**Supplementary data for**

***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](mailto:ktraynor@asu.edu) (K.S. Traynor).

**Varroa mite distribution and haplotypes:**

*Problems associated with identification of Varroa mites before 2000s:*

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 honey bee colony losses became essential. Given that Varroa mites forms a **cryptic species complex**[1](https://paperpile.com/c/uUhUQm/UCcV), 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[2](https://paperpile.com/c/uUhUQm/XIB6). Varroa mites and the disease associated named varroosis, is an animal notifiable disease by the OIE. The development of molecular markers was a game-changer and allows a major taxonomic revision in 2000. As its name indicates, “*V. destructor*” is the real identity of the cosmopolitan Western honey bee nightmare while *V. jacobsoni* remained unable to reproduce on this host (Figure S1). Despite its status as notifiable infection disease, V. destructor’s presence is not systematically reported or 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*, 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[3](https://paperpile.com/c/uUhUQm/MtuE). 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*[*4–6*](https://paperpile.com/c/uUhUQm/ExHC+AXI8+pr06), and that ii) honey bee-Varroa is a dynamic co-evolutive system in which arm races for survival shape both host and parasite populations[7](https://paperpile.com/c/uUhUQm/tZdC). As a striking case, Varroa populations in South America[8](https://paperpile.com/c/uUhUQm/aymE), North America[9,10](https://paperpile.com/c/uUhUQm/L55u+71C4), and Japan[4,11](https://paperpile.com/c/uUhUQm/ExHC+NtmY) have been experiencing a rather quick turnover as the less “virulent” Japanese *V. destructor* was replaced by the more “virulent” Korean one.

*Varroa mites mtDNA haplotype or haplogroup? Confusion and classification*

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)[1](https://paperpile.com/c/uUhUQm/UCcV). 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[26](https://paperpile.com/c/uUhUQm/i55s)and Borneo 2 AY037890 [27](https://paperpile.com/c/uUhUQm/N2Pq)). 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 (2010) 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 [4](https://paperpile.com/c/uUhUQm/ExHC). 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) [4](https://paperpile.com/c/uUhUQm/ExHC) which could naively be considered the former described China 2 (AY372063) [26](https://paperpile.com/c/uUhUQm/i55s). To help clarify this, we proposed to redefine the haplogroups and give some advice for future naming (see Table S1):

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.

**Distribution of V. destructor haplotypes on original and new hosts**

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[28](https://paperpile.com/c/uUhUQm/8lH9) between the two sister species *V. destructor* and *V. jacobsoni* found on their original host and sympatry with the related *V. underwoodi*[*25*](https://paperpile.com/c/uUhUQm/8PBD).

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[29](https://paperpile.com/c/uUhUQm/ZPYB). We collected distribution data about Varroa species identity, mtDNA haplogroup, date of sampling, geographical localization, honey bee 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 (Table S2).

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 (see Table S3)[1,4,6,26,27,30–33](https://paperpile.com/c/uUhUQm/UCcV+N2Pq+i55s+N1E8+ExHC+QUKm+pr06+yUiF+fzzx). 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 (see Table S2). 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/](https://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.

**References:**

1. [Anderson, D. L. & Trueman, J. W. Varroa jacobsoni (Acari: Varroidae) is more than one species. *Exp. Appl. Acarol.* **24**, 165–189 (2000).](http://paperpile.com/b/uUhUQm/UCcV)

2. [Wilfert, L. *et al.* Deformed wing virus is a recent global epidemic in honeybees driven by Varroa mites. *Science* **351**, 594–597 (2016).](http://paperpile.com/b/uUhUQm/XIB6)

3. [Dietemann, V. *et al.* Standard methods for varroa research. *J. Apic. Res.* **52**, 1–54 (2013).](http://paperpile.com/b/uUhUQm/MtuE)

4. [Navajas, M. *et al.* New Asian types of Varroa destructor: a potential new threat for world apiculture. *Apidologie*  **41**, 181–193 (2010).](http://paperpile.com/b/uUhUQm/ExHC)

5. [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).](http://paperpile.com/b/uUhUQm/AXI8)

6. [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).](http://paperpile.com/b/uUhUQm/pr06)

7. [Beaurepaire, A. L. *et al.* Population genetics of ectoparasitic mites suggest arms race with honeybee hosts. *Sci. Rep.* **9**, 11355 (2019).](http://paperpile.com/b/uUhUQm/tZdC)

8. [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).](http://paperpile.com/b/uUhUQm/aymE)

9. [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).](http://paperpile.com/b/uUhUQm/L55u)

10. [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).](http://paperpile.com/b/uUhUQm/71C4)

11. [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:](http://paperpile.com/b/uUhUQm/NtmY)[10.1007/s13355-020-00667-w](http://dx.doi.org/10.1007/s13355-020-00667-w)[.](http://paperpile.com/b/uUhUQm/NtmY)

12. [Oudemans, A. C. Note VIII. On a new genus and species of parasitic Acari. 216–222 (1904).](http://paperpile.com/b/uUhUQm/k3Mx)

13. [Crane, E. Living with varroa in Japan. *Bee World* **65**, 149–150 (1984).](http://paperpile.com/b/uUhUQm/za1y)

14. [Delfinado, M. D. Mites of the Honeybee in South-East Asia. *J. Apic. Res.* **2**, 113–114 (1963).](http://paperpile.com/b/uUhUQm/AXPh)

15. [Crane, E. Beekeeping round the World. *Bee World* **49**, 113–114 (1968).](http://paperpile.com/b/uUhUQm/tHGW)

16. [Grobov, O. F., Pulenetz, N. M. & Sofronov, G. L. Geographical variability of the size of the dorsal scutellum in females of Varroa jacobsoni Oudemans. *Proceedings of the XXVIIth* (1980).](http://paperpile.com/b/uUhUQm/DDtY)

17. [Delfinado-Baker, M. & Aggarwal, K. A new Varroa (Acari: Varroidae) from the nest of Apis cerana (Apidae). *Int. J. Acarology* **13**, 233–237 (1987).](http://paperpile.com/b/uUhUQm/Q4zU)

18. [Biasiolo, A. Lack of allozyme variability amongVarroa mite populations. *Exp. Appl. Acarol.* **16**, 287–294 (1992).](http://paperpile.com/b/uUhUQm/t1i8)

19. [Kraus, B. & Hunt, G. Differentiation of Varroa jacobsoni Oud populations by random amplification of polymorphic DNA (RAPD). *Apidologie*  **26**, 283–290 (1995).](http://paperpile.com/b/uUhUQm/Rjbr)

20. [de Guzman, L. I. & Delfinado-Baker, M. A new species of Varroa (Acari: Varroidae) associated with Apis koschevnikovi (Apidae: Hymenoptera) in Borneo. *Int. J. Acarology* **22**, 23–27 (1996).](http://paperpile.com/b/uUhUQm/Ju9i)

21. [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).](http://paperpile.com/b/uUhUQm/Eer4)

22. [Evans, J. D. Microsatellite loci in the honey bee parasitic mite Varroa jacobsoni. *Mol. Ecol.* **9**, 1436–1438 (2000).](http://paperpile.com/b/uUhUQm/vSto)

23. [Evans, J. D. & Lopez, D. L. Complete mitochondrial DNA sequence of the important honey bee pest, Varroa destructor (Acari: Varroidae). *Exp. Appl. Acarol.* **27**, 69–78 (2002).](http://paperpile.com/b/uUhUQm/D9K3)

24. [Navajas, M., Le Conte, Y., Solignac, M., Cros-Arteil, S. & Cornuet, J.-M. The complete sequence of the mitochondrial genome of the honeybee ectoparasite mite Varroa destructor (Acari: Mesostigmata). *Mol. Biol. Evol.* **19**, 2313–2317 (2002).](http://paperpile.com/b/uUhUQm/EVD8)

25. [Techer, M. A. *et al.* Divergent evolutionary trajectories following speciation in two ectoparasitic honey bee mites. *Commun Biol* **2**, 357 (2019).](http://paperpile.com/b/uUhUQm/8PBD)

26. [Zhou, T. *et al.* Identification of Varroa mites (Acari: Varroidae) infesting Apis cerana and Apis mellifera in China. *Apidologie*  **35**, 645–654 (2004).](http://paperpile.com/b/uUhUQm/i55s)

27. [Koeniger, G., Koeniger, N., Anderson, D. L., Lekprayoon, C. & Tingek, S. Mites from debris and sealed brood cells of Apis dorsata colonies in Sabah (Borneo) Malaysia, including a new haplotype of Varroa jacobsoni. *Apidologie*  **33**, 15–24 (2002).](http://paperpile.com/b/uUhUQm/N2Pq)

28. [Chantawannakul, P., de Guzman, L. I., Li, J. & Williams, G. R. Parasites, pathogens, and pests of honeybees in Asia. *Apidologie*  **47**, 301–324 (2016).](http://paperpile.com/b/uUhUQm/8lH9)

29. [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).](http://paperpile.com/b/uUhUQm/ZPYB)

30. [Warrit, N., Smith, D. R. & Lekprayoon, C. Genetic subpopulations of Varroa mites and their Apis cerana hosts in Thailand. *Apidologie*  **37**, 19–30 (2006).](http://paperpile.com/b/uUhUQm/N1E8)

31. [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).](http://paperpile.com/b/uUhUQm/QUKm)

32. [Dietemann, V. *et al.* Population genetics of ectoparasitic mites Varroa spp. in Eastern and Western honey bees. *Parasitology* **146**, 1429–1439 (2019).](http://paperpile.com/b/uUhUQm/yUiF)

33. [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).](http://paperpile.com/b/uUhUQm/fzzx)

**List of articles reviewed for DNA confirmation of Varroa species (old to recent)**

* Kraus, B. & Hunt, G. Differentiation of Varroa jacobsoni Oud populations by random amplification of polymorphic DNA (RAPD). *Apidologie* **26**, 283–290 (1995)
* 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)
* 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)
* De Guzman, L., RINDERER, STELZER & Anderson, D. Congruence of RAPD and mitochondrial DNA markers in assessing Varroa jacobsoni genotypes. **37**, 49–51 (1998)
* de Guzman, L. I. & Rinderer, T. E. Identification and comparison of Varroa species infesting honey bees. *Apidologie* **30**, 85–95 (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)
* 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)
* Anderson, D. L. & Trueman, J. W. Varroa jacobsoni (Acari: Varroidae) is more than one species. *Exp. Appl. Acarol.* **24**, 165–189 (2000)
* Evans, J. D. Microsatellite loci in the honey bee parasitic mite Varroa jacobsoni. *Mol. Ecol.* **9**, 1436–1438 (2000)
* 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)
* 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)
* 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)
* Zhou, T. *et al.* Identification of Varroa mites (Acari: Varroidae) infesting Apis cerana and Apis mellifera in China. *Apidologie* **35**, 645–654 (2004)
* 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)
* Warrit, N., Smith, D. R. & Lekprayoon, C. Genetic subpopulations of Varroa mites and their Apis cerana hosts in Thailand. *Apidologie* **37**, 19–30 (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)
* Muñoz, I. *et al.* Genetic profile of Varroa destructor infesting Apis mellifera iberiensis colonies. *J. Apic. Res.* **47**, 310–313 (2008)
* 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)
* Navajas, M. *et al.* New Asian types of Varroa destructor: a potential new threat for world apiculture. *Apidologie* **41**, 181–193 (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)
* 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)
* Fazier, M. *et al.* A scientific note on Varroa destructor found in East Africa; threat or opportunity? *Apidologie* **41**, 463–465 (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)
* 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)
* 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)
* 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)
* Maggi, M. *et al.* Genetic structure of Varroa destructor populations infesting Apis mellifera colonies in Argentina. *Exp. Appl. Acarol.* **56**, 309–318 (2012)
* 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)
* 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)
* Dietemann, V. *et al.* Standard methods for varroa research. *J. Apic. Res.* **52**, 1–54 (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)
* 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)
* 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)
* 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)
* 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)
* 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)
* 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)
* 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)
* Tsevegmid, K., Neumann, P. & Yañez, O. The Honey Bee Pathosphere of Mongolia: European Viruses in Central Asia. *PLoS One* **11**, e0151164 (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)
* Page, P. *et al.* Social apoptosis in honey bee superorganisms. *Sci. Rep.* **6**, 27210 (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)
* 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)
* 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)
* 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)
* Rasolofoarivao, H. *et al.* Genetic diversity of Varroa destructor parasitizing Apis mellifera unicolor in Madagascar. *Apidologie* **48**, 648–656 (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)
* 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)
* 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)
* 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)
* 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)
* 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)
* 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)
* 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)
* 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)
* 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)
* 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)
* 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
* Gajić, B. *et al.* Coexistence of genetically different Varroa destructor in Apis mellifera colonies. *Exp. Appl. Acarol.* **78**, 315–326 (2019)
* Beaurepaire, A. L. *et al.* Population genetics of ectoparasitic mites suggest arms race with honeybee hosts. *Sci. Rep.* **9**, 11355 (2019)
* Dietemann, V. *et al.* Population genetics of ectoparasitic mites Varroa spp. in Eastern and Western honey bees. *Parasitology* **146**, 1429–1439 (2019)
* Techer, M. A. *et al.* Divergent evolutionary trajectories following speciation in two ectoparasitic honey bee mites. *Commun Biol* **2**, 357 (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)
* 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
* 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)
* 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
* 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