

SYMBIOSIS

A symbiotic mosaic

Many insects that feed on plant sap can survive on such a nutritionally poor substrate owing to their association with nutrient-providing bacterial endosymbionts. In *Planococcus citri* mealybugs, this association is particularly interesting, as it involves a nested symbiosis in which the *P. citri* betaproteobacterial endosymbiont, 'Candidatus Tremblaya princeps str. PCIT' (*Tremblaya* PCIT), harbours its own endosymbiont, the gammaproteobacterium 'Candidatus Moranella endobia'.

Writing in *Cell*, John McCutcheon and colleagues now reveal that this complex tripartite relationship requires genetic input from at least six different organismal lineages to be metabolically functional.

At just 139 kb, the genome of *Tremblaya* PCIT is the smallest bacterial genome reported to date. Although obligate endosymbionts are known to have severely reduced genomes, the *Tremblaya* PCIT genome is unusual, as it lacks functional homologues for many crucial components of translation. It has been suggested that *Tremblaya* PCIT remains metabolically viable by utilizing essential

gene products supplied by its own endosymbiont, 'Ca. Moranella endobia'. However, it is also possible that the missing functions are encoded by the host, *P. citri*, or that genes from *Tremblaya* PCIT or other bacteria have undergone horizontal gene transfer to the *P. citri* genome and the products of these genes are transported back into the *Tremblaya* PCIT cytoplasm.

To begin to distinguish between these different possibilities, the authors sequenced the complete genome of a *Tremblaya* strain that lacks an intracellular symbiont ('Candidatus Tremblaya phenacola str. PAVE' (*Tremblaya* PAVE)). They found that the *Tremblaya* PAVE genome is much less degenerate than that of *Tremblaya* PCIT, suggesting that the unusual degree of degeneracy in *Tremblaya* PCIT stems from the acquisition of 'Ca. Moranella endobia'. Many of the translation-related genes that were absent from *Tremblaya* PCIT were present in *Tremblaya* PAVE. Importantly, however, both *Tremblaya* PAVE and *Tremblaya* PCIT lacked the genes required for lysine and histidine biosynthesis.

So how are these essential enzymatic gaps filled? The authors used RNA sequencing to identify expressed genes in the *P. citri* bacteriome (the cellular structure

housing the endosymbionts). This revealed 22 expressed horizontally transferred genes, including lysine biosynthesis genes, as well as genes encoding proteins involved in the biosynthesis of other nutrients and in bacterial cell wall maintenance. Surprisingly, phylogenetic analysis showed that none of the horizontally transferred genes clustered with genes from the class Betaproteobacteria. Instead, they seem to have been transferred from various members of the classes Alphaproteobacteria or Gammaproteobacteria or the phylum Bacteroidetes. The authors confirmed that the identified genes were encoded in the insect genome by generating a low-pass draft genome sequence for *P. citri*.

So, this complicated symbiosis turns out to be even more genetically complex than previously thought. The combined genomic and transcriptomic data suggest that the essential metabolic pathways in this symbiotic mosaic are completed by heterologous complementation from an extraordinary variety of sources.

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ORIGINAL RESEARCH PAPER Husnik, F. et al. Horizontal gene transfer from diverse bacteria to an insect genome enables a tripartite nested mealybug symbiosis. *Cell* **153**, 1567–1578 (2013)
FURTHER READING McCutcheon, J. P. & Moran, N. A. Extreme genome reduction in symbiotic bacteria. *Nature Rev. Microbiol.* **10**, 13–26 (2012)

