For certain orchids, relatives more important than pollinators in shaping floral attractants

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This is an inflorescence close-up of Pterygodium cooperi, an orchid indigenous to the grasslands of the Drakensberg Mountains in eastern South Africa. This flower secretes non-volatile oil as a pollinator reward and is pollinated by specialized solitary bees in the genus Rediviva (Melittidae). To collect the oil, the bee pushes back on the upper lip with its head while simultaneously inserting its forelegs into the central cup-like lip appendage that curves back into the flower. Using its forelegs with their specialized scraping and absorptive trichomes, it scrapes and wicks up the oil. The oil is transported back to the nest and used for provisioning and construction of the bee's nest cells. The waxy projections of the lower lip cause the bee to slip as it positions itself on the flower and this results in the bee contacting and extracting the pollen sacs (pollinaria) with its hind legs. Unlike many orchids, this species provides a distinctive scent as well as a food reward to attract its specialized pollinators. The floral scent is dominated by the unusual benzenoid ketone 2-Methoxy-6-methyl-acetophenone (64.6%), as well as a variety of the aliphatic compounds including (E)-3-Methyl-4-Decenoic acid (9.1%), Heneicosane (5.0%), (E)-3-Methyl-4-decenal (2.9%), (E,Z)-2,6-Dodecadienal (2.8%), and Decanal (1.1 %). The dominance of benzenoids and/or aliphatic compounds is typical of the scents of the oil-secreting orchids in both Summer and Winter Rainfall regions despite the presence of different pollinator species. Thus phylogeny appears to be more important than pollinators in determining scent constituents of oil-secreting orchids in southern Africa. This is especially true for P. cooperi and other species in the Ommatodium clade that are dominated by 2-Methoxy-6-methyl-acetophenone regardless of pollinator or region of occurrence. Credit: Kim Steiner

Bees, bats, and moths all follow their noses in search of food from flowers. Plants that rely on such animals for pollination often produce particular chemical scents that attract specific pollinators. However, the ability to produce certain chemicals is also determined by a plant's genetics, or phylogenetic history, which can potentially limit its ability to respond to pollinator pressures. So which is more important in the evolution of floral scents: pollinator-induced natural selection or phylogenetic constraints?

While pollinators are often thought to be the driving force behind the type of chemicals plants produce to attract them, no matter how closely related the plants are to each other, a new study by Kim Steiner and colleagues published in the October issue of the American Journal of Botany reveals that phylogeny may be more important than pollinators in determining floral scent characteristics in a group of specialized South African orchids.

"The evolution of any plant or animal character, be it morphological or something as seemingly intangible as a floral scent composed of many specific compounds, is a product of the balancing forces of natural selection and phylogenetic constraint," notes Steiner (University of Kwazulu-Natal, Pietermaritzburg, South Africa).

"While the results of natural selection, or pollinator-mediated selection, generally produce the most fascinating examples of evolution -- such as the extraordinarily long spurs of the Angraecum orchid (Darwin's orchid) and the equally extraordinarily long proboscis of its hawkmoth pollinator -- many characteristics are shared between closely related species simply as the result of their common ancestry, and it is important to be aware that this common ancestry can have a strong influence on the outcome of natural selection," Steiner says.

While Steiner was conducting fieldwork in South Africa, he noticed that the Redivia bees he was catching had small yellow objects attached to their legs. These turned out to be pollen packets (pollinaria) from orchid flowers. "By matching up the varied shapes and sizes of the different pollinaria found on the bees with those I extracted from the various orchid flowers I encountered, I was able to determine which orchid species these bees were visiting and what the attractant might be," Steiner comments. "For each orchid whose pollinaria the oil-collecting bees carried, I found that the flowers secreted a non-volatile oil rather than nectar as a reward. And, by examining as many orchid flowers as I could find, I discovered that over 100 orchid species in southern Africa produce oil as a pollinator reward and that these species are pollinated by oil-collecting bees."

The scents of these orchids, which are usually described as unpleasant, pungent, cloying, or smelling like soap, fascinated Steiner, and he sent as many scents as he could collect to a well-known authority on orchid scents, Roman Kaiser. According to Steiner, "Once we had a good sample of scents from the different oil-secreting orchids, we could begin to compare them and ask questions regarding whether closely related species had more similar scents than distantly related species and whether species pollinated by the same bee species also shared the same floral scent, even when they were not closely related. In other words, is phylogeny more important than natural selection in determining the composition of floral scents in this group of orchids?"

Steiner and his colleagues, Kaiser and Dötterl, predicted that because these oil-secreting orchids seem so specialized, the scent profiles of species pollinated by the same bee species would be similar regardless of phylogeny. They also predicted that the scents of orchids within a rainfall region (winter vs. summer) would be more similar to each other than to related species found in other regions.

Using a method called headspace adsorption, the authors sampled the scents of 39 oil-secreting Coryciinae orchids. Flowering stems for each species were enclosed in a glass vessel, and air was pumped through the vessel forcing scents to pass through a glass capillary tube, after which their distinct chemical compound signatures were captured via gas chromatography.

While 257 compounds from nine different compound classes were identified, each orchid species on average had 26 different compounds—more than 60% of the compounds were found in only one or two orchid species, and only 3% were found in more than half of the taxa.

Contrary to Steiner et al.'s expectations, in the winter rainfall region, phylogenetics seems to play a significantly greater role than pollinator selection pressure. Here the scent profiles fell along phylogenetic lines—related taxa had similar scents, while specific bee species pollinated taxa with different scents, and taxa with similar scents were pollinated by different bee species. Similarly, in the summer rainfall region, scent profiles also fell along phylogenetic lines, although the authors could not examine pollinator effects because most of the orchids in this region shared the same pollinators.

Interestingly, almost all the orchids in the two regions emitted similar scent compounds even though the Rediviva bee pollinator species differed between the two regions. This was also contrary to the authors' expectations.

Overall Steiner et al. found overwhelming support for the fact that phylogeny played a more important role in scent variation than pollinator selection, even in a group of closely related plant species pollinated by a single class of pollinator.

"We have shown that although there is evidence for pollinator-mediated selection in the chemical composition of some of the scents we analyzed," concludes Steiner, "for the group of oil-secreting orchids as a whole, the role of phylogenetic constraint is more important for determining overall scent composition of the fragrances than natural selection."

The authors are still hot on the trail of this flower/bee puzzle and are currently working on identifying the compounds that stimulate the olfactory sensilla of the bee's antennae. As Steiner notes, "We still need to examine the individual chemical constituents in the fragrances of oil-secreting orchids and to test which of these compounds can be detected physiologically by the oil-collecting bees. Then we can determine which of the myriad of compounds in the scents we have already analyzed are attractive to the oil-collecting bees."

More information: Kim E. Steiner, Roman Kaiser, and Stefan Dötterl. (2011). Strong phylogenetic effects on floral scent variation of oil-secreting orchids in South Africa. American Journal of Botany 98(10): 1663-1679. DOI: 10.3732/ajb.1100141

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