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Chemical Mimicry in Sexually Deceptive Orchids of the Genus *Ophrys*

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The most spectacular case of floral mimicry is sexual deception, also called pseudocopulation, a pollination mechanism which is not known outside the *Orchidaceae* (AYASSE 2006). In sexually deceptive orchids the flowers mimic in shape, color and odor females of their pollinators, and thereby attract males for pollination. Male aculeate Hymenoptera are mostly involved in pollination of sexually deceptive orchids. Our investigations clearly demonstrated that odor signals are of primary importance for the attraction of the pollinating males (SCHIESTL & al. 1999, AYASSE & al. 2003). *Ophrys* flowers produce the same compounds in more or less similar relative amounts to the sex pheromone of females of their pollinators (AYASSE 2006). In *O. sphegodes*, saturated and unsaturated hydrocarbons triggered EAG responses in male antennae, and synthetic copies of these hydrocarbons, blended in the relative amounts found in the odor samples of females and the orchid flower, elicited copulatory attempts in males (SCHIESTL & al. 2000). Almost the same alkanes and alkenes were found to be biologically active in several allopatric and sympatric species of the *Ophrys fusca* group and in one species of the *O. sphegodes/mammosa* group pollinated by either Andrena nigroaenea or A. flavipes (STÖKL & al. 2005).

In contrast to the Andrena pollinated species, investigations in the mirror orchid *O. speculum* have shown that pollinator attraction in sexually deceptive orchids may be also based on a few specific chemical compounds (AYASSE & al. 2003). *O. speculum* flowers produce many volatiles, including trace amounts of (ω-1)-hydroxy- and (ω-1)-oxo acids, especially 9-hydroxydecanoic acid. These compounds, which are novel in plants,

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proved to be the major components of the female sex pheromone in the scoliid wasp Campsoscolia ciliata, and stimulate male copulatory behavior in this pollinator species. The specificity of the signal depends primarily on the structure and enantiomeric composition of the oxygenated acids, which is the same in wasps and in the orchids. The overall composition of the blend differed significantly between orchid and its pollinator and is of secondary importance.

Scent Variation

The highly specific *Ophrys*-pollinator relationship represents the main mechanism of reproductive isolation between the often interfertile *Ophrys* species (EHRENDORFER & al. 1980) and the species-specific scent is mainly responsible for pre-zygotic isolation (SCHIESTL & AYASSE 2002). In the sympatric, closely related orchid species *O. fusca* and *O. bilunulata*, which are pollinated by A. nigroaenea and A. flavipes, SCHIESTL & AYASSE 2002 identified and compared the pollinator attracting scent. They found that the difference in scent between both species is rather small. Among the biologically active compounds the pattern of alkanes was mostly the same, whereas the relative proportions of alkenes differed. Based on behavioral experiments, SCHIESTL & AYASSE 2002 found that the pattern of alkenes has an important function in selectively attracting pollinators of both species, a result that was later supported by investigations by STÖKL & al. 2005. Using electrophysiology (GC-EAD) and chemical analyses they studied the odor bouquets of several allopatric and sympatric species of the *Ophrys fusca* group and one species of the *O. sphegodes/ mammosa* group, all pollinated by either A. nigroaenea or A. flavipes. A comparison of the investigated species based on the proportions of all GC-EAD active compounds revealed that allopatrically occurring *Ophrys* species with the same pollinator, independent of their phylogenetic relationship, use the same odor compounds for pollinator attraction. Therefore, there is a convergent evolution of pollinator attracting volatiles in *Ophrys* orchids. Differences between the *Ophrys* species pollinated either by A. nigroaenea or by A. flavipes mainly involve different odor bouquets.

Hybridization and Speciation

Hybridization and introgression is thought to be an important mechanism for speciation in many plants (EHRENDORFER 1980). In the *Ophrys fusca* group, speciation may be brought about by changing the patterns of alkenes, which lead to the attraction of a different pollinator and reproductive isolation (SCHIESTL & AYASSE 2002). Such plants would successfully reproduce, being reproductively isolated from other sympatrically occurring plants, and the new odor would be established by stabilizing selection. However, if a mutant would attract the pollinators of sympatrically occurring species, hybridization may take place.

Floral scent of *Ophrys* hybrids supports the finding that hybrids may produce intermediate scent (AYASSE 2006). *O. tenthredinifera* and *O. bombyliflora* are both pollinated by Eucera bees and different degrees of cross-attraction can be observed, which may lead to hybrid formation. In a comparison of the odor bouquets of hybrids identified by morphological traits and both parent species, several specimens of the hybrid swarm clustered together with one of the parent species. If the specimens that produce intermediate scent by chance attract a new pollinator, speciation may take place. Hybridization may favorably occur in *Ophrys* species that are visited by pollinators of the same genus of bees, like for example in the *Ophrys fusca* group, where most species are pollinated by Andrena males. Future investigations, combining molecular techniques, chemical analyses, behavioral experiments and electrophysiology will help to clarify the potential hybrid origin of Ophrys populations and may demonstrate processes of sympatric speciation.

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References

AYASSE M. 2006. Floral scent and pollinator attraction in sexually deceptive orchids. – In: DUDAREVA N. & PICHERSKY E. (eds.), Biology of Floral Scent. – CRC Press, Boca Raton.

— , SCHIESTL F., PAULUS H. F., IBARRA F. & FRANCKE W. 2003. Pollinator attraction in a sexually deceptive orchid by means of unconventional chemicals. – Proc. R. Soc. Lond. B, 270: 517–522.

EHRENDORFER F. 1980. Hybridisierung, Polyploidie und Evolution bei europäisch-mediterranen Orchideen. – Die Orchidee, Sonderheft, p.15–34.

NILSSON L. A. 1992. Orchid pollination biology. – Tree 7(8): 255–259.

SCHIESTL F. P. & AYASSE M. 2002. Do changes in floral odor cause sympatric speciation in sexually deceptive orchids? – Plant Syst. Evol. 234: 111–119.

— , AYASSE M., PAULUS H. F., LOFSTEDT C., HANSSON B. S., IBARRA F. & FRANCKE W. 1999. Orchid pollination by sexual swindle. – Nature 399(6735): 421–422.

— , AYASSE M., PAULUS H. F., LOFSTEDT C., HANSSON B. S., IBARRA F. & FRANCKE W. 2000. Sex pheromone mimicry in the early spider orchid *(Ophrys sphegodes)*: patterns of hydrocarbons as the key mechanism for pollination by sexual deception. – J. comp. Physiol. A 186(6): 567–574.

STÖKL J., PAULUS H. F., DAFNI A., SCHULZ C., FRANCKE W. & AYASSE M. 2005. Pollinator attracting odour signals in sexually deceptive orchids of the *Ophrys fusca* group. – Plant Syst. Evol. 254: 105–120.