



The Latest Bee Science Distilled

by Scott McArt

The origin and evolution of the Western honey bee

As I sit down to write the fiftieth Notes from the Lab, I find myself thinking about how this column got started.

Notes from the Lab was inspired by Roger Morse, the famed former professor of apiculture at Cornell, who penned a monthly column called “Research Review” for over forty years. When I started at Cornell, it seemed appropriate to revive a column with a similar goal: highlighting the latest cool bee research. I’ve been writing this column for four years now, so I

guess I have thirty-six to go until I catch up to Morse. It’s been a lot of fun so far!

With this origin story in mind, perhaps it’s appropriate that the topic for this month’s Notes from the Lab is the origin of our Western honey bee, *Apis mellifera*. Have you ever looked at your bees and wondered where they originally came from? What about all those *A. mellifera* subspecies and lineages; where and when did they evolve, how are they related to each other, and what parts of their genetic code do they share? These are the topics for our fiftieth Notes from the Lab, where we summarize “*Thrice out of Asia and the adaptive radiation of the western honey bee*,” written by Kathleen Dogantzis and colleagues and published in *Science Advances* [2021].

For their study, Dogantzis and colleagues analyzed the genomes of 251 individual *A. mellifera* samples representing 14 subspecies. The authors added to an existing *A. mellifera* database by collecting 160 new bee samples from throughout Europe, Africa, and Asia. In other words, they collected lots of *A. mellifera* from its entire natural range with the goal of revealing and comparing as much of its genetic variation as possible.

All samples were sequenced and aligned, and single-nucleotide polymorphisms (SNPs, pronounced “snips”) were identified. If you’ve never heard of a SNP, its name describes it fairly well: a place in the ge-

nome where a single nucleotide (i.e., an A, T, C, or G) is different for some individuals compared to others. For example, your honey bees might have an A at a particular position, while my bees might have a G at that same position. That’s a SNP.

Looking in detail at all of the SNPs allowed the authors to determine genetic variation among all 251 bee samples, how they were related, and with a couple of assumptions, when particular lineages diversified. In total, Dogantzis and colleagues analyzed 11.8 million SNPs – a very impressive dataset!

So, what did they find? Is there clear separation between the current *A. mellifera* lineages? Yes. As seen in Figure 1, the data reveal there are seven distinct lineages of Western honey bees. Lineage A (gray in Figure 1) is present across most of Africa, lineage L (orange) is present in Egypt, lineage U (yellow) is present in Madagascar, lineages Y and O (red and blue) are present in Asia, lineage C (turquoise) is present in Europe, and lineage M (purple) is present in Eurasia.

But look closely at panel B of Figure 1. Each narrow vertical column represents one of the 251 individual *A. mellifera* samples. As you can see, the colors for each lineage aren’t completely solid. This means some of the bees from a particular lineage share genes with another lineage. In other words, clearly there’s some recent mating that’s occurred between those

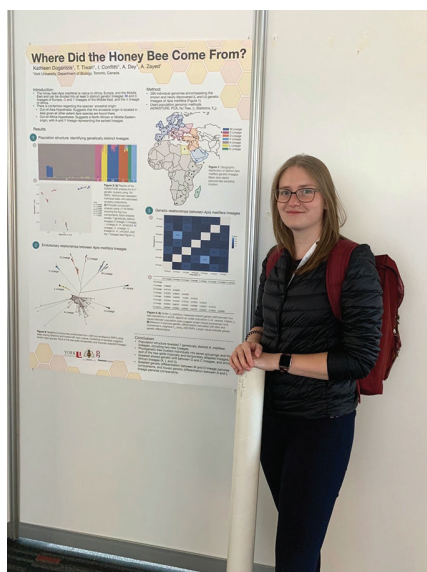


Photo 1 Lead author Kathleen Dogantzis presented her work in pre-COVID times at the 2019 Apimondia conference in Montreal, Quebec.

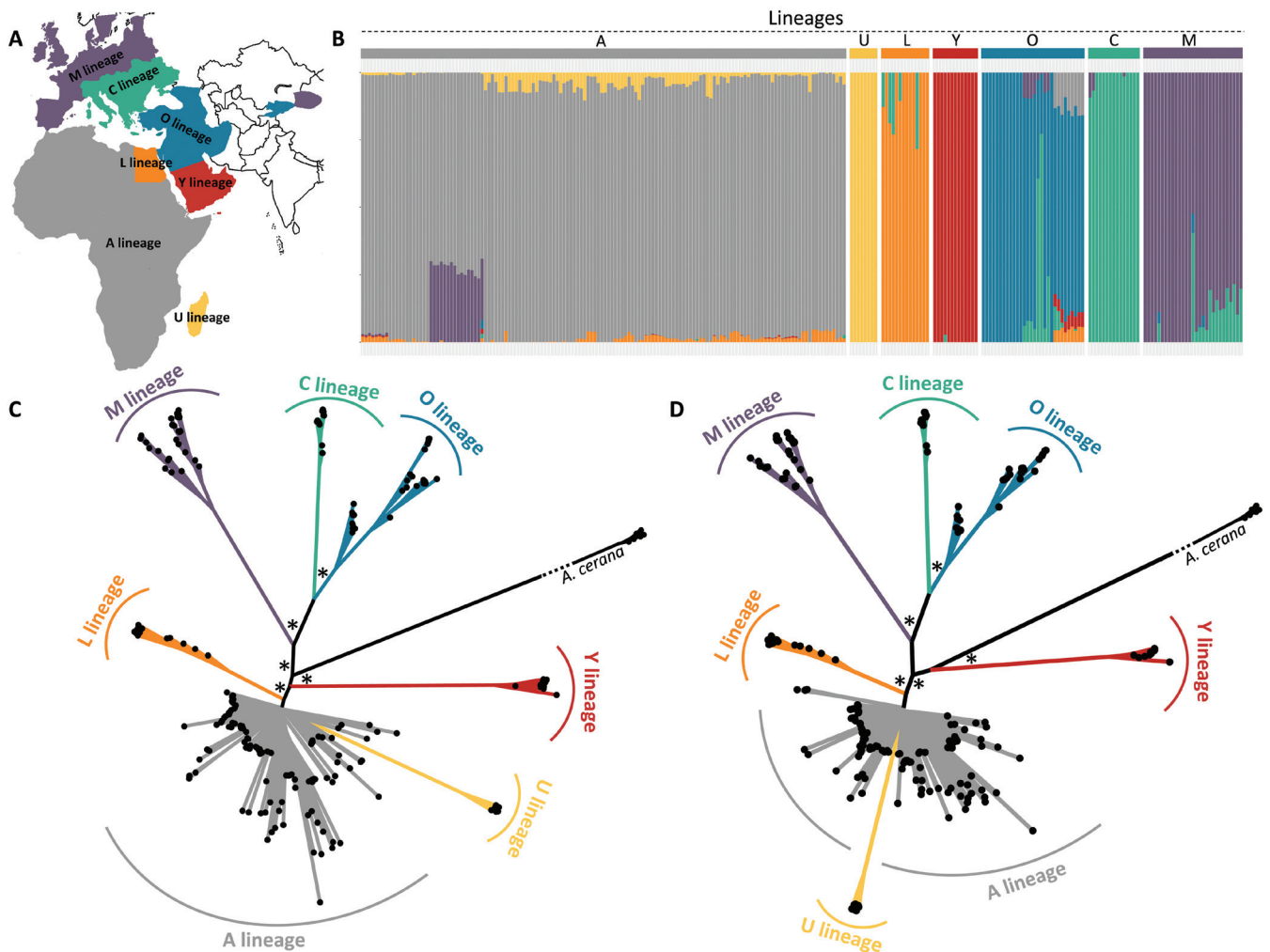


Fig. 1 Population structure and phylogenetic reconstruction of *A. mellifera*. (A) Map of the native distribution of the seven genetically distinct lineages. (B) Patterns of ancestry and population structure. Vertical bars represent individual bees, and colored segments represent the proportion of ancestry to the different clusters. (C) Evolutionary relationships among *A. mellifera* samples reconstructed with a neighbor-joining tree using SNPs located genome-wide. Asterisks represent node support of 100%. (D) Evolutionary relationships among *A. mellifera* samples constructed with a neighbor-joining tree using SNPs located within protein-coding regions. Asterisks represent node support of 100%.

particular lineages. This is especially clear for the O lineage (blue), which includes the subspecies *A.m. syriaca*. This subspecies shares 76.8% of its genome with lineage O, but it also shares 12.6% of its genome with lineage A, 4.4% with Y, and 4.4% with L. Given its geographic position between Africa and Asia, perhaps this evidence of recent cross-lineage mating should not be surprising.

How are the *A. mellifera* lineages related to each other? As seen in Figure 1C-D, the seven lineages are related to each other very similarly no matter how the data are analyzed (i.e., using SNPs in the whole genome (i.e., using SNPs in the whole genome, as shown in panel A, or only protein-coding SNPs, as shown in panel B). This means we're very confident in the overall pattern of relatedness among lineages, which allows the authors to ask more so-

phisticated questions about relatedness and evolution.

OK, let's get to it. When and where did *A. mellifera* originate and evolve? About six million years ago in Asia, with at least three expansions into Europe/Africa since. As seen in Figure 2, the authors assigned dates to the origin of each subspecies and traced those origins through time, again using the two methods of analysis (whole-genome vs. protein-coding SNPs, shown in panels A and B, respectively). The stories are very similar.

First, look at the left side of each panel. Because the circles are mostly yellow, this means the earliest *A. mellifera* lineages evolved in Asia. If you look at the top of each panel, you can also see the species that's the most likely closest ancestor to *A. mellifera*: the Eastern honey bee, *Apis cerana*. I doubt this will surprise many people,

especially since *A. cerana* and *A. mellifera* look so similar and share parasites such as varroa and nosema.

Next, trace the colored circles from left to right in each panel. Some of the colored circles stay yellow; this means those subspecies evolved in Asia and stayed in Asia. But something interesting happens when you look at the red and turquoise circles. Can you see the group of red circles sticking together as you move from left to right? This means there was likely one common origin of African *A. mellifera*, then a diversification of subspecies once it arrived in Africa. Contrast this pattern with the two distinct groups of turquoise circles in the middle and bottom of each panel. This means there were likely two origins of European *A. mellifera*, followed by diversification of subspecies. Adding it all up, the evidence

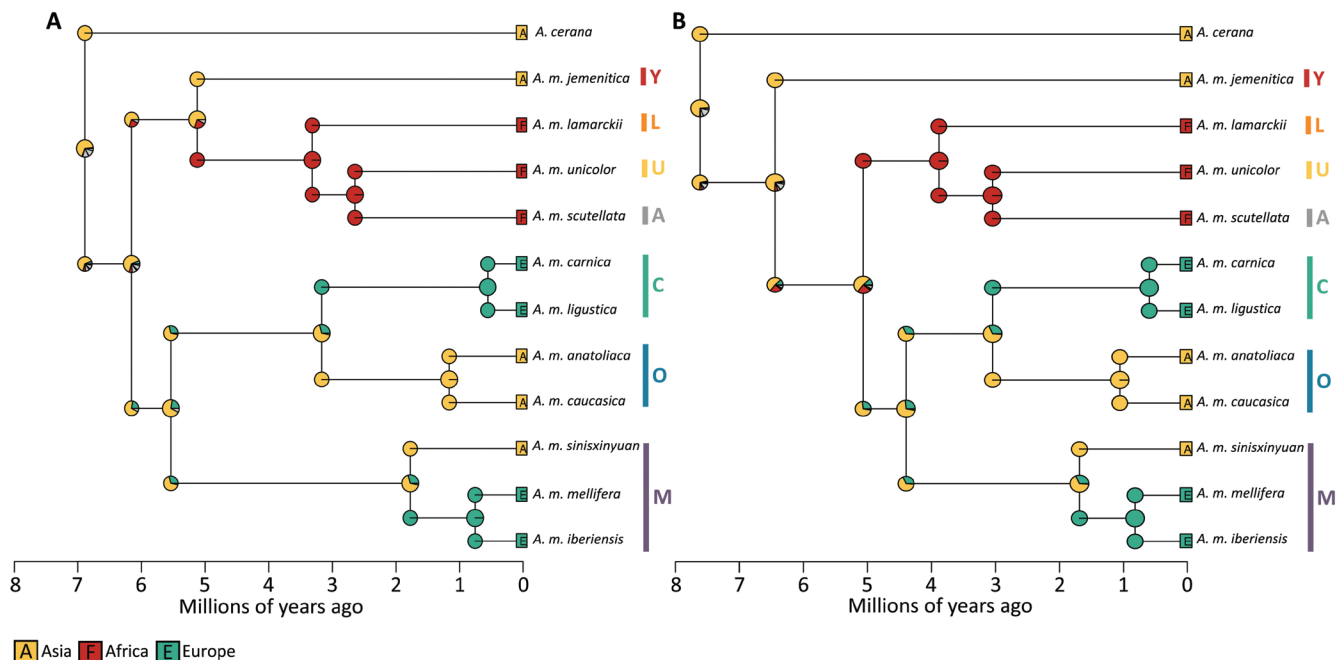


Fig. 2 Ancestral biogeographic range reconstruction of *A. mellifera* using two resolved topologies. The current geographic range of subspecies is indicated at branch tips by letters A (Asia), F (Africa), and E (Europe). Colored bars to the right of the trees indicate the lineage association of the subspecies. Pie charts at nodes indicate the marginal maximum likelihood probabilities for the estimated ancestral range. The ancestral range is predicted to be in Asia, with an estimated probability of 64 to 73%. (A) represents the topology reconstructed using SNPs located throughout the genome, while (B) represents the topology reconstructed with SNPs located in protein-coding regions.

shows that *A. mellifera* originated in Asia, then expanded once into Africa and twice into Europe, with various subspecies diversifying from there.

So there you have it. You wanted to know where your bees came from, and the ultimate answer is Asia. Though how every one of their genes got to you is a more complicated story, likely involving many paths through many regions and lineages, perhaps including all three expansions out of Asia.

Where will your bees' genetics go from here? That's partially up to you and partially up to the environment. As I sit here finishing the fiftieth Notes from the Lab, I think something similar is true. I certainly have a say in what gets written, but it's my environment (i.e., the scientists who publish their cool new work, and you, the engaged audience) who also have a say. So here's to the next fifty. Whether you're a scientist or engaged reader, don't be shy about shaping my environment and letting me know what science you want to see highlighted!

Until next time, bee well and do good work.

Scott McArt

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