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EVOLUTIONARY BIOLOGY

# Flowers with bad breath

How an old gene acquired a new function to exploit an insect's sense of smell

**Lorenzo Caputi** *and* **Sarah E. O'Connor**

Plants and insects have coexisted for millions of years (*1*). The evolution of flowers—the reproductive organs of angiosperms—has played a foundational role in shaping interactions between plants and insects (*2*). In addition to visual and structural adaptations, flowers evolved the ability to produce complex mixtures of volatile compounds that allow the plant to communicate with insects, often conveying specific messages (*3*). The emission of these floral scents can either seduce insects to visit the plant's reproductive organs, thereby increasing the chances of successful pollination, or repel unwanted visitors. During evolution, plants have modulated the molecular composition of these scents to address specific insect audiences. On page 656 of this issue, Okuyama *et al.* (*4*) report one example of a molecular mechanism by which plants can add a chemical message to their scent language.

Plants belonging to the genera *Aristolochia*, *Rafflesia*, and *Asarum* use sulfur-containing chemicals, namely oligosulfides, in their flower scents. These oligosulfides confer to the flower a foul odor that mimics a rotten carcass (*5*). This represents a strategic deception in which insects that normally feed on decaying organic matter are tricked into paying a visit to these flowers, which results in inadvertent pollination by the insects. Hence, the inclusion of these sulfur-containing molecules has allowed the plants to hijack insect behaviors while offering nothing to the insects in return.

In plants, oligosulfides originate from methanethiol, which is an intermediate formed during the catabolism of the amino acid methionine (*6*). Methanethiol is also produced in the human body through microbial metabolism in the mouth and the gut. Poor oral hygiene favors the accumulation of high amounts of this compound in the mouth, leading to halitosis (bad breath). Humans also produce methanethiol endogenously in the liver. Some diseases, including certain cancers, disrupt cellular metabolic processes, thus causing accumulation of this compound in the body and extraoral halitosis (*7*, *8*). In both plants and humans, methanethiol can spontaneously oxidize to form oligosulfides, such as dimethyl disulfide (DMDS). DMDS is a major scent component emitted by the flowers of *Asarum*. Some plant species produce higher amounts of oligosulfides than others, which led Okuyama *et al.* to hypothesize that specific enzymes are required for the formation of these foul-smelling volatile chemicals.

Okuyama *et al.* found a correlation between the amount of DMDS emitted by the flowers and the expression levels of a gene belonging to a family that encodes selenium-binding proteins (SBPs). In humans, an SBP called SELENBP1 acts as a methanethiol oxidase and detoxifies methanethiol into hydrogen peroxide, hydrogen sulfide, and formaldehyde (*9*). Mutations in *SELENBP1* are associated with

PHOTOS: OKUYAMA *ET AL.*

*Asarum simile*, *Eurya japonica*, and *Symplocarpus renifolius* (from left to right) each independently evolved the ability to mimic the smell of rotten flesh through disulfide synthase activity.

increased amounts of methanethiol, leading to breath that has a cabbage-like smell (*9*). Although genes encoding methanethiol oxidases are highly conserved among land plants, their function in the plant kingdom is unclear.

Okuyama *et al.* noticed that *Asarum* contains a number of SBP genes, which can be grouped into three major classes. To determine whether any of these SBP genes were involved in DMDS formation, the authors heterologously expressed the corresponding proteins in *Escherichia coli* and then assessed their enzymatic activity using methanethiol as substrate. They found that the protein products of one of these classes of gene, which they named SBP1, can produce DMDS from methanethiol. Therefore, SBP1 does not perform the canonical methanethiol oxidase reaction—conversion of methanethiol into formaldehyde, hydrogen sulfide, and hydrogen peroxide—but instead oligomerizes methanethiol to DMDS.

How did this chemical reactivity of SBP1 evolve from the canonical methanethiol oxidase? Okuyama *et al.* used phylogenetic relationships to infer what the protein sequence of the ancestral methanethiol oxidase would have been. These phylogenetic reconstructions also revealed what amino acid changes likely occurred in the protein throughout evolution. The authors identified three amino acids responsible for the functional shift between methanethiol oxidase and SBP1 enzymatic activity. In their survey of 12 plant genera, from which the authors assayed the activity of a subset of SBP enzymes, enzymes with disulfide synthase activity were only found in *Asarum*, *Symplocarpus*, and *Eurya* (see the photos). In all three genera, which are phylogenetically distant, disulfide synthases evolved independently through the same process, which involved gene duplication events.

Gene duplication is the driving force for evolutionary innovation. In this process, the original gene maintains the original function, whereas the new copy is subject to mutations. These mutations may lead to the acquisition of a new function. This process, called neofunctionalization, plays a substantial role in the evolution of specialized traits in all living organisms. Okuyama *et al.* report a notable example of gene neofunctionalization. In this case, the newly acquired function confers a direct ecological advantage to oligosulfide-emitting plants, one that enables these organisms to establish new olfactory relationships with an insect population and to adapt to diverse ecological niches. This is accomplished by only a few amino acid substitutions in one protein.

It is notable that although methanethiol oxidation, the ancestral enzymatic activity, is also observed in humans, enzymatic oligosulfide synthase activity has only evolved in plants. This is likely to be because plants are under constant evolutionary pressure to produce complex chemistry for communication and defense. □

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Department of Natural Product Biosynthesis, Max Planck Institute for Chemical Ecology, Jena, Germany. Email: lcaputi@ice.mpg.de

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