New research deepens mystery about evolution of bees' social behavior

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Examples of bee species analyzed include (clockwise from top left) Apis dorsata, a member of the honey bee tribe Apini; Bombus pauloensis, of the bumble bee tribe Bombini, Melipona quadrifasciata, of the stingless bee tribe Meliponini, and Exaerete smaragdina, of the orchid bee tribe Euglossini. Note: Images are not to scale. (Photos by Eduardo Alemeida, Ph.D., University of São Paulo). Credit: Eduardo Alemeida, Ph.D., University of São Paulo

A new study has mounted perhaps the most intricate, detailed look ever at the diversity in structure and form of bees, offering new insights in a long-standing debate over how complex social behaviors arose in certain branches of bees' evolutionary tree.

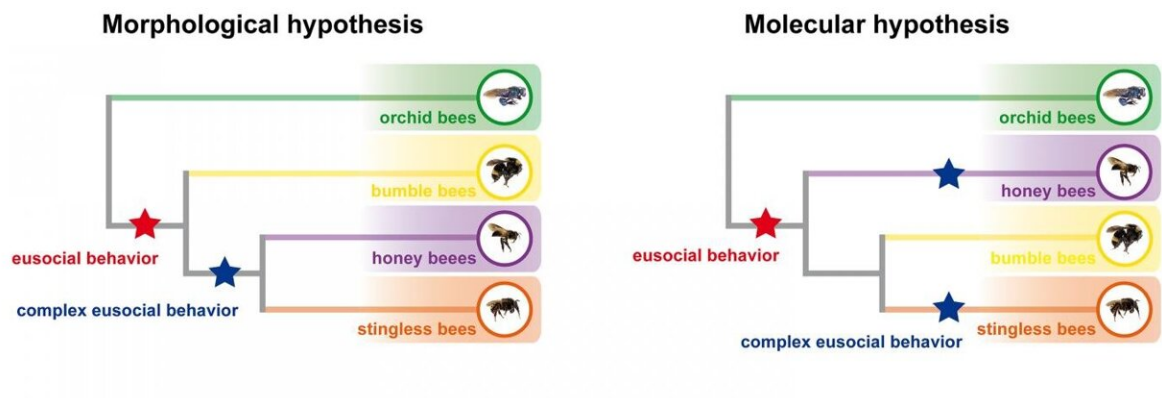
Published today in *Insect Systematics and Diversity*, the report is built on an analysis of nearly 300 morphological traits in bees, how those traits vary across numerous species, and what the variations suggest about the evolutionary relations between bee species. The result offers strong evidence that complex social behavior developed just once in pollen-carrying bees, rather than twice or more, separately, in different evolutionary branches—but researchers say the case is far from closed.

Diego Sasso Porto, Ph.D., has been studying the structure and form, or morphology, of bees for more than a decade, and his latest effort ventures into a longstanding conundrum about bee evolution. Corbiculate bees—those that possess corbicula, or pollen baskets, on their hind legs—encompass honey bees, stingless bees, bumble bees, and orchid bees. Among them, honey bees and stingless bees are the only groups with highly complex social behaviors, such as forming large colonies with queens, workers, and drones. Bumble bees display less complex sociality, and orchid bees are mostly solitary. Traditional morphological analyses have long indicated that honey bees and stingless bees are most closely related and that complex social behavior developed in their common ancestor before the groups diverged. However, in the 1990s, emergent techniques in molecular genetic analysis began to show that stingless bees and bumble bees were the more closely related "sister" groups, which would mean that honey bees and stingless bees each developed their complex social behavior independently, after their ancestral paths diverged.

Ever since, these different lines of evidence have persisted as a notorious case of incongruence between molecular and morphological data sets in animals. Porto, now a postdoctoral researcher in the Department of Biological Sciences at Virginia Tech, made his foray into the debate amid his doctoral work at the University of São Paulo in Brazil, under the guidance of Eduardo Almeida, Ph.D., co-author on the new study.

"The main criticism from some molecular researchers against morphology, and even from morphologists themselves, was we don't have enough data," Porto says. "This work was a big effort to try to get the best morphological data set we could ever get for this group of bees, and we tried several analyses to see if the problem is with morphological data itself or the way we interpret morphological data."

Porto evaluated past morphological studies of bees and then conducted new analysis of specimens from 53 species, dissecting each, imaging anatomical structures under optical and scanning electron microscopes, and ultimately scoring all of the specimens across 289 different traits. Often minute or even microscopic in detail, these traits ranged from the number of teeth on a bee's mandibles to the arrangement of barbs on its stinger.



Credit: Diego Sasso Porto, Ph.D., Virginia Tech

With this massive trove of morphological data in hand, Porto applied multiple types of computerized statistical analyses to evaluate the possible phylogenies, or "family trees," that delineate the relationships among bee species. The results strongly support previous morphological findings, that honey bees (tribe Apini) and stingless bees (Meliponini) are most closely related. "The evidence from our dataset, if we just take it at plain sight, is really strong. We have a lot of traits supporting this," says Porto.

But, he sought to further explore the discrepancy between what molecular genetic analysis shows and what his own morphological data supports. To do so, Porto ran his data through a separate analysis that evaluated how well the morphological data could fit with the evolutionary tree supported by molecular analysis—that Meliponini and Bombini (bumble bees) are most closely related. As expected, it was not a great fit—a bit like putting a square peg in a round hole—but they were not completely incompatible, he says.

In their report in *Insect Systematics and Diversity*, Porto and Almeida offer a few hypotheses for evolutionary processes that could explain the continuing discrepancy in lines of evidence about corbiculate bee evolution.

"Morphological data is telling us one story, and molecular data is telling us another story. We are not going anywhere if we just keep these conflicting discussions," says Porto. "So, our decision was ... let's try to interpret the alternative scenario with our data. If the hypothesis given by molecular data is true, how can we interpret our strong morphological evidence for the other hypothesis?"

One possible explanation, they say, is that, if bumble bees and stingless bees share a common ancestor that first branched away from honey bees, they then rapidly diverged in a short time frame and evolved separately for much longer, gradually obscuring the shared traits bumble bees and stingless bees once had. Moreover, the earliest ancestor of stingless bees is believed to have been relatively small, and "miniaturization" is known to drive structural simplifications in anatomical traits, which would have further contributed to erasing similarities between bumble bees and stingless bees.

However, these possibilities don't explain why stingless bees then evolved to become more morphologically similar to honey bees, but Porto and Almeida posit that similar functional roles or similar social behaviors among stingless bees and honey bees could have driven them to evolve in similar ways.

Testing these hypotheses is what Porto says he would like to explore next—and encourages other researchers to do, as well. "It would be really good to have maybe the same data set, but including more specimens from fossils, and run the analysis again," he says.

More information: Diego Sasso Porto, Eduardo A B Almeida.

Corbiculate Bees (Hymenoptera: Apidae): Exploring the Limits of Morphological Data to Solve a Hard Phylogenetic Problem. *Insect Systematics and Diversity*. May 2021. doi.org/10.1093/isd/ixab008

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