



The Latest Bee Science Distilled

by Scott McArt

The genealogy of honey bees in the United States

The Western honey bee, *Apis mellifera*, is not native to the United States. Most beekeepers know this.

But do you know the genealogy of *A. mellifera* (hereafter, the “honey bee”) in the United States? In other words, do you know the full story of when honey bees came to the USA, how many times they were introduced, where each of those introductions occurred, how quickly they spread from one part of our country to another, and which lineages are most abundant in your neighborhood as a result of this history? These are the topics for our fortieth Notes from the Lab, where we summarize “**Genetic past, present, and future of the honey bee (*Apis mellifera*) in the United States of America,**” written by Madeline Carpenter and Brock Harpur and published in *Apidologie* [2021].

More than 25 million people have used 23andMe, Ancestry.com, or other genetic tests to trace their genealogies. Many of us are clearly curious about where our great-great-grandparents came from! Similarly, I can assure you from talking with hundreds of beekeepers over the years that every single one of us is interested in the genealogy of our bees.

Some beekeepers are simply curious to know the lineage of their bees. *Do I have Italian bees? Are my bees Carniolans?* But many beekeepers also know that specific traits, such as varroa resistance, have a genetic basis (e.g., Purdue “mite biting” bees). This means

that the pedigree of your bees matters since those genes are passed down from the previous generation. In other words, knowing the genetics and genealogy of honey bees can help us understand their history, but it can also allow us to understand their future in terms of the diversity of traits that can be improved through breeding.

For their study, Carpenter and Harpur tapped into two major resources. First, they did some good old-fashioned work in the library. Because honey bees have been intensively managed for nearly 11,000 years, we humans have been pretty good about noticing them and writing down our observations. So, if you want to know when and where honey bees were present, you can read old documents to see when and where someone mentions them in historical records. The authors pored over thousands of documents, ultimately finding nearly 200 records that indicated the first time honey bees were observed in a particular geographic location in the USA.

Second, nearly two dozen honey bee population genetic studies have been conducted in the United States to date, and more studies are in the works. Carpenter and Harpur summarized all existing scientific literature on this topic. Ultimately, these genetic studies allow us to understand how introductions of various lineages have shaped the genetic diversity and differentiation of honey bee populations across the USA. It is

this diversity and differentiation that provides the raw material necessary for breeding.

So, when and where were honey bees first introduced to the United States? 1622 in Jamestown, Virginia (see Figure 1). If you’re sitting in Virginia right now and reading this article, you’re sitting in the region that’s enjoyed the longest history of honey bees in the USA, starting with the first introduction by the Virginia Company from England.

Three other locations were relatively quick to follow. Honey bees were introduced by English colonists to Plymouth and Boston, Massachusetts in 1637 and 1640, respectively, and by English colonists to Long Island, New York in 1670 (Figure 1). Between 1670 and 1845, only two additional importation records exist; Pensacola, Florida in 1763, and Mobile, Alabama in 1773.

During this time, honey bees spread west to the Mississippi by two mechanisms: trade among humans and natural swarming. For example, in the 1700s, it was common for “bee trees” to be found throughout the Carolinas and Pennsylvania. Then, in the mid-1800s, importations started to pick up in the western United States. In 1845, honey bees were imported to Texas by German settlers, and numerous introductions occurred on the west coast (California, Oregon, Washington) and Hawaii in the 1850s (Figure 1).

Which lineages were introduced? At least nine subspecies from four of the five *A. mellifera* lineages have been

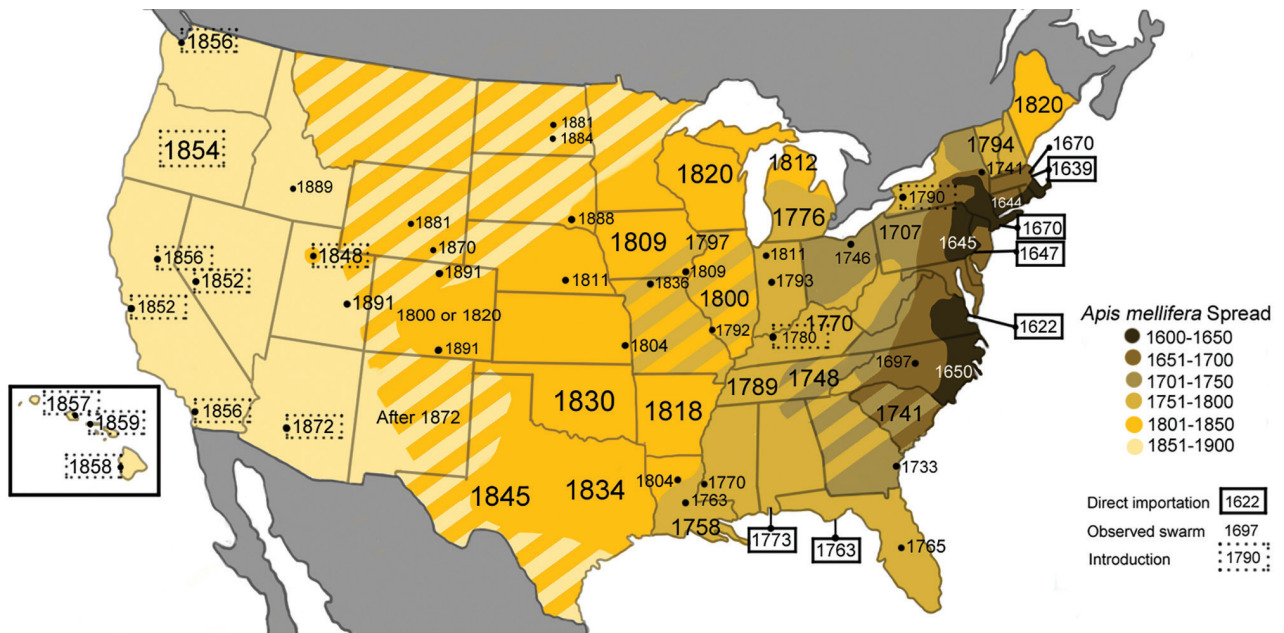


Fig. 1 Estimated *A. mellifera* population expansions in the mainland United States. Locations have been recorded or estimated from digitized importation records of European colonialists or their accounts of swarm sightings. Sightings are given a specific location if possible; otherwise, the date text is larger and imposed over the state or area the sighting occurred. Color gradients are proposed ranges estimated by combining known sightings and introductions with an estimation of average yearly spread as (50 years – establishment date) x 16.5 km. Alaska has been excluded because honey bees were first introduced to the state in 1924 and cannot be attributed to a source population. Dates before 1859 are exclusively *A.m. mellifera* sightings, but dates after 1859 can be attributed to *A.m. ligustica*, *A.m. mellifera*, *A.m. ligustica* x *A.m. mellifera* hybrids, and/or various *A. mellifera* hybrids.

introduced to the USA. But for over 200 years (between 1622 and 1859), the only honey bee subspecies present in the United States was *A.m. mellifera* (*Apis mellifera mellifera*). Bees from this lineage (lineage M) come from

northern Europe and central Asia and include the English “dark bees,” which were the first honey bees to arrive in Jamestown.

Italian bees (*A.m. ligustica*; lineage C, from central and southern Europe)

were the next to arrive, imported in 1859 to New York City and Philadelphia from Germany and Switzerland (Figure 2, red square). In the 1860s, Italian queens were imported to several locations in the USA from the

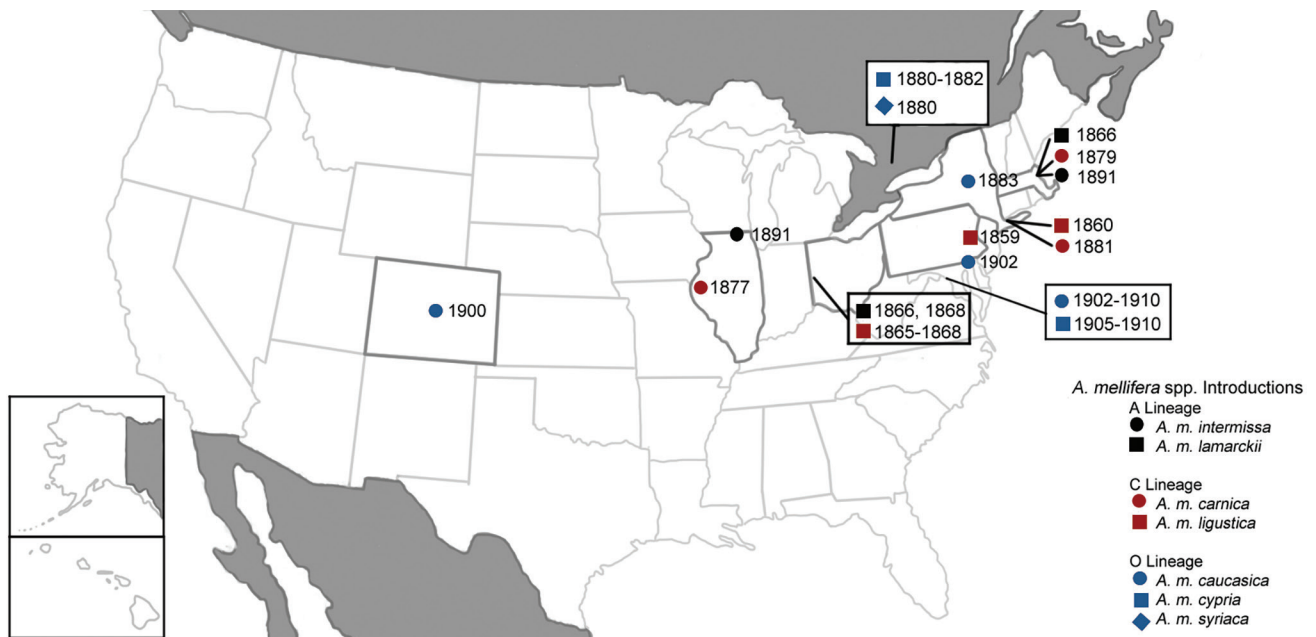


Fig. 2 Seven subspecies were introduced to the mainland United States between 1859 and 1922: *A.m. ligustica* (1859), *A.m. lamarckii* (1866), *A.m. carnica* (1877), *A.m. cyprica* (1880), *A.m. syriaca* (1880), *A.m. caucasica* (1882), and *A.m. intermissa* (1891). Here, we have highlighted the first 5 years of a recorded importation of a given subspecies into the mainland United States. The exceptions are *A.m. caucasica* and *A.m. cyprica*, both of which were imported sporadically or for a short time before importations ceased and were continued under Benton. One series of *A.m. cyprica* and *A.m. syriaca* importations to Beeton (now New Tecumseth), Canada is recorded because these were the source of importations to the USA. The boxes represent large-scale operations in Ohio (Rev. L.L. Langstroth); Washington, D.C. (Frank Benton); and Canada (D. A. Jones).

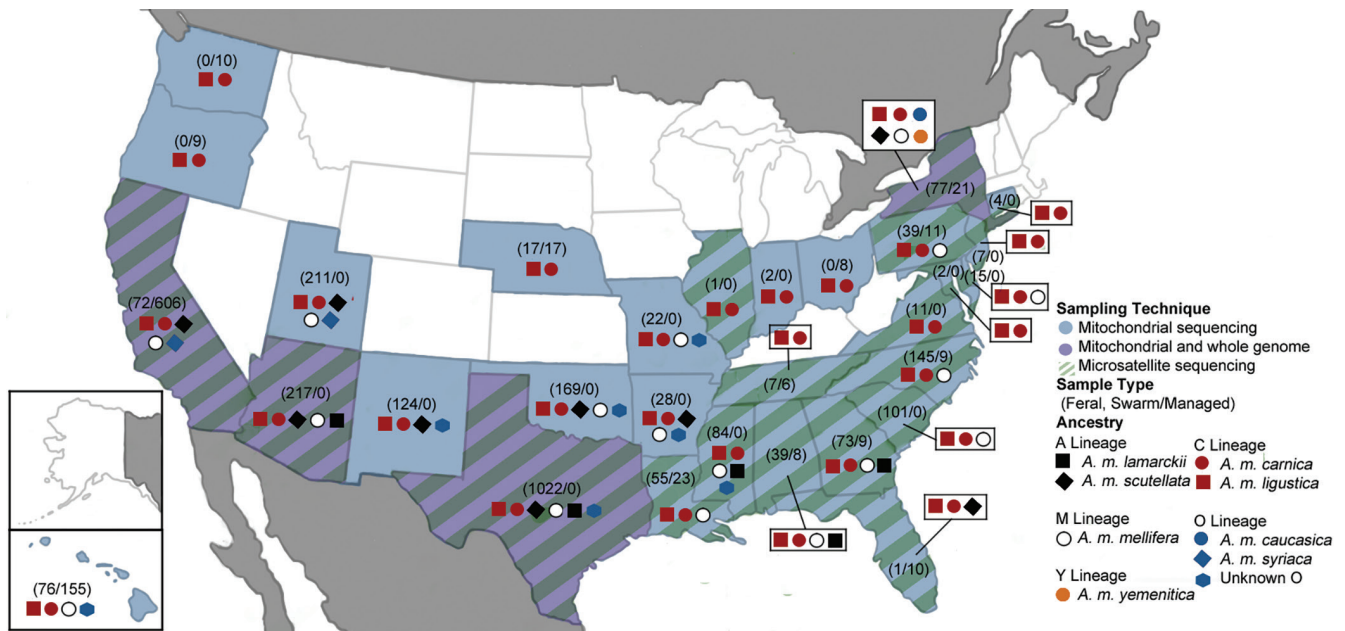


Fig. 3 Summary of locations, methods, and sample sizes of honey bee genetic studies in the U.S., as well as lineages or subspecies (when identifiable) detected. Both managed and feral populations are included in each state, but there is considerable — if not complete — overlap between lineages and/or mitotypes found within a state's feral and commercial colonies. The studies represented in this figure specified the ancestry of individual samples. Overall, the figure highlights two major shortcomings in U.S. honey bee genomics: small sample sizes (11 states have fewer than 11 samples) and biases toward either managed or feral colonies within states. Furthermore, despite the documented presence of AHB in Louisiana, Alabama, Mississippi, and Georgia, sampling methods have missed them there.

Lake Maggiore region of northern Italy, until it became more common in the 1890s to import from Milan and Bologna.

Carniolan bees (*A.m. carnica*; lineage C) were first imported in 1877 to Hamilton, IL (Figure 2, red circle) by none other than Charles Dadant, the founder of Dadant & Sons, which publishes the fine magazine you're currently reading. Carniolan bees were imported throughout the late 1800s from areas in Dalmatia and Carniola (modern-day Croatia and Slovenia) and Hungary.

Caucasian bees (*A.m. caucasica*; lineage O, from the Middle East and western Asia) were first imported in 1883 to upstate New York (Figure 2, blue circle). These bees were initially imported from beekeepers in Germany, but in the early 1900s, queens were imported directly from operations on the shores of the Black and Caspian seas.

Four additional subspecies of *A. mellifera* have been imported to the USA: The Cyprian honey bee (*A.m. cypria*; lineage O), Syrian honey bee (*A.m. syriaca*; lineage O), Egyptian honey bee (*A.m. lamarkii*; lineage A, from Africa), and Tellian honey bee (*A.m. intermissa*; lineage A). Records indicate they weren't distributed widely because each of the lineages was prone to swarming, abscond-

ing, and/or defensive behavior. This is why most readers in the USA have probably rarely heard of Cyprian, Syrian, Egyptian, or Tellian bees; they are not common lineages of bees in the United States due to their importation history.

Well, there were certainly a lot of introductions, especially in the 1800s! What's happened since then? Two events in the early 1900s reduced honey bee importations in the USA. Isle of Wight disease (1906-1916) and World War I (1914-1918) dramatically reduced the number of colonies imported from Europe; the former ultimately led to the Bee Act of 1922, which forbade the importation of live honey bees and hive products to the USA. This act was expanded in the 1960s to include germplasm, due to concern about Africanized honey bees (AHB) from South and Central America. In 1987, importations from Canada were also restricted over concerns about AHB.

Limited importations commenced again in 1989 after the identification of varroa-resistant strains in Europe. Importation of varroa-tolerant strains were also allowed from Russia between 1997 and 2002. From 2004-2010, importations from New Zealand and Australia occurred, but were halted in 2010 out of concern that the Eastern honey bee, *Apis cerana*, could

potentially arrive. Finally, since 2009 there have been at least 11 USDA-approved importations of germplasm to Washington State for use in breeding efforts.

Which subspecies of honey bees are most common in the USA right now? Italians and Carniolans. Or, more precisely, current genetic evidence shows the two most common mitotypes of honey bees in the United States are C1 (*A.m. ligustica*) and C2 (*A.m. carnica*), as shown in Figure 3.

The fact that lineage C (*A.m. ligustica* and *A.m. carnica*) is currently more common than lineage M (*A.m. mellifera*) likely says something about how popular Italian and Carniolan bees were in the late 1800s and how popular some of their traits are with beekeepers today. Even though *A.m. mellifera* was the only subspecies present in the USA for over 200 years (between 1622 and 1859), the late 1800s saw a dramatic increase in importation and distribution of *A.m. ligustica* and *A.m. carnica*. That period in the late 1800s appears to have had a large and lasting impact on present-day honey bee genetics in the United States.

Is there enough genetic diversity and differentiation to select for traits that will keep my bees strong and healthy? This, of course, is the million-dollar question. Can it be

answered? Well, on the one hand, the study by Carpenter and Harpur shows we definitely need more genetic and genomic data for honey bees in the United States (for example, see the big blank areas in Figure 3).

But on the other hand, genetic diversity of honey bees in the USA is high. Several studies have shown that genetic diversity of bees in the USA is just as high as (or higher than) genetic diversity in Europe. In addition, new genomic studies show there are regional differences in honey bees, and genetically unique feral populations exist. Thus, the evidence to date indicates honey bees in the USA have high genetic diversity and differentiation.

In other words, breeders have quite a bit of raw material to work with when selecting for traits in their bees. While it's impossible to know whether it will be enough raw material given all the current and future stresses that bees may face, it certainly seems promising. Especially if we recognize the importance of good breeders (and genetic/genomic researchers!) and give them as much support as we can.

Until next time, bee well and do good work.

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REFERENCE:

Carpenter, M. H. and B. A. Harpur. Genetic past, present, and future of the honey bee (*Apis mellifera*) in the United States of America. *Apidologie* (2021). <https://doi.org/10.1007/s13592-020-00836-4>

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