three distinct mites from the Philippines.

5. GENETIC VARIATION IN *V. JACOBSONI* INFESTING *A. MELLIFERA* WORLDWIDE

Initial studies reported detectable allozyme differences between *V. jacobsoni* collected from *A. mellifera* in Brazil and Germany [27]. However, no allozyme differences were subsequently detected among *V. jacobsoni* collected from *A. mellifera* colonies at 12 different localities in Europe (six different countries) and at one locality in China [7]. In a more recent study that employed RAPD and a restricted set of polymerase chain reaction (PCR) primers from the larger primer set first used by Kraus and Hunt [30], two different *V. jacobsoni* genotypes were located in the US [14]. One of these (referred to as the Japanese or J genotype because it was assumed to have originated from Japan) was first found in Brazil and Puerto Rico, but was then later found at low incidences in North America and Canada [16] and in Thailand [12]. The other genotype (called the Russian or R genotype
because it was assumed to have originated from Russia) was first found in Russia and several states of the US [14], but was then found in Morocco and other parts of Europe [13].

As part of a search for variation in *V. jacobsoni* on *A. cerana* in Asia, Anderson and Trueman [5, 6] also conducted an extensive search for variation in *V. jacobsoni* infesting and reproducing in *A. mellifera* colonies in 32 different countries. This search also employed comparisons of mtDNA CO-I gene sequences as the means of detecting variation. The results showed that only two genetically distinct mites have become major parasites of *A. mellifera* worldwide. Both of these mites are also natural parasites of specific populations of *A. cerana* in Asia. The most prevalent was the Korea haplotype, which is a natural parasite of *A. cerana* in Korea. It was detected on *A. mellifera* in Africa, Europe, the Middle East, Asia and the Americas. Much less common was the Japan/Thailand haplotype, which is a natural parasite of *A. cerana* in Japan and Thailand. It was detected on *A. mellifera* in Japan, Thailand and the Americas. These two mites do not belong to the newly redefined *V. jacobsoni* but to the mainland Asia group of mites, for which a new species name has been proposed and which will soon appear in publication [6]. Some characteristics of the Korea and Japan/Thailand haplotypes are compared with those of the Java haplotype in Table I.

6. CONCLUSIONS

The recent discoveries of morphological, behavioural and genetic variation in *V. jacobsoni* have emphasised the value of studying a pest on its native host. The extent of genetic variation that has been uncovered among *V. jacobsoni* infesting *A. cerana* in Asia is remarkable, and probably reflects a long period of co-evolution between the mite and the bee. However, it is still premature to speculate on such co-evolution because phylogenetic data for Asian bees are not yet conclusive [47], and further phylogenetic information is still required for *Varroa* mites that infest *A. cerana* in certain parts of Asia, particularly in India and Pakistan [6].

Of particular interest from the recent work on genetic variation in *V. jacobsoni* is the finding that only two out of 18 genetically different mites that have been concealed within the *V. jacobsoni* species complex have successfully switched host to *A. mellifera* and become serious pests. These two mites, the Japan/Thailand and Korea haplotypes, now occur sympatrically in the US. Each has been referred to in previous studies from the US as the Japan or J genotype and the Russian or R genotype respectively [12–16], while the Korea haplotype has also been referred to in yet another study as the GER genotype [4] (Tab. I). The system used by Anderson and Trueman [6] of naming these and other mites in the *V. jacobsoni* species complex after the countries from which they occur naturally on their native host *A. cerana* is more conventional.

In recent years there has been much conjecture about the presence and source of the Japan/Thailand and Korea haplotypes in the US. In the recent work reported by Anderson and Trueman [6], the Japan/Thailand haplotype was the only mite detected in samples collected from *A. mellifera* in Brazil during the late 1980s and early 1990s, whereas mites that were collected from the same bee in Brazil in 1997 were a mixture of Japan/Thailand and Korea haplotypes, with the Japan/Thailand haplotype being most common. Similarly, all the mites that were examined from North America in the early 1990s were solely Korea haplotypes, whereas those examined from 1997 onwards were mixtures of the Japan/Thailand and Korea haplotypes, with the Korea haplotype being by far the most common. Hence it is likely that two separate introductions of *Varroa* mites occurred into the Americas, as another study has already indicated [13].
Table I. Characteristics of the Korea, Japan/Thailand and Java haplotypes.

<table>
<thead>
<tr>
<th>Haplotype</th>
<th>Synonyms</th>
<th>Natural parasite of <em>A. cerana</em> (location)</th>
<th>Infests and reproduces on <em>A. mellifera</em> (location)</th>
<th>Species*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Korea</td>
<td>Russian genotype [14]</td>
<td>Korea</td>
<td>Europe, Middle East, South Africa, Asia, North and South America</td>
<td>New species [6]</td>
</tr>
<tr>
<td></td>
<td>R genotype [13]</td>
<td></td>
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<tr>
<td></td>
<td>GER genotype [4]</td>
<td></td>
<td></td>
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<tr>
<td>Japan/Thailand</td>
<td>Japan genotype [14]</td>
<td>Japan and Thailand</td>
<td>Japan, Thailand, North and South America</td>
<td>New species Same species as the Korean haplotype [6]</td>
</tr>
<tr>
<td></td>
<td>J genotype [13]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Java</td>
<td>PNG genotype [4]</td>
<td>Indonesia (Java, Sulawesi, Timor, Irian Jaya), Papua New Guinea</td>
<td>Does not reproduce on <em>A. mellifera</em></td>
<td><em>V. jacobsoni</em> [6, 38]</td>
</tr>
</tbody>
</table>

* The new species name proposed for the Korea and Japan/Thailand haplotypes will soon appear in *Experimental and Applied Acarology*. 
The detection of only the Japan/Thailand haplotype in early collections from Brazil is consistent with a report that *V. jacobsoni* was first introduced to Brazil on *A. mellifera* imported from Japan via Paraguay in 1972 [19]. Hence, it is most likely that this event introduced the Japan/Thailand haplotype to the Americas. However, the source of introduction of the Korea haplotype into the Americas will probably remain unknown, as this mite is the commonest mite on *A. mellifera* worldwide and therefore could have been introduced from any one of many different locations. Now that the Japan/Thailand and Korea haplotypes are sympatric in the US it is likely they will interbreed, as they are genetically very close. To examine the interactions between these mites, new genomic DNA diagnostic markers will be needed, and should be developed from genetically pure populations of each mite, which can be found on *A. cerana* in either Japan or Korea.

Finally, the recent finding that only two out of the 18 genetically different mites that have been concealed within the *V. jacobsoni* species complex have switched to *A. mellifera* raises the question of why other mites closely related to those mites (e.g., the Vietnam, China and Nepal haplotypes) have not. Recent studies in Vietnam have indicated that the Vietnam haplotype, which infests the indigenous strain of *A. cerana*, and the Korea haplotype, which infests the imported *A. mellifera*, are isolated, and that this isolation seems to be linked with the inability of the Vietnam haplotype to reproduce on *A. mellifera* [24]. Finding the reasons why some *Varroa* mites can reproduce on *A. mellifera* while others cannot may well provide the key to determining methods for controlling the Japan/Thailand and Korea haplotypes on *A. mellifera*, without the need to resort to chemical acaricides.

Résumé – Diversité chez l’acarien *Varroa jacobsoni* Oud., parasite des abeilles. Les études initiales sur la morphologie ont montré peu de différences, à l’exception de la taille, entre les femelles de *Varroa jacobsoni*. Puisque les acariens parasitant la petite abeille *Apis cerana* sont significativement plus petits que ceux qui parasitent l’abeille *A. mellifera* plus grosse, on a tout d’abord supposé que les différences de taille dépendaient de l’espèce hôte. On connaissait depuis longtemps l’existence de différences dans la reproduction de l’acarien sur son nouvel hôte, *A. mellifera*. Les femelles de l’acarien se reproduisent sans difficultés sur le couvain de mâles et le couvain d’ouvrières d’*A. mellifera* en Europe, au Moyen-Orient, en Asie et dans certaines régions d’Amérique. La plupart des colonies ne survivent pas à l’attaque parasitaire sans méthode de lutte efficace. Dans quelques régions tropicales et subtropicales d’Amérique, les acariens se reproduisent nettement moins qu’en Europe ou au Moyen-Orient. La mortalité des acariens est plus élevée qu’en Angleterre, si bien qu’*A. mellifera* se montre tolérante à *V. jacobsoni* dans la zone tropicale de l’Amérique du Sud. Pourtant, lors de recherche en Indonésie, on a mis en évidence que les acariens de Java, qui avaient été décrits en 1904 sous le nom de *V. jacobsoni*, ne pouvaient pas du tout se reproduire sur *A. mellifera*. D’autres facteurs, comme des différences dans le génotype des acariens, pourraient influer la capacité à se reproduire.

Au début, la recherche de différences génétiques s’est limitée presqu’unique aux populations présentes sur le nouvel hôte, *A. mellifera*, et on a trouvé peu de diversité. Les études plus récentes utilisant les techniques de séquençage de l’ADN ont porté sur un beaucoup plus grand nombre d’échantillons d’acariens de l’hôte originel, *A. cerana*, provenant de toute l’Asie. Au total 18 types différents d’acariens (haplotypes) ont été décelés. Le nom du pays ou de l’île d’où il était issu a été attribué à chaque haplotype. Les analyses assistées par ordinateur ont classé les 18 haplotypes en deux groupes principaux, plus trois haplotypes distincts venant des Philippines. L’un des
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Deux groupes principaux comprend les acariens de la région malaise-indonésienne (Malaisie, Sumatra, Bornéo, Java, Bali, Lombok, Sumbawa, Flores et Ambon). Dans l’autre groupe principal on trouve les acariens du continent asiatique (Japon, Corée, Chine, Vietnam, Népal et Sri Lanka). La distance génétique moyenne des haplotypes au sein de chaque groupe principal est inférieure à 2%. Cette valeur est si petite qu’il s’agit là bien de variations au niveau de la population. La distance génétique moyenne entre les deux groupes principaux est de 6,2 % ; cette différence est suffisamment grande pour indiquer une séparation au niveau des espèces.

D’autres recherches non génétiques ont montré que les acariens du continent sont nettement plus gros et moins ronds que ceux du groupe Malaisie-Indonésie (Fig. 1). On a trouvé en outre que l’haplotype de Java était génétiquement isolé de l’haplotype de Corée. Outre les différences génétiques, les différences phénotypiques et les barrières de reproduction indiquent qu’il s’agit de deux espèces différentes correspondant aux deux groupes principaux. Dans la nouvelle classification, V. jacobsoni est redéfini comme étant le type malais-indonésien, alors que le type du continent asiatique reçoit un nouveau nom (à paraître dans Experimental and Applied Acarology).


Varroa jacobsoni / variabilité / variabilité génétique / variabilité morphologique / variabilité reproductive / Apis mellifera / A. cerana

Variation. Die neueren Arbeiten mit einer DNA Sequenzierung untersuchten sehr viele Milbenproben vom ursprünglichen Wirt A. cerana aus ganz Asien. Insgesamt wurden 18 unterschiedliche Typen von Milben (Haplotypen) nachgewiesen. Jedem Haplo-
typ wurde der Name des Landes oder der Insel zugeordnet, aus denen er stammte. Computer-gestützte Analysen ordneten die 18 Haplotypen in zwei Hauptgruppen und in drei zusätzliche distinkte Haplotypen aus den Philippinen ein. Eine der beiden Haupt-
gruppen umfasst die Milben der malayisch-
indonesischen Region (Malaysia, Sumatra, Borneo, Java, Bali, Lombok, Sumbawa, Flo-
res und Ambon). In der anderen Haupt-
gruppe fanden sich Milben vom Festland Asien (Japan, Thailand, Korea, China, Viet-
nam, Nepal und Sri Lanka). Die mittlere 
genetische Distanz der Haplotypen inner-
halb der Malaysia-Indonesien bzw. der Fest-
land-Gruppe war weniger als 2 %. Dieser Wert ist so klein, dass es sich hier wohl um Populationsvariationen handelt. Die mitt-
lere genetische Distanz zwischen den Haupt-
gruppen betrug 6,2 %. Der Unterschied ist 
groß genug, um eine Trennung auf der 
Ebene von Arten vorzunehmen. Weitere

derschnittliche Artenhandelt. Der Unterschied ist

Ein Teil dieser Untersuchungen bezog sich auch auf die genetischen Variationen der Milben auf A. mellifera in 32 Ländern. Nur zwei genetisch unterschiedliche Milbentypen haben sich weltweit zu Parasiten von A. mellifera entwickelt. Beide sind natürli-
che Parasiten von spezifischen A. cerana Populationen. Am weitesten hat sich der Korea Haplo-
typ verbreitet. Er wurde in Afrika, Europa, Asien, im Mittleren Osten und in Amerika entdeckt. Der Japan/Thail-
land Haplo-
typ ist seltener. Er wurde nur in Japan, Thailand und Amerika gefunden. Diese beiden Milbentypen gehören zur Fest-
landgruppe und werden den neuen Namen erhalten. Die Konsequenzen dieser neuen 
Befunde für die zukünftige Forschung und

die alternativen Behandlungsmethoden
werden diskutiert.

**Varroa jacobsoni** / **Typenvielfalt** / **Morphologie** / **Reproduktion** / **Genetik** / **Apis mellifera** / **A. cerana**

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