**Supplementary material**

***Varroa destructor*: A complex parasite, crippling honeybees worldwide**

Kirsten S. Traynor,1\* Fanny Mondet,2 Joachim R. de Miranda,3 Maeva Techer,4 Vienna Kowallik,4 Melissa A. Y. Oddie,3 Panuwan Chantawannakul,5 and Alison McAfee6

1. Global Biosocial Complexity Institute, Arizona State University, Tempe, AZ, USA

2. INRAE, Abeilles et Environnement, Avignon 84914, France

3. Department of Ecology, Swedish University of Agricultural Sciences, Uppsala 750 07, Sweden

4. Ecology and Evolution Unit, Okinawa Institute of Science and Technology Graduate University (OIST), Okinawa, 904-0495, Japan

5. Environmental Science Research Center (ESRC), Faculty of Science, Chiang Mai University, 50200, Chaing Mai, Thailand

6. Department of Entomology and Plant Pathology, North Carolina State University, Raleigh, North Carolina, USA

\*Correspondence: ktraynor@asu.edu (K.S. Traynor).

**Box S1. Varroa species identification**

The presence of varroa mites on their hosts and into newly introduced areas has been notified in different ways. As the global invasion by varroa mites became a rapidly growing problem, developing methods to accurately identify the culprit behind Western honeybee colony losses became essential. Given that varroa mites form a cryptic species complex [S1], an on-field glance diagnosis made by a non-taxonomist expert is challenging or almost impossible. Since the 1970s and with the help of beekeeping movements, what was described as “*V. jacobsoni*”, expanded its range out of Asia by conquering several countries each year [S2]. Varroa is an animal notifiable by the OIE. The development of molecular markers was a game-changer and allowed a major taxonomic revision in 2000. As its name indicates, “*V. destructor*” is the real identity of the cosmopolitan Western honeybee nightmare while *V. jacobsoni* remained unable to reproduce on this host. Despite its status as notifiable infectious disease, *V. destructor’s* presence is not systematically reported nor confirmed in the OIE database even when confirmed by molecular approaches

When its presence is reported, some still prefer the rapidity and affordability of morphometrics to report *V. destructor*: the slightly larger and wider in body size than *V. jacobsoni*. Nonetheless, the mtDNA barcoding of the COX1 gene slowly grew as standard method to report the novel presence of Varroa [S3]. One consequence of the later availability of molecular tools in Varroa invasion is that all observations of “*V. jacobsoni*” made before the 2000 research milestone may be difficult to confirm and more so in Asia where several species coexist. Another problem is that once the parasite settled in a new area, varroa population species and strains composition are not systematically checked if so, it is rare that the process is repeated over time. Considering that varroa populations in a region remained the same over the course of the invasion could be a big bias in mite control as i) more jumps than expected occurred in the varroa genus onto *A. mellifera* [S4-S6], and that ii) honeybee-varroa is a dynamic co-evolutive system in which arm races for survival shape both host and parasite populations [S7]. As a striking case, varroa populations in South America [S8], North America [S9, S10], and Japan [S4, S11] have been experiencing a rather quick turnover as the less “virulent” Japanese *V. destructor* was replaced by the more “virulent” Korean one.

**Box S2. Classification of haplotypes and haplogroups**

The concept of varroa haplotype has changed almost every decade as different mitochondrial markers were adopted to study their genetic variability in native and invasive populations. Following the taxonomic revision in 2000, haplotype for Varroa mites was considered to correspond to the 458-nucleotide identity of the partial COX1 mtDNA sequence (except 426-nt for *V. rindereri* AF107261) [S1]. A total of 18 haplotypes were named by the geographical location they were first obtained and depending on their phylogenetic relationship: “LOCATION”. Building on that basis is a novel haplotype with at least one SNP difference was found and the country name already used, then a number was simply added as “LOCATION+NUMBER” (e.g., China 2 AY372063 [S12] and Borneo 2 AY037890 [S13]). This unspoken rule was respected until 2010, where haplotype meaning changed to the 2696 nucleotide identity of partial COX1, COX3, ATP6 and CYTB mtDNA genes concatenated sequences. These new haplotypes were supposedly building on the basis of previous COX1 458-nt identity and if variation was detected in other mtDNA genes then sub named with “LOCATION+NUMBER+SUB-NUMBER” (e.g., Japan J1-1, J1-2, J1-3, J1-4, J1-5 and J1-6). Additionally, Navajas et al. [S4] defined that “mites with identical COX1 sequences were regarded as members of the same ‘haplogroup’ and, mites of the same haplogroup that showed variation within their concatenated sequences were regarded as variants of a particular haplogroup.”

However, by aligning all sequences from these studies, we found some possibly undetected confusion regarding this naming rule that could be problematic when referring in the future to one haplotype. First, *V. destructor* Korean K1-1 and K1-2 sequences are 100% identical and should be considered as K1-1/2. Haplotypes K1-1, K1-2, K1-3 and K1-4 were claimed identical on the 458 bp of the mitochondrial COX1 gene and to be part of the same K1 haplogroup [S4]. Yet, contrary to other haplogroups like J1 or we found that K1-4 differed from one transition in position 1125 (A > G) from other K1 haplotypes. Other confusion arises with Chinese haplogroup C2 (GQ379067) [S4] which could naively be considered the former described China 2 (AY372063) [S12]. To help clarify this, we proposed to redefine the haplogroups and give some advice for future naming (underlying supplementary data is all available via the interactive map weblink – see bottom of Box S3):

1. Mites with identical COX1 sequence based on the region chosen by Anderson and Trueman (2000) (AJ493124.2 COX1 positions 698 to 1155, included) should be considered as part of the same haplogroup.

2. If at least one SNP appears on the 458 nucleotide COX1 fragment, then the novel haplotype should be named “LOCATION+NUMBER”.

3. If additional non-described variation is found in COX3, ATP6 or CYTB standard markers is found, then the new haplotype should be named as “LOCATION+NUMBER+SUB-NUMBER” following the previous existing order.

In the near future, the availability of two varroa reference genomes will offer huge opportunities to get genome-wide and population informative markers as diagnostic tools. We advise that this nomenclature is followed as much as possible to allow temporal tracking the evolution Varroa population genetic diversity and structure.

**Box S3. Host distribution of haplotypes**

To better understand the temporal dynamic of *V. destructor* populations during the worldwide invasion, we visually reported the distribution of species and strains/lineages only confirmed by mtDNA COX1 sequencing. Such an approach has previously provided a distribution map emphasizing the supposed parapatry trend [S14] between the two sister species *V. destructor* and *V. jacobsoni* found on their original host and sympatry with the related *V. underwoodi* [S15].

For this, we reviewed 68 articles from 1995 to 2020 using either RAPD, mtDNA analysis (PCR-RFLP, sequencing) and/or nuclear microsatellites on varroa mites or environmental honey DNA [S16]. We collected distribution data about varroa species identity, mtDNA haplogroup, date of sampling, geographical localization, honeybee host. For geographical localization, three cases occurred: a) exact coordinates were available, b) city or locality was available and c) no localization was available outside of the country level. In the second case, we approximated the geographical position as the center of the city/locality or placed it to the nearest Agricultural Institute or Academic Center/University as some past sampling was known to be carried in experimental research apiaries (Supplementary Data 2).

In addition, 485 mitochondrial sequences were downloaded from NCBI Genbank (last update on the 01 February 2020) for which for the same information if not included in the previous papers list. We obtained three mitogenomes, 387 partial COX1 sequences (length ranging from 188 to 1088bp), 36 partial COX3 sequences (ranging from 323 to 436 bp), 36 partial ATP6 sequences (ranging from 287 to 339 bp), 23 partial CYTB sequences (ranging from 899 to 985 bp). All COX1 sequences were blasted and aligned to 44 reference mtDNA haplotypes (Supplementary Data 3) [S1, S4, S6, S12, S13, S17-S19]. Despite highly variable length and inconsistent sequence overlapping due to the usage of variable primers and high sequences trimming, we expanded the known COX1 haplogroups (Supplementary Data 2). Following the nomenclature rules, we found that *V. destructor* is the most diverse with 31 haplogroups (including 22 K-like), followed by *V. jacobsoni* with 19, five for *V. underwoodi*, for undetermined *Varroa* sp. and one for *V. rindereri*. We use these haplogroups to build an interactive distribution map of the varroa mites on their honey bee hosts mikheyevlab.github.io/varroa-mtDNA-world-distrib/.

The R code for these interactive maps are freely available on the GitHub link with the data tables used to build the points and country layers.

**Box S4**. **How can we ethically cull colonies?**

The decision to kill a bee colony is never easy, nor taken lightly. It is done out of necessity, to protect other colonies or to comply with the law. However, once a decision has been made to euthanize a colony, the most ethical approach is to make this as quick, painless and thorough as possible. The methods used vary by region and country. We advocate that individuals check with their apiary inspection service or veterinary institutions for the legal and most humane ways to eliminate the colony. Some will eliminate the entire colony. Others will sacrifice the queen, treat the remaining bees and brood with a miticide and then recombine with healthy colonies or add a new queen, depending on the appropriate situation and the health of the bees. Recombining can inadvertently allow the virulent virus to continue to exist even though varroa infestation is reduced, and risks perpetuating miticide-resistant varroa. Hence, long term it may be wiser to eliminate the entire colony, though not all beekeepers are comfortable with euthanization. These types of choices are never easy, as you weigh the benefits and drawbacks of protecting bees from individual colonies versus the entire apiary population.

**Table S1. Summary of current knowledge about honeybee viruses**.1

|  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **VIRUS** | **Major Strains** | **Family** | **Order** | **Genome** | **TRANSMISSION** | | | | | **SEASON** | | |
| ORAL-FECAL | VARROA | CONTACT | VERTICAL | ENVIRONMENT | SPRING | SUMMER | AUTUMN |
| Deformed wing virus | DWV-A | Iflaviridae | Picornavirales | ssRNA(+) | **+** | **+** | - | **+** | **+** | + | ++ | **+++** |
| DWV-B | **+** | **+** | - | **+** | **+** | + | ++ | **+++** |
| DWV-C | **?** | **?** | ? | **?** | **?** | ? | ? | ? |
| Egypt bee virus\* | EBV | ? | ? | ? | ? | ? | ? | ? | ? |
| Bundaberg bee virus 6 | QLD-14 | **?** | **?** | ? | **?** | **?** | ? | ? | ? |
| NT-12 | ? | ? | ? | ? | ? | ? | ? | ? |
| Slow bee paralysis virus | SBPV | **+** | **+** | - | ? | **+** | + | + | + |
| Moku virus | MV | ? | ? | ? | ? | ? | ? | ? | ? |
| Renmark bee virus 2\* | SA-5 | ? | ? | ? | ? | ? | ? | ? | ? |
| Varroa destructor virus-2 | VDV-2 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 3\* | WA2-20 | ? | ? | ? | ? | ? | ? | ? | ? |
| VN2-2 | ? | ? | ? | ? | ? | ? | ? | ? |
| VN2-6 | ? | ? | ? | ? | ? | ? | ? | ? |
| Robindale bee virus 4 | VN3-43 | ? | ? | ? | ? | ? | ? | ? | ? |
| Bundaberg bee virus 5 | QLD-13 | ? | ? | ? | ? | ? | ? | ? | ? |
| Bundaberg bee virus 4 | QLD-11 | ? | ? | ? | ? | ? | ? | ? | ? |
| Sacbrood virus | SBV | **+** | - | - | ? | **+** | **+++** | ++ | + |
| TSBV | **+** | ? | ? | ? | ? | ? | ? | ? |
| Darwing bee virus 2\* | NT-6 | **?** | **?** | ? | **?** | **?** | ? | ? | ? |
| NT-17 | ? | ? | ? | ? | ? | ? | ? | ? |
| Acute bee paralysis virus | ABPV | Dicistroviridae | **+** | **+** | - | **+** | **+** | + | **+++** | ++ |
| KBV | **+** | **+** | - | **+** | **+** | + | ++ | **+++** |
| IAPV | **+** | **+** | - | **+** | **+** | + | ++ | ++ |
| Robindale bee virus 2\* | VN1-57 | ? | ? | ? | ? | ? | ? | ? | ? |
| Empeyrat virus | NT-5 | **?** | **?** | ? | **?** | **?** | ? | ? | ? |
| QLD-7 | **?** | **?** | ? | **?** | **?** | ? | ? | ? |
| Bundaberg bee virus 1 | QLD-6 | ? | ? | ? | ? | ? | ? | ? | ? |
| Bundaberg bee virus 2\* | QLD-4 | ? | ? | ? | ? | ? | ? | ? | ? |
| Aphid lethal paralysis virus | ALPV | ? | ? | ? | ? | **+** | - | **+++** | - |
| Rhopalosiphum padi virus | RhPV | ? | ? | ? | ? | ? | ? | ? | ? |
| Big Sioux river virus | BSRV | ? | ? | ? | ? | **+** | - | **+++** | ++ |
| Apis dicistrovirus | ADV | ? | ? | ? | ? | ? | ? | ? | ? |
| Robinvale bee virus 1\* | VN1-10 | ? | ? | ? | ? | ? | ? | ? | ? |
| Hobart bee virus 1\* | TAS-7 | ? | ? | ? | ? | ? | ? | ? | ? |
| Robindale bee virus 3\* | VN1-50 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 1\* | WA2-13 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 2\* | WA1-14 | ? | ? | ? | ? | ? | ? | ? | ? |
| Black queen cell virus | BQCV | **+** | **~** | - | **+** | **+** | + | **+++** | + |
| Renmark bee virus 1\* | SA-7 | ? | ? | ? | ? | ? | ? | ? | ? |
| Arkansas bee virus\*\* | ArkBV | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Berkeley bee virus\*\* | BerkBPV | ? | ? | ? | ? | ? | ? | ? | ? |
| Renmark bee virus 3 | SA4 | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Robinvale bee virus 8 | VN1-22 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 5\* | WA1-24 | ? | ? | ? | ? | ? | ? | ? | ? |
| Robinvale bee virus 5\* | VN1-15 | ? | ? | ? | ? | ? | ? | ? | ? |
| Darwin bee virus 6 | NT-8 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 4\* | WA2-63 | ? | ? | ? | ? | ? | ? | ? | ? |
| Robinvale bee virus 9\* | VN3-31 | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Darwin bee virus 5 | NT1 | ? | ? | ? | ? | ? | ? | ? | ? |
| Robinvale bee virus 7\* | VN1-35 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 7\* | WA1-16 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 6\* | WA2-62 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 9\* | WA1-9 | ? | ? | ? | ? | ? | ? | ? | ? |
| Renmark bee virus 4 | SA-10 | ? | ? | ? | ? | ? | ? | ? | ? |
| Renmark bee virus 5\* | SA-8 | ? | ? | ? | ? | ? | ? | ? | ? |
| Perth bee virus 8\* | WA1-18 | ? | ? | ? | ? | ? | ? | ? | ? |
| Bundaberg bee virus 7\* | QLD-8 | ? | ? | ? | ? | ? | ? | ? | ? |
| Darwin bee virus 8\* | NT-7 | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Robinvale bee virus 6\* | VN1-8 | ? | ? | ? | ? | ? | ? | ? | ? |
| Darwin bee virus 7\* | NT-15 | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Bundaberg bee virus 8\* | QLD-9 | ? | ? | ? | ? | ? | ? | ? | ? |
| Tobacco ringspot virus | TSRV | Secoviridae | ? | ? | ? | ? | ? | ? | ? | ? |
| Seco-like virus\* | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Nodamura-like virus\* | ? | Nodaviridae | ? | ? | ? | ? | ? | ? | ? | ? |
| Apis Nora virus | ANV | ? | ? | ? | ? | ? | ? | ? | ? |
| Chronic bee paralysis virus | CBPV | ? | ? | **+** | - | **+** | ? | **+** | **++** | **++** | + |
| Bee virus\*\* | BVX | ? | **+** | ? | ? | ? | ? | **+++** | + | + |
| BVY | **+** | ? | ? | ? | ? | + | **+++** | + |
|  | LSV-1 | ? | ? | ? | ? | **+** | ++ | **+++** | ++ |
| Lake Sinai virus | LSV-2 | ? | ? | ? | ? | **+** | **+++** | + | + |
|  | LSV-3 | ? | ? | ? | ? | **+** | + | + | + |
|  | LSV-4 | ? | ? | ? | ? | **+** | + | + | + |
| Bee Macula-like virus | BeeMLV | Tymoviridae | Tymovirales | ? | **+** | ? | ? | **+** | + | ++ | **+++** |
| Varroa Tymo-like virus\* | VTLV | ? | **+** | ? | ? | ? | ? | ? | ? |
| Cloudy wing virus\*\* | CWV | ? | ? | ? | - | **~** | ? | ? | + | + | + |
| Varroa destructor virus-3 | VDV-3 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Varroa destructor virus-4 | VDV-4 | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Varroa orthomyxovirus-1 | VOV-1 | Orthomyxoviridae | Articulavirales | ssRNA(-) | ? | ? | ? | ? | ? | ? | ? | ? |
| Apis rhabdovirus-1 | ARV-1 | Rhabdoviridae | Mononegavirales | ? | ? | ? | ? | ? | ? | ? | ? |
| Apis rhabdovirus-2 | ARV-2 | ? | ? | ? | ? | ? | ? | ? | ? |
| Apis bunyavirus-1\* | ABV-1 | Arenaviridae | Bunyavirales | ? | ? | ? | ? | ? | ? | ? | ? |
| Apis bunyavirus-2\* | ABV-2 | Phasmaviridae | ? | ? | ? | ? | ? | ? | ? | ? |
| Partiti-like virus\* | ? | Partitiviridae | ? | dsRNA | ? | ? | ? | ? | ? | ? | ? | ? |
| Circo-like virus-1\* | ? | Circoviridae | ? | ssDNA | ? | ? | ? | ? | ? | ? | ? | ? |
| Circo-like virus-2\* | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Apis mellifera filamentous virus | AmFV | Baculoviridae | Megavirales | dsDNA | **+** | ? | ? | ? | ? | **+++** | + | + |
| Apis iridescent virus\* | AIV | Iridoviridae | ? | ? | **?** | ? | ? | + | **++** | + |

**1** The viruses are organized taxonomically (**Virus**, **Major Strains**, **Family**, **Order**), with those viruses belonging to the same taxonomic group at each level bound by a box. Undetermined or unclear taxonomic identities are indicated by a question mark (?). The highest organizational trait shown is the type of virus **genome**: single-stranded positive sense RNA genome (ssRNA(+); single-stranded negative sense RNA genome (ssRNA(-); double-stranded RNA genome (dsRNA); single-stranded DNA genome (ssDNA) and double-stranded DNA genome (dsDNA). Viruses for whom only partial genome sequence data is available are marked with a single asterisk (\*), while those for whom no genome sequence data is available are marked with two asterisks (\*\*). Viruses with a DNA genome are marked in purple font. Viruses identified primarily in Varroa destructor are marked in red font. The newly discovered potential bee viruses identified by Roberts et al. 2018 [S20] are marked in blue font. These should be considered provisional bee-infecting viruses until positive evidence of host status is obtained.

The columns on the right summarize the current experimental evidence for the presence (+, highlighted), absence (-) or unknown status (?) of the different transmission routes for the various viruses (green = oral-fecal transmission; red = vector-mediated transmission; black = contact transmission; blue = sexual-vertical transmission; orange = environmental transmission), as well as the evidence for their seasonal incidence (spring, summer, autumn), marked on a three-point scale (+, ++, +++).

**Table S2. Landmark discoveries in varroa research**

|  |  |
| --- | --- |
| **Year** | **Reference** |
| 1995 | Kraus, B. & Hunt, G. Differentiation of Varroa jacobsoni Oud populations by random amplification of polymorphic DNA (RAPD). *Apidologie* **26**, 283–290 (1995) |
| 1997 | de Guzman, L. I., Rinderer, T. E. & Stelzer, J. A. DNA evidence of the origin of Varroa jacobsoni Oudemans in the Americas. *Biochem. Genet.* **35**, 327–335 (1997) |
| 1998 | Anderson, D. L. & Fuchs, S. Two genetically distinct populations of Varroa jacobsoni with contrasting reproductive abilities on Apis mellifera. *J. Apic. Res.* **37**, 69–78 (1998) |
| 1998 | De Guzman, L., RINDERER, STELZER & Anderson, D. Congruence of RAPD and mitochondrial DNA markers in assessing Varroa jacobsoni genotypes. **37**, 49–51 (1998) |
| 1999 | de Guzman, L. I. & Rinderer, T. E. Identification and comparison of Varroa species infesting honey bees. *Apidologie* **30**, 85–95 (1999) |
| 1999 | de Guzman, L. I., Rinderer, T. E. & Anthony Stelzer, J. Occurrence of two genotypes of Varroa jacobsoni Oud. in North America. *Apidologie* **30**, 31–36 (1999) |
| 2000 | Fuchs, S., Anderson, D. L. & Others. A scientific note on the genetic distinctness of Varroa mites on Apis mellifera L. and on Apis cerana Fabr. in North Vietnam. *Apidologie* **31**, 459–460 (2000) |
| 2000 | Anderson, D. L. & Trueman, J. W. Varroa jacobsoni (Acari: Varroidae) is more than one species. *Exp. Appl. Acarol.* **24**, 165–189 (2000) |
| 2000 | Evans, J. D. Microsatellite loci in the honey bee parasitic mite Varroa jacobsoni. *Mol. Ecol.* **9**, 1436–1438 (2000) |
| 2003 | Garrido, C., Rosenkranz, P., Paxton, R. J. & Gonçalves, L. S. Temporal changes in Varroa destructor fertility and haplotype in Brazil. *Apidologie* **34**, 535–541 (2003) |
| 2003 | Solignac, M. *et al.* Characterization of microsatellite markers for the apicultural pest Varroa destructor (Acari: Varroidae) and its relatives. *Mol. Ecol. Notes* **3**, 556–559 (2003) |
| 2004 | Warrit, N., Hagen, T. A. R., Smith, D. R. & Çakmak, I. A survey of Varroa destructor strains on Apis mellifera in Turkey. *J. Apic. Res.* **43**, 190–191 (2004) |
| 2004 | Zhou, T. *et al.* Identification of Varroa mites (Acari: Varroidae) infesting Apis cerana and Apis mellifera in China. *Apidologie* **35**, 645–654 (2004) |
| 2005 | Solignac, M. *et al.* The invasive Korea and Japan types of Varroa destructor, ectoparasitic mites of the Western honeybee (Apis mellifera), are two partly isolated clones. *Proc. Biol. Sci.* **272**, 411–419 (2005) |
| 2006 | Warrit, N., Smith, D. R. & Lekprayoon, C. Genetic subpopulations of Varroa mites and their Apis cerana hosts in Thailand. *Apidologie* **37**, 19–30 (2006) |
| 2006 | Cornuet, J. M., Beaumont, M. A., Estoup, A. & Solignac, M. Inference on microsatellite mutation processes in the invasive mite, Varroa destructor, using reversible jump Markov chain Monte Carlo. *Theor. Popul. Biol.* **69**, 129–144 (2006) |
| 2008 | Muñoz, I. *et al.* Genetic profile of Varroa destructor infesting Apis mellifera iberiensis colonies. *J. Apic. Res.* **47**, 310–313 (2008) |
| 2009 | Strapazzon, R., Carneiro, F. E., Guerra, J. C. V., Jr & Moretto, G. Genetic characterization of the mite Varroa destructor (Acari: Varroidae) collected from honey bees Apis mellifera (Hymenoptera, Apidae) in the state of Santa Catarina, Brazil. *Genet. Mol. Res.* **8**, 990–997 (2009) |
| 2010 | Navajas, M. *et al.* New Asian types of Varroa destructor: a potential new threat for world apiculture. *Apidologie* **41**, 181–193 (2010) |
| 2010 | Awad, N. S., Allam, S. F. M., Rizk, M. A., Hassan, M. F. & Zaki, A. Y. Fingerprinting and assessment of genetic variability of Varroa destructor in Egypt. *J. Apic. Res.* **49**, 251–256 (2010) |
| 2010 | Guerra, J. C. V., Jr, Issa, M. R. C., Carneiro, F. E., Strapazzon, R. & Moretto, G. RAPD identification of Varroa destructor genotypes in Brazil and other regions of the Americas. *Genet. Mol. Res.* **9**, 303–308 (2010) |
| 2010 | Fazier, M. *et al.* A scientific note on Varroa destructor found in East Africa; threat or opportunity? *Apidologie* **41**, 463–465 (2010) |
| 2010 | Cornman, S. R. *et al.* Genomic survey of the ectoparasitic mite Varroa destructor, a major pest of the honey bee Apis mellifera. *BMC Genomics* **11**, 602 (2010) |
| 2011 | Awad, N. S., Allam, S. F. M., Rizk, M. A., Hassan, M. F. & Zaki, A. Y. Identification of Varroa mite (Acari: Varroidae) parasitizing honeybee in Egypt using DNA sequencing, morphometric and SEM analysis. *Arab J. Biotechnol.* **14**, 41–48 (2011) |
| 2011 | Rueppell, O., Hayes, A. M., Warrit, N. & Smith, D. R. Population structure of Apis cerana in Thailand reflects biogeography and current gene flow rather than Varroa mite association. *Insectes Soc.* **58**, 445–452 (2011) |
| 2012 | Akinwande, K. L., Badejo, M. A. & Ogbogu, S. S. Incidence of the Korean haplotype of Varroa destructor in southwest Nigeria. *J. Apic. Res.* **51**, 369–370 (2012) |
| 2012 | Maggi, M. *et al.* Genetic structure of Varroa destructor populations infesting Apis mellifera colonies in Argentina. *Exp. Appl. Acarol.* **56**, 309–318 (2012) |
| 2013 | Badejo, M. A., Ogbogu, S. S. & Akinwande, K. L. Morphometrics and parasitic load of Varroa mites (Acari: varroidae) on colonies of Apis mellifera adansonii (Hymenoptera: apidae) in south Western Nigeria. *Acarina* **21**, 17–26 (2013) |
| 2013 | Akinwande, K. L., Badejo, M. A. & Ogbogu, S. S. Challenges associated with the honey bee ( Apis Mellifera Adansonii ) colonies establishment in South Western Nigeria. *Afr. J. Food Agric. Nutr. Dev.* **13**, (2013) |
| 2013 | Dietemann, V. *et al.* Standard methods for varroa research. *J. Apic. Res.* **52**, 1–54 (2013) |
| 2013 | Yang, B., Peng, G., Li, T. & Kadowaki, T. Molecular and phylogenetic characterization of honey bee viruses, Nosema microsporidia, protozoan parasites, and parasitic mites in China. *Ecol. Evol.* **3**, 298–311 (2013) |
| 2013 | Rasolofoarivao, H. *et al.* Spread and strain determination of Varroa destructor (Acari: Varroidae) in Madagascar since its first report in 2010. *Exp. Appl. Acarol.* **60**, 521–530 (2013) |
| 2013 | Gajic, B. *et al.* Variability of the honey bee mite Varroa destructor in Serbia, based on mtDNA analysis. *Exp. Appl. Acarol.* **61**, 97–105 (2013) |
| 2015 | Thapa, R. *et al.* SEM Observations of Korean Haloptype Varroa destructor (Acari: Varroidae) Collected from Apis mellifera Colonies. *Journal of Apiculture* **30**, 143–153 (2015) |
| 2015 | Alattal, Y., Javed Ansari, M., Al-Ghamdi, A. & Single, A. Surveillance and genotyping of Varroa destructor (Acari: Varroidae) parasitizing Apis mellifera jemenitica (Hymenoptera: Apidae) in Saudi Arabia. *Revista Colombiana de Entomología* **41**, 180–183 (2015) |
| 2015 | Roberts, J. M. K., Anderson, D. L. & Tay, W. T. Multiple host shifts by the emerging honeybee parasite, Varroa jacobsoni. *Mol. Ecol.* **24**, 2379–2391 (2015) |
| 2015 | Beaurepaire, A. L. *et al.* Host Specificity in the Honeybee Parasitic Mite, Varroa spp. in Apis mellifera and Apis cerana. *PLoS One* **10**, e0135103 (2015) |
| 2015 | Strachecka, A., Borsuk, G., Olszewski, K. & Paleolog, J. A new detection method for a newly revealed mechanism of pyrethroid resistance development in Varroa destructor. *Parasitol. Res.* **114**, 3999–4004 (2015) |
| 2016 | Tsevegmid, K., Neumann, P. & Yañez, O. The Honey Bee Pathosphere of Mongolia: European Viruses in Central Asia. *PLoS One* **11**, e0151164 (2016) |
| 2016 | Elbeaino, T. *et al.* Occurrence of Deformed wing virus, Chronic bee paralysis virus and mtDNA variants in haplotype K of Varroa destructor mites in Syrian apiaries. *Exp. Appl. Acarol.* **69**, 11–19 (2016) |
| 2016 | Page, P. *et al.* Social apoptosis in honey bee superorganisms. *Sci. Rep.* **6**, 27210 (2016) |
| 2016 | Dynes, T. L. *et al.* Fine scale population genetic structure of Varroa destructor, an ectoparasitic mite of the honey bee (Apis mellifera). *Apidologie* **2016**, 1–9 (2016) |
| 2016 | Gajić, B. *et al.* Haplotype identification and detection of mitochondrial DNA heteroplasmy in Varroa destructor mites using ARMS and PCR-RFLP methods. *Exp. Appl. Acarol.* **70**, 287–297 (2016) |
| 2017 | Kelomey, A. E. *et al.* Genetic characterization of the honeybee ectoparasitic mite Varroa destructor from Benin (West Africa) using mitochondrial and microsatellite markers. *Exp. Appl. Acarol.* **72**, 61–67 (2017) |
| 2017 | Cham, D. T., Fombong, A. T., Ndegwa, P. N., Irungu, L. W. & Raina, S. K. Scientific note on the first report of Varroa destructor in Cameroon. *J. Apic. Res.* **56**, 397–399 (2017) |
| 2017 | Rasolofoarivao, H. *et al.* Genetic diversity of Varroa destructor parasitizing Apis mellifera unicolor in Madagascar. *Apidologie* **48**, 648–656 (2017) |
| 2017 | Octaviano-Salvadé, C. E. *et al.* A scientific note on genetic profile of the mite Varroa destructor infesting apiaries in Rio Grande do Sul state, Brazil. *Apidologie* **48**, 621–622 (2017) |
| 2017 | Pakwan, C. *et al.* Bacterial communities associated with the ectoparasitic mites Varroa destructor and Tropilaelaps mercedesae of the honey bee (Apis mellifera). *FEMS Microbiol. Ecol.* **93**, (2017) |
| 2017 | Ayan, A., Aldemir, O. S. & Selamoglu, Z. Analysis of COI Gene Region of Varroa destructor in Honey Bees (Apis mellifera) in Province of Siirt. **1**, 20–23 (2017) |
| 2018 | Hajializadeh, Z., Asadi, M. & Kavousi, H. First report of Varroa genotype in western Asia based on genotype identification of Iranian Varroa destructor populations (Mesostigmata: Varroidae) using RAPD marker. *Systematic and Applied Acarology* **23**, 199–205 (2018) |
| 2018 | Kelomey, A., Paraïso, A. A., Sina, H., Legout, H. & Baba-Moussa, L. Genetic Variability of the Mitochondrial DNA in Honeybees (Apis mellifera L.) from Benin. **2017**, (2018) |
| 2018 | Ayan, A. & Aldemir, O. S. Genetic characterization of Varroa destructor (Family: Varroidae) prevalent in honeybees (Apis mellifera) in the province of Aydin in Turkey. **6**, 26–32 (2018) |
| 2018 | Farjamfar, M., Saboori, A., González-Cabrera, J. & Hernández Rodríguez, C. S. Genetic variability and pyrethroid susceptibility of the parasitic honey bee mite Varroa destructor (Acari: Varroidae) in Iran. *Exp. Appl. Acarol.* **76**, 139–148 (2018) |
| 2019 | Esnault, O., Meenowa, D., Sookar, P., Chauzat, M.-P. & Delatte, H. Spread and strain determination of Varroa destructor following its introduction to Mauritius and interactions with the bee louse Braula pretoriensis in honey bee colonies. *J. Apic. Res.* **58**, 75–83 (2019) |
| 2019 | Beaurepaire, A. L., Ellis, J. D., Krieger, K. J. & Moritz, R. F. A. Association of Varroa destructor females in multiply infested cells of the honeybee Apis mellifera. *Insect Sci.* **26**, 128–134 (2019) |
| 2019 | Utzeri, V. J. *et al.* A next generation sequencing approach for targeted Varroa destructor (Acari: Varroidae) mitochondrial DNA analysis based on honey derived environmental DNA. *J. Invertebr. Pathol.* **161**, 47–53 (2019) |
| 2019 | Wang, S. *et al.* Ectoparasitic Mites Varroa underwoodi (Acarina: Varroidae) in Eastern Honeybees, but not in Western Honeybees. *J. Econ. Entomol.* **112**, 25–32 (2019) |
| 2019 | Hajializadeh, Z., Asadi, M., Ahmadi, K. & Balvasi, A. Varroa destructor (Acari: Varroidea) populations from Southern Iran belong to haplotype K of the mitochondrial COI. (2019) doi:10.22073/pja.v8i2.43363 |
| 2019 | Gajić, B. *et al.* Coexistence of genetically different Varroa destructor in Apis mellifera colonies. *Exp. Appl. Acarol.* **78**, 315–326 (2019) |
| 2019 | Beaurepaire, A. L. *et al.* Population genetics of ectoparasitic mites suggest arms race with honeybee hosts. *Sci. Rep.* **9**, 11355 (2019) |
| 2019 | Dietemann, V. *et al.* Population genetics of ectoparasitic mites Varroa spp. in Eastern and Western honey bees. *Parasitology* **146**, 1429–1439 (2019) |
| 2019 | Techer, M. A. *et al.* Divergent evolutionary trajectories following speciation in two ectoparasitic honey bee mites. *Commun Biol* **2**, 357 (2019) |
| 2019 | Li, W., Wang, C., Huang, Z. Y., Chen, Y. & Han, R. Reproduction of Distinct Varroa destructor Genotypes on Honey Bee Worker Brood. *Insects* **10**, 372 (2019) |
| 2019 | Bhatta, C. P., Reddy, M. S. & Smith, D. R. Scientific note:Varroa jacobsoni and V. destructor on hill and plains strains of Apis cerana in southern India. *Apidologie* (2019) doi:10.1007/s13592-019-00723-7 |
| 2020 | Harada, R., Yoshioka, M., Okuyama, H., Kato, M. & Takahashi, J. Complete mitochondrial DNA sequence of the parasitic honey bee mite Varroa destructor (Mesostigmata: Varroidae). **5**, 635–636 (2020) |
| 2020 | Muntaabski, I. *et al.* Genetic variation and heteroplasmy of Varroa destructor inferred from ND4 mtDNA sequences. *Parasitol. Res.* (2020) doi:10.1007/s00436-019-06591-5 |
| 2020 | Ogihara, M. H., Yoshiyama, M., Morimoto, N. & Kimura, K. Dominant honeybee colony infestation by Varroa destructor (Acari: Varroidae) K haplotype in Japan. *Appl. Entomol. Zool.* (2020) doi:10.1007/s13355-020-00667-w |

**Supplementary References**

S1. Anderson, D. and Trueman, J. (2000) Varroa jacobsoni (Acari: Varroidae) is more than one species. Experimental & applied acarology 24 (3), 165-189.

S2. Wilfert, L. et al. (2016) Deformed wing virus is a recent global epidemic in honeybees driven by Varroa mites. Science 351 (6273), 594-7.

S3. Dietemann, V. et al. (2013) Standard methods for varroa research. Journal of apicultural research 52 (1), 1-54.

S4. Navajas, M. et al. (2010) New Asian types of Varroa destructor: a potential new threat for world apiculture. Apidologie 41 (2), 181-193.

S5. Roberts, J. et al. (2015) Multiple hostáshifts by the emerging honeybee parasite, Varroa jacobsoni. Molecular Ecology 24 (10), 2379-2391.

S6. Beaurepaire, A.L. et al. (2015) Host Specificity in the Honeybee Parasitic Mite, Varroa spp. in Apis mellifera and Apis cerana. PLoS One 10 (8), e0135103.

S7. Beaurepaire, A.L. et al. (2019) Population genetics of ectoparasitic mites suggest arms race with honeybee hosts. Sci Rep 9 (1), 11355.

S8. Garrido, C. et al. (2003) Temporal changes in Varroa destructor fertility and haplotype in Brazil. Apidologie 34 (6), 535-541.

S9. de Guzman, L.I. et al. (1999) Occurrence of two genotypes of Varroa jacobsoni Oud. in North America. Apidologie 30 (1), 31-36.

S10. Solignac, M. et al. (2005) The invasive Korea and Japan types of Varroa destructor, ectoparasitic mites of the Western honeybee (Apis mellifera), are two partly isolated clones. Proceedings of the Royal Society B: Biological Sciences 272 (1561), 411-419.

S11. Ogihara, M.H. et al. (2020) Dominant honeybee colony infestation by Varroa destructor (Acari: Varroidae) K haplotype in Japan. Applied Entomology and Zoology, 1-9.

S12. Zhou, T. et al. (2004) Identification of Varroa mites (Acari: Varroidae) infesting Apis cerana and Apis mellifera in China. Apidologie 35 (6), 645-654.

S13. Koeniger, G. et al. (2002) Mites from debris and sealed brood cells of Apis dorsata colonies in Sabah (Borneo) Malaysia, including a new haplotype of Varroa jacobsoni. Apidologie 33 (1), 15-24.

S14. Chantawannakul, P. et al. (2016) Parasites, pathogens, and pests of honeybees in Asia. Apidologie 47 (3), 301-324.

S15. Techer, M.A. et al. (2019) Divergent evolutionary trajectories following speciation in two ectoparasitic honey bee mites. Commun Biol 2, 357.

S16. Utzeri, V.J. et al. (2019) A next generation sequencing approach for targeted Varroa destructor (Acari: Varroidae) mitochondrial DNA analysis based on honey derived environmental DNA. Journal of invertebrate pathology 161, 47-53.

S17. Warrit, N. et al. (2006) Genetic subpopulations of Varroa mites and their Apis cerana hosts in Thailand. Apidologie 37 (1), 19-30.

S18. Gajic, B. et al. (2013) Variability of the honey bee mite Varroa destructor in Serbia, based on mtDNA analysis. Experimental and Applied Acarology 61 (1), 97-105.

S19. Wang, S. et al. (2019) Ectoparasitic Mites Varroa underwoodi (Acarina: Varroidae) in Eastern Honeybees, but not in Western Honeybees. Journal of economic entomology 112 (1), 25-32.

S20. Roberts, J.M.K. et al. (2018) Metagenomic analysis of Varroa-free Australian honey bees (Apis mellifera) shows a diverse Picornavirales virome. Journal of General Virology 99, 818–826.