# The sweet stench of decay

The scents of flowers have long inspired writers such as Shakespeare, who had Juliet consider: 'That which we call a rose by any other word would smell as sweet.' Beautiful flowers are also frequently the subjects of painters, and, combined, these artistic endeavours conjure up a natural world that is all vibrant colour and heady fragrance, as gorgeous blooms attract butterflies, moths and bees for pollination. So far, so pleasant: but such a view is somewhat restricted, because flowers that attract pollinators such as blowflies and dung beetles with the unlikely lures of putrefaction, decay and fermentation have also evolved in many plant families, including the Araceae, Aristolochiaceae, Orchidaceae and Apocynaceae. The scents of relatively few such species have been chemically characterized, but now a paper in this issue of *New Phytologist* by Andreas Jürgens, Stefan Dötterl and Ulrich Meve (pp. 452–468) has for the first time analysed the flower scents of stapeliads, the so-called 'carrion flowers' of the Apocynaceae (subfamily Asclepiadoideae, tribe Ceropegieae, subtribe Stapeliinae).

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Stapeliads are milkweeds of semiarid Africa and Asia with a special place in the lore of succulent plant enthusiasts: they can be challenging to cultivate in temperate climes, and their flowers frequently have putrid odours, filling a glasshouse with the scent of carrion or faeces. These sombre, often bizarrely coloured, blooms, have evolved to attract flies as pollinators, with colours, patterns, textures and, especially, odours that mimic the decaying animal and plant material on which they feed and lay their eggs, and which would nourish their larvae. By using a highly sensitive trapping method, microsolid phase extraction (micro-SPE; Gordin & Amirav, 2000), combined with gas chromatography-mass spectrometry (GC-MS) to analyse the scents of 15 stapeliad species from 11 genera, Jürgens *et al.* have identified the volatile compounds that lend such distinctively unpleasant notes to the flowers' faecal, urinous and cadaverous odours.

Their findings are provocative for several reasons. Striking variation in the number and identity of floral volatiles was observed among species, and was visualized as discrete clusters in 'odour space' using nonmetric multidimensional scaling (NMDS) analysis. These clusters were dominated by compounds that suggested distinct sources of putrification: hexanoic acid, carboxylic acids and pyrazines (urine), heptanal and octanal (rotting carcasses), and varying combinations of dimethyl oligosulphides (decaying meat, carnivore dung) and indole and cresol (herbivore dung). The word 'foetid' is frequently used by botanists to describe any one of these odours. However, this study, combined with research on flowers that mimic rotting fruit (Goodrich *et al.*, 2006), reveals that this term is insufficiently precise to enable accurate predictions of scent chemistry. The authors, drawing from an extensive literature on the chemistry of decay and fly attraction, propose that stapeliad species from each cluster have evolved flowers that mimic very specific (and distinct) models, albeit inanimate ones. These patterns emerged repeatedly within and among stapeliad genera, without obvious phylogenetic constraints. Thus, the telltale odours in each cluster, although biosynthetically distinct, are evolutionarily labile. It remains to be discovered what role floral odours have had in determining the specificity of pollination systems in stapeliads, and whether this has promoted the speciation (and adaptive radiation?) of the *c.* 350 species within this clade.

## Convergent evolution of pollination systems

Intriguingly, the major scent components found in these stapeliads are very similar to those used by inflorescences of some species of *Arum*, *Amorphophallus* and *Pseudodracontium* in the wholly unrelated family Araceae to attract flies and beetles (Kite & Hetterscheid, 1997; Kite *et al.*, 1998). An analysis of scent space for these genera, combined with the stapeliads of Jürgens *et al.* shows that, although the clades occupy discrete portions of the two-dimensional space (where species have distinct odour profiles), they also overlap where taxa utilize the same scent components (Fig. 1). The stapeliad study provides a wonderful example of convergent evolution at the fine phenotypic scale of scent biosynthesis, confirming the universality of olfactory mimicry of urine, carrion and faeces across angiosperm orders and geographical regions. The fixed information content of these odours (and their loci in the odour topology of Fig. 1) can be thought of as 'adaptive peaks' in floral phenotype space (Raguso, 2003), by analogy with the adaptive landscapes used by Wright (1932) and Niklas (1997) to visualize evolutionary random walks between alternative genotypes or phenotypes. Thus, flowers (or even fungi) that emit dimethyl disulphide may reliably attract blowflies as potential pollen or spore-dispersal agents in any suitable habitat on earth (Burger *et al.*, 1988; Borg-Karlson *et al.*, 1994; Stensmyr *et al.*, 2002; Bänziger & Pape, 2004). Equally intriguing are the ways by which the stapeliads studied by Jürgens *et al.* differ from aroids and other angiosperms (e.g. *Aristolochia*) that use utricles or 'trap
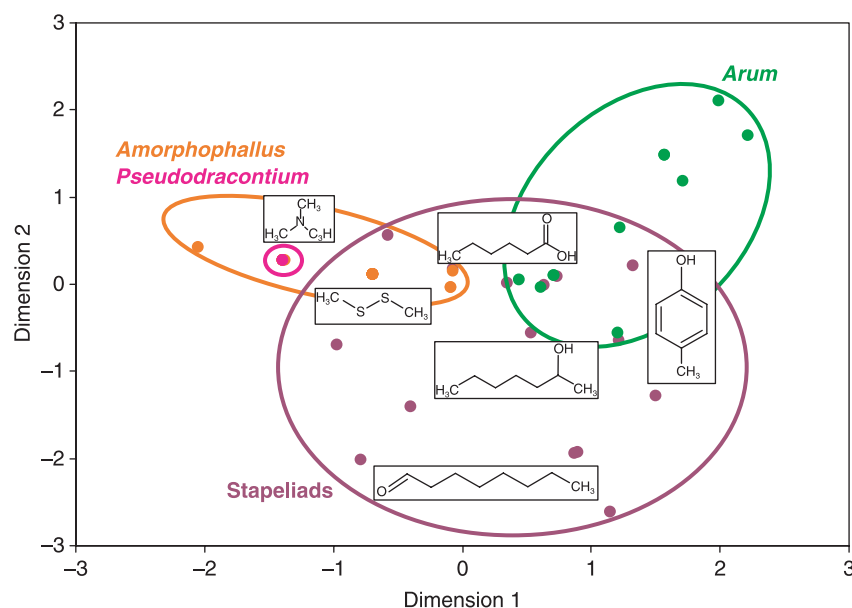
**Fig. 1** The scent space of sapromyiophilous stapeliads and aroids. Nonmetric multidimensional scaling (NMDS) analysis of the major scent compounds present in the odour profiles of 15 species of stapeliads (Apocynaceae subfamily Asclepiadoideae, tribe Ceropegieae, subtribe Stapeliinae; data from Jürgens *et al.*, 2006), plus 11 species of *Arum*, 20 species of *Amorphophallus* and two species of *Pseudodracontium* (Araceae; data from Kite *et al.*, 1998). NMDS was performed using a binary (presence-absence) matrix of the 48 plant species and the 54 most abundant (≥ 10% volume) compounds from their scent profiles, resulting in a two-dimensional plot using Euclidean distances between species. Unidentified compounds were omitted from the analysis. Several *Amorphophallus* species have identical oligosulphide odours and thus occupy the same loci in scent space. Chemical structures indicate scent components that contributed most to the separation of clusters in scent space (Jürgens *et al.*, 2006), and are (clockwise from top): hexanoic acid, p-cresol, octanal, dimethyl disulphide and 2-heptanol (centre). Trimethyl amine (upper left) confers a dead-fish odour to *Amorphophallus brachyphyllus* (Kite & Hetterscheid, 1997), and is predicted to be present in stapeliads such as *Huernia thuretii* (not yet studied), which would expand the stapeliad domain in scent space.

flowers' to imprison their pollinators overnight, and respiratory bursts (thermogenesis, $CO_2$ emission) to enhance the sensory mimicry of rotting flesh (Seymour *et al.*, 2003; Angioy *et al.*, 2004). This is one of the few areas of pollination biology in which odours have been more commonly manipulated in experiments than floral form or colour. The authors identify the need for further research on the reproductive ecology of stapeliads, particularly on the interaction between complex visual and tactile stimuli with the odours described herein, and the function(s) of nectar in these interactions.

Convergences in the evolution of floral traits have previously been considered to reflect 'pollination syndromes', a framework for classifying flowers, and, by default, for understanding the evolution of plant–pollinator interactions, which has its origins in the 19th-century work of Federico Delpino (Knuth, 1906) and which subsequent researchers have modified and fine-tuned. A century later, the predictive utility of pollination syndromes remains controversial (Herrera, 1996; Waser *et al.*, 1996; Ollerton & Watts, 2000; Fenster *et al.*, 2004). The stapeliads studied by Jürgens *et al.* are traditionally thought to belong to the syndrome of 'sapromyiophily' – 'pollination by insects associated with decaying organic matter' (Proctor *et al.*, 1996). However as Jürgens *et al.* discuss, even a relatively limited survey of these

stapeliads has shown that the broad concept of sapromyiophily subsumes flowers which may be mimicking different kinds of mammalian faeces, rotting flesh and urine. Further analyses will no doubt provide other specific mimicry systems (e.g. rotting fish; Kite & Hetterscheid, 1997), but intensive ecological field studies of the pollinators of sapromyiophilous species are required in order to assess the link between odour profiles and particular pollen vectors.

## Specialization, generalization and outstanding ecological questions

An unresolved aspect of decay mimicry pollination systems such as these stapeliads possess is the extent to which the plants are ecologically specialized (pollinated by only one or a few species) as well as phenotypically and functionally specialized (i.e. they have specific adaptations to pollination by a discrete functional group of pollinators) (Fenster *et al.*, 2004; Ollerton *et al.*, 2006). Judging from records in the online ASCLEPOL database (http://www.uni-bayreuth.de/departments/planta2/research_wgl/pollina/as_pol_t.html), in some cases stapeliads may be quite ecologically generalized, but more extensive data of this nature are needed. Another possibility is suggested by nearly continuous variation

among a subset of stapeliads in the relative ratios of oligosulphides to cresol, indicators of carrion/carnivore dung vs herbivore dung, respectively. Some stapeliads may utilize omnivore dung (with mixed dietary metabolites) as a sensory model, or may adopt a generalized mimicry strategy as a bet-hedge against instability in pollinator abundance (Waser *et al.*, 1996; Johnson *et al.*, 2003). Field studies of pollinator diversity, abundance and effectiveness over several sites and seasons are needed to test such predictions.

The reproductive success of stapeliads as mimics depends on the presence of suitable saprophilic insects, which in turn is provisional on the availability of carrion, faeces and other nourishment. However, we know nothing of the role of these decaying substrates, and how their abundance affects pollinator population dynamics. The population dynamics of the plants may also be important. If the mimicking flowers are too common relative to the models, they may negatively affect the abundance of insects, which not only waste time and energy visiting the flowers, but can also directly lose fitness by laying eggs within them. Stapeliad populations are often in low density, with individuals scattered over a wide area – is this because of negative frequency-dependent selection? Similar arguments have been made for rewardless flowers which mimic rewarding flowers, and more generally for any Batesian mimic-model system (Anderson & Johnson, 2006). However, there are reasons to suppose that mimicry of egg-laying sites, such as carrion and excrement, may depart from traditional negative frequency dependence. First, the mimics do not negatively affect the models (e.g. as they may do in sexually deceptive pollination systems; see Wong & Schiestl, 2002), because the models are dead or inanimate! Second, depending on phenology, more models may breed more pollinators, or at least increase their local abundance, such that mimics could thrive in model hotspots, *sensu* the magnet species effect documented by Johnson *et al.* (2003) for orchids with generalized food deception. This is also suggested by the abundance of stinkhorn fungi (*Phallus impudicus*) near badger setts with their associated badger corpses (Sleeman *et al.*, 1997). Finally, such flowers are frequently short-lived, persisting only for 1 or 2 d (Burgess *et al.*, 2004), and their models (e.g. the seagull carcasses among Mediterranean populations of *Helicodiceros* (Araceae)) may only be attractive to saprophilic insects for a short period (Angioy *et al.*, 2004). They would therefore not compete with a corpse or dung heap model for fly attraction for more than a short period, or the models may not ever saturate fly visits.

Stapeliads and other asclepiads provide extremely good systems for studying plant–pollinator interactions because, like orchids, they disperse their pollen as discrete masses (pollinia) which firmly attach to flower visitors, making the identification of pollinators more straightforward than for other angiosperms (Wyatt & Broyles, 1994; Fishbein & Venable, 1996; Ollerton & Liede, 1997). Using such plants, an achievable goal is to relate the detailed laboratory studies such as that by Jürgens *et al.* to field studies of plant–pollinator interactions, and experimental manipulations of floral traits (including floral scent) and the phenotype space occupied by the flowers. This would provide us with a deeper understanding of ecological pattern, evolutionary convergence and phylogenetic constraint in this most fascinating group of plants.

Despite the romantic connotations of floral colours and aromas in art and literature, flowers often mediate sexual reproduction in plants through surprisingly exploitative, deceptive and unpleasant means. The writer H. L. Mencken is quoted as saying: 'A cynic is a man who, when he smells flowers, looks around for a coffin.' Mencken probably didn't realize it, but that's a statement which is close to the truth of stapeliad scent biology.

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# *Letters*

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# Ferns represent an untapped biodiversity for improving crops for environmental stress tolerance

Ferns, which comprise *c.* 10 000 species and 250 genera, are the most conspicuous spore-bearing land plants. They have evolved remarkable adaptations to extreme environments, from tropical to cold temperate regions, from lowland to alpine zones and from xeric to aquatic conditions. Because the majority of living ferns result from a more recent diversification that is independent of angiosperm evolution, ferns represent a crucial, hitherto-unexplored genetic diversity that may be exploited for improving plants via gene-transfer technologies. The development of genome resources for select fern species, and the identification of functions for networks of genes, are crucial to achieve this.

## Ferns represent an important early node in land plant evolution

Ferns are the second-largest group of vascular plants, comprising *c.* 10 000 living species. Molecular phylogenetic studies have revealed three monophyletic groups of early