Mechanisms and evolution of deceptive pollination in orchids

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ABSTRACT

The orchid family is renowned for its enormous diversity of pollination mechanisms and unusually high occurrence of non-rewarding flowers compared to other plant families. The mechanisms of deception in orchids include generalized food deception, food-deceptive floral mimicry, brood-site imitation, shelter imitation, pseudoantagonism, rendezvous attraction and sexual deception. Generalized food deception is the most common mechanism (reported in 38 genera) followed by sexual deception (18 genera). Floral deception in orchids has been intensively studied since Darwin, but the evolution of non-rewarding flowers still presents a major puzzle for evolutionary biology. The two principal hypotheses as to how deception could increase fitness in plants are (i) reallocation of resources associated with reward production to flowering and seed production, and (ii) higher levels of cross-pollination due to pollinators visiting fewer flowers on non-rewarding plants, resulting in more outcrossed progeny and more efficient pollen export. Biologists have also tried to explain why deception is overrepresented in the orchid family. These explanations include: (i) efficient removal and deposition of pollinaria from orchid flowers in a single pollinator visit, thus obviating the need for rewards to entice multiple visits from pollinators; (ii) efficient transport of orchid pollen, thus requiring less reward-induced pollinator constancy; (iii) low-density populations in many orchids, thus limiting the learning of associations of floral phenotypes and rewards by pollinators; (iv) packaging of pollen in pollinaria with limited carry-over from flower to flower, thus increasing the risks of geitonogamous self-pollination when pollinators visit many flowers on rewarding plants. All of these general and orchid-specific hypotheses are difficult to reconcile with the well-established pattern for rewardlessness to result in low pollinator visitation rates and consequently low levels of fruit production. Arguments that deception evolves because rewards are costly are particularly problematic in that small amounts of nectar are unlikely to have a significant effect on the energy budget of orchids, and because reproduction in orchids is often severely pollen-, rather than resource-limited. Several recent experimental studies have shown that deception promotes cross-pollination, but it remains unknown whether actual outcrossing rates are generally higher in deceptive orchids. Our review of the literature shows that there is currently no evidence that deceptive orchids carry higher levels of genetic load (an indirect measure of outcrossing rate) than their rewarding counterparts. Cross-pollination does, however, result in dramatic increases in seed quality in almost all orchids and has the potential to increase pollen export (by reducing pollen discounting). We suggest that floral deception is particularly beneficial, because of its promotion of outcrossing, when pollinators are abundant, but that when pollinators are consistently rare, selection may favour a nectar reward or a shift to autopollination. Given that nectar-rewardlessness is likely to have been the ancestral condition in orchids and yet is evolutionarily labile, more attention will need to be given to explanations as to why deception constitutes an 'evolutionarily stable strategy'.

Key words: cross-pollination, floral deception, geitonogamy, inbreeding, nectar, Orchidaceae, pollinaria, reward, self-pollination.

CONTENTS

I. INTRODUCTION

Orchidaceae with approximately 19 500 species (Dressler, 1993) is considered one of the largest families in the plant kingdom (it is rivalled only by the Asteraceae, which contains approximately 23 000 species: Bremer, 1994). However, the radiation of the orchid family has probably taken place in a comparatively short period (the earliest orchid fossils appear in the Eocene) in comparison to most flowering plant families, which had already started to diversify in the Mid-Cretaceous (Beck, 1976; Crane, Friis & Pederson, 1995; van der Cingel, 1995). Orchids show a wide diversity of epiphytic and terrestrial growth forms and have successfully colonized almost every habitat on earth. However, it is their staggering variation in floral form that has long attracted the interest of evolutionary biologists. Although earlier botanists had described the structure of orchid flowers and observed visits by insects, the nature and variations of pollination mechanisms in orchids were first fully appreciated by Charles Darwin. His book *On the various contrivances by which British and foreign orchids are fertilised by insects*, first published in 1862, is the record of a great deal of painstaking and perceptive observation. Darwin considered the adaptations of orchid flowers to their animal pollinators as being among the best examples of his idea of evolution through natural selection.

Pollination systems in orchids are often mistakenly assumed to be the outcome of co-evolutionary processes (van der Pijl & Dodson, 1966; Dressler, 1968; Dodson, 1975). Co-evolution between orchids and their pollinators is probably uncommon (Szentesi, 2002) and most of the

evolution is unilateral on the orchid side without any evolutionary changes in the pollinator (Williams, 1982). Unilateral evolution can be attributed to orchids having appeared when most key pollinator groups had already evolved and established complex mutualisms with flowering plants (Labandeira *et al.*, 1994; Dilcher, 2000), orchids typically constituting a minor element in plant guilds on which pollinators depend for nectar (Jermy, 1999), and orchids often being deceptive (see below) and therefore unlikely to influence the evolution of pollinator traits (*cf.* Johnson & Steiner, 1997).

Orchids frequently exploit existing plant-pollinator relationships or even sexual systems of insects. This is exemplified by species that achieve pollination through deception (i.e. an absence of floral rewards for pollinators). The discovery by Sprengel (1793) that many orchid flowers do not contain nectar, and thus deceive their insect pollinators, was greeted with incredulity and disbelief. Darwin (1877, p. 37) rejected the idea of floral deception on the grounds that insects, particularly bees would be too intelligent to fall for 'so gigantic an imposture'. He also believed that the apparently empty spurs of many orchid flowers might contain nectar which would be released when 'insects penetrate the lax inner membrane of the nectaries' with their proboscides to 'suck the copious fluid between the two membranes' (Darwin, 1877, p. 40). There is now overwhelming evidence that Darwin was mistaken and that non-rewarding flowers are actually rather widespread among Orchidaceae – between 6500 and 9000 species (approximately one-third of the total) are believed to deceive insect pollinators (van der Pijl & Dodson, 1966; Dressler, 1981; Ackerman, 1986; Renner, 2005). In this review we

Table 1. *Classification of deception mechanisms in the Orchidaceae and their occurrence. The number of genera was estimated according to van der Cingel (1995, 2001)*

Mechanism	Exploited insect behaviour	No. of genera
Generalized food deception	Food foraging	38
Batesian floral mimicry	Food foraging	9
Brood-site imitation	Oviposition	11
Shelter imitation	Sleep/warmth	1
Pseudoantagonism	Territoriality	2
Rendezvous attraction	Sexual	4
Sexual deception	Sexual	18

refer to orchid pollinators as insects for sake of convenience. Birds are known to pollinate several orchid species, but have not thus far been implicated in any system of floral deception.

Non-rewarding flowers have evolved in at least 32 angiosperm families (Renner, 2005). However, of the 7500 angiosperm species pollinated through deception, approximately 6500 are orchids (Renner, 2005). Clearly there is something about orchids that predisposes them to the evolution of deceptive pollination systems. However, a clear explanation of why the occurrence of deceptive pollination systems is concentrated in the Orchidaceae has proved elusive. In the past ten years renewed efforts have been made to formulate and test hypotheses about the evolution and maintenance of deceptive pollination systems in orchids.

The aim of this review is to summarise the mechanisms of floral deception in orchids, evaluate their occurrence within the family, discuss potential fitness benefits of non-rewarding flowers in the light of former and recent studies, and consider the evolutionary stability of deceptive strategies.

II. DECEPTION MECHANISMS IN ORCHIDS

The mechanisms by which non-rewarding orchids attract pollinators vary from generalized food deception, through specific mimicry of other flowers and deceptive sapromyophily, to sexual deceit (leading in many cases to pseudocopulation). The terminology and earlier literature on mimicry and deception in plant pollination, including orchids are summarised in van der Pijl (1966), Little (1983), Dafni (1984, 1986), Ackerman (1986), Dafni & Bernhardt (1990), and van der Cingel (1995). However, during the recent decade numerous new studies on orchid pollination systems have been published and have given new insights into the function of deceptive mechanisms. The most common types of deceptive pollination in orchids involve food and sexual deception (Table 1).

(1) Generalized food deception

Most orchids with deceptive pollination mechanisms exploit the innate food-foraging behaviour of pollinators (Nilsson, 1980; Dafni, 1983). In order to attract pollinators, orchids advertise general floral signals, which are typical for rewarding plant species, such as inflorescence shape, flower colour, scent, nectar guides, spurs and pollen-like papillae (Gumbert & Kunze, 2001; Galizia *et al.*, 2005). Consequently, Little (1983) termed this type as 'mimicry based on naïveté'. Dafni (1986) suggested replacing it with the term 'non-model mimicry', as he believed other examples of mimicry (i.e. Batesian mimicry and imitation of male flowers by female ones in plants with unisexual flowers) are based also on visits from inexperienced pollinators. However, since orchids adopting this strategy do not imitate any specific rewarding plants and Batesian mimicry usually involves experienced (conditioned) pollinators (Johnson, 2000), the term 'mimicry' seems to be inappropriate. The pollinators may be recently emerged insects, immigrants, or exploratory pollinators whose food resources are becoming depleted. The term 'generalized food deception' (Steiner, 1998) has become widely used to describe this form of deception in orchids.

Relatively few orchid genera attract pollinators by offering pseudopollen or false anthers, most notably *Polystachya* (Davies, Roberts & Turner, 2002), *Maxillaria* (van der Pijl & Dodson, 1966; Davies, Winters & Turner, 2000), certain species of *Eria* (Beck, 1914; Davies & Turner, 2004c) and *Dendrobium* (Kjellsson & Rasmussen, 1987; Davies & Turner, 2004b). The bright yellow tufts of hairs on the lips attract pollen-foraging bees in *Arethusa bulbosa*, *Pogonia ophioglossoides*, *Calopogon tuberosus* and *Cephalanthera longifolia* (Thien & Marcks, 1972; Dressler, 1981; Dafni & Ivri, 1981b). Dummy anthers occur in *Caladenia* (Bates, 1985), *Glossodia*, *Elythranthera*, and *Eriochilus* species (Dafni & Bernhardt, 1990). In *Polystachya*, *Maxillaria* and *Eria* species, the labellar papillae and trichomes are rich in protein and starch, and are actively collected by the pollinators (Dodson & Frymire, 1961; Dodson, 1962; Goss, 1977; Beardsell & Bernhardt, 1982; Dressler, 1993; Davies, Turner & Gregg, 2003). However, we have no direct evidence that pseudopollen is used for nutrition by pollinators. Most papillae contain pigments or act as osmophores and probably represent visual or tactile cues that guide pollinators into flowers (Davies & Turner, 2004a).

Orchids associated with generalized food deception very often flower gregariously in early spring, exhibit floral colour polymorphism and exploit newly emerged bees and bumblebees after hibernation (Heinrich, 1975). Sometimes rewardless species benefit from growing in the vicinity of nectariferous co-flowering species, as these increase abundance of pollinators in the orchids' local habitat (viz a viz the magnet species effect: Laverty, 1992; Lammi & Kuitunen, 1995; Johnson *et al.*, 2003b).

Deception based on instinctive foraging behaviour occurs in numerous, unrelated orchid genera, e.g. in *Orchis* (Dafni, 1983, 1987; Nilsson, 1983a; Johnson & Nilsson, 1999), *Dactylorhiza* (Nilsson, 1980; Lammi & Kuitunen, 1995), *Disa* (Johnson, 1993; Johnson & Steiner, 1995, 1997; Johnson, Linder & Steiner, 1998), *Calypso* (Ackerman, 1981; Boyden, 1982; Alexandersson & Agren, 1996), *Cypripedium* (Stoutamire, 1971; Nilsson, 1979), *Anacamptis* (Nilsson, 1984; Johnson *et al.*, 2003b; Johnson, Peter & Agren, 2004),

Brassavola (Schemske, 1980), *Calopogon* (Firmage & Cole, 1988), *Pogonia* (Ushimaru & Nakata, 2001), and *Dipodium* (Bernhardt & Burns-Balogh, 1983).

(2) Batesian floral mimicry

Deceptive orchids that achieve pollination through the resemblance of their flowers to those of particular rewarding species have been termed Batesian mimics (Brown & Kodric-Brown, 1979; Bierzychudek, 1981; Dafni, 1984; Johnson, 1994; Roy & Widmer, 1999). Some authors, such as Little (1983), have rejected this term on the grounds that Batesian mimicry in animals involves repulsion of predators (Bates, 1862), rather than attraction, as is the case with flowers and their pollinators. Nevertheless, the evolution of Batesian mimicry in plants and animals is essentially similar, involving rare species that benefit from an adaptive resemblance to more common species (*cf.* Starrett, 1993). There is increasing evidence that flowers of some Batesian mimics bear such a close resemblance to their models that pollinators are literally unable to distinguish between the two kinds of inflorescences (Dafni & Ivri, 1981*a*; Johnson, 1994, 2000; Johnson, Alexandersson & Linder, 2003*a*). Matching of the model's flower colour by the mimic appears to be critical for successful attraction of pollinators. Food-deceptive floral mimicry is associated with pollinators that use mainly colour, rather than scent, as their primary foraging cue (Johnson, 1994, 2000; Johnson *et al.*, 2003*a*; Anderson, Johnson & Carbutt, 2005). Nevertheless, even bees can be deceived by mimics that match the flower colour of models, yet differ substantially in floral scent (Gumbert & Kunze, 2001; Galizia *et al.*, 2005).

Batesian mimics often form part of pollination guilds involving several rewarding plant species that show convergent evolution to common pollinator(s) (Brown & Kodric-Brown, 1979; Dafni & Bernhardt, 1990; Johnson *et al.*, 2003*a*). Dafni & Bernhardt (1990) used the term 'guild mimicry' to describe a situation where at least two of the rewarding species resemble each other. Although they attributed such resemblance to 'Müllerian floral mimicry' (Müller, 1878; Proctor & Yeo, 1973), in reality Müllerian mimicry is almost impossible to distinguish from convergent evolution. However, in such guilds it is not uncommon for a non-rewarding species to mimic other rewarding species. This pattern has been termed 'advergent' evolution as it is the mimic, rather than the models, that undergoes the evolutionary modification that results in resemblance (Brower & Brower, 1972; Johnson *et al.*, 2003*a*). Guild mimicry has been reported for the southern Australian genera *Diuris* (Beardsell *et al.*, 1986) and *Thelymitra* (Dafni & Calder, 1987), which resemble legumes and buzz-pollinated lilioids or dicots, respectively. In the South African genus *Disa*, several species form part of guilds pollinated by butterflies (Johnson, 1994) or long-proboscid flies (Johnson, 2000; Johnson *et al.*, 2003*a*; Anderson *et al.*, 2005). The convergence among guild members includes similarities in flowering time, spur or flower tube length, and flower colour (Johnson & Steiner, 1997; Johnson *et al.*, 2003*a*).

(3) Brood-site imitation

This category describes plants that employ deceitful attraction of insects that are seeking an appropriate place to lay their eggs. The flowers tend to mimic standard oviposition sites such as carrion (sapromyophily), dung (copromyophily, coprocantharophily), or the fruiting body of fungi (mycetophily). The victims are mostly Diptera and Coleoptera. Apart from Orchidaceae, this strategy is found in Aristolochiaceae, Asclepiadaceae, and Araceae. Among orchids, this deception mechanism is mainly confined to tropical and subtropical areas and is completely missing from Europe (but see *Epipactis consimilis* below).

Various orchids in both the Old and New World floras are pollinated by flies, attracted by the brownish or dull reddish floral colours and foul odours. Such species often posses' trap flowers with a one-way passage pouch or trap insects by movement of the lip, e.g. genera *Pterostylis*, *Paphiopedilum*, *Bulbophyllum*, *Cirrhopetalum*, *Megaclinium* (closely related to *Bulbophyllum*), *Anguloa*, *Masdevallia* and *Pleurothalis* (van der Pijl, 1966; Proctor, Yeo & Lack, 1996; Borba & Semir, 2001).

Some orchids show features of the fungus-gnat syndrome. The Australian genus *Corybas* has geoflorous, dark-coloured flowers, which are pollinated by ovipositing fungus gnats (Jones, 1970). The orchid seems to mimic the fruiting bodies of basidiomycetes. Similarly the South American genus *Dracula* has a fungus-like or fishy scent and fungus-like shaped lip (Vogel, 1978). A Japanese *Cypripedium* species bears modified flowers that droop near the ground, in which the entrance to the pouched lip has the appearance of a small mushroom (Proctor *et al.*, 1996).

The Afro-Asiatic species *Epipactis veratrifolia* (syn. *E. consimilis*) combines oviposition-site mimicry with a nectar reward. The species misleads female syrphids in laying eggs on the labellum, which bears a combination of orange and black structures probably perceived as aphids (Ivri & Dafni, 1977). Egg-laying is triggered by a combination of visual, tactile and olfactory stimuli. The hoverfly males defend a territory around these orchids and contribute to pollination in a more traditional way as nectar feeders. A similar mechanism was reported for the genus *Paphiopedilum* (section *Coryopedilum*), where syrphid flies are deceived into laying their eggs in the flowers, especially on the staminode (Atwood, 1985).

(4) Shelter imitation

Some flowers offer insects a floral tube in which to rest or sleep, as a hiding place during windy and rainy weather (Gumprecht, 1977), or for thermoregulation, because the temperature in the flower tube may exceed the ambient temperature by up to 3 °C during the morning hours (Dafni, Ivri & Brantjes, 1981; Felicioli *et al.*, 1998). In orchids, this mechanism appears to be confined to the Mediterranean genus *Serapias*, whose extremely dark red-coloured flowers appear to mimic bee nest entrances (Dafni *et al.*, 1981). Given that bees probably obtain real shelter in the flowers of *Serapias* (Dafni *et al.*, 1981), the characterisation of this system as 'deceptive' is open to debate.

(5) Pseudoantagonism

Orchids with this mechanism exploit the territorial behaviour of some Hymenoptera, which attack the flowers when they are vibrating in the wind and pollinate them in the process. The defensive behaviour of territorial *Centris* spp. bees may be exploited by some *Oncidium* and *Tolumnia* species (Dodson & Frymire, 1961; Neirenberg, 1972). This mechanism has not been thoroughly studied and seems to be extremely rare. Ackerman (1986) suggested that this interaction may be mutualistic as bees become better territorial defenders with practice. However, no evidence yet supports this hypothesis.

(6) Rendezvous attraction

Some orchids exploit the sexual drive of male bees during mate-seeking flights. Male bees, when inspecting surrounding flowers for females foraging on pollen or nectar, are deceived by orchids with similar colour, shape and scent as co-blooming rewarding plants. This mechanism has been reported in the European orchid species, *Cephalanthera rubra* (Nilsson, 1983b) and *Orchis papilionacea* (Vogel, 1972), as well as in the African *Disa obtusa* and *Ceratandra grandiflora* species (Johnson & Steiner, 1994; Steiner, 1998).

(7) Sexual response

The evolution of sexual deceit was seen as one of the major enigmas of orchid evolution in the past. In this case, the flowers mimic female insect mating signals, especially their pheromones, and are pollinated by the lured male insects, which often try to copulate with the flower. The sexual response ranges from a less advanced stage, in which the orchids deceive pollinators mainly by olfactory cues (Bino, dafni & Meeuse, 1982; Stoutamire, 1983), towards highly adapted flowers which elicit 'pseudocopulation' by male insects (Correvon & Pouyanne, 1916; Pouyanne, 1917; Coleman, 1927; Ames, 1937; Kullenberg, 1961; Priesner, 1973; Kullenberg & Bergström, 1973, 1976b; Vogel, 1976; Kullenberg, Borg-Karlson & Kullenberg, 1984; Vöth, 1984; Paulus & Gack, 1990; Peakall & Beattie, 1996; Ayasse *et al.*, 2000, 2003; Schiestl & Ayasse, 2002; Schiestl *et al.*, 1999, 2000, 2003). Roy and Widmer (1999) and Schiestl (2005) extend the concept of Batesian mimicry in plants to cover not only food-deceptive floral mimicry (see above), but also floral mimicry of insects (sexual deception), on the basis that deceptive mimics in both systems should experience negative frequency-dependent pollination success.

Dressler (1981) suggested that rendezvous attraction might have been the first step in evolution towards pseudocopulation. This would be followed by a stage in which flowers emit signals releasing at least certain phases of the male sexual behaviour (Bergström, 1978). This step is represented in the East Mediterranean species *Orchis galilaea*, which is pollinated exclusively by males of *Lasiglossum marginatum* (syn. *Halictus marginatus*), while females visit the flowers of other plant families (Bino *et al.*, 1982). The behaviour of the males landing on dark spots on the labellum suggests that the strong, musk-like scent of the flowers is similar to that of the pheromone of the females. This intermediate state also appears in the South Australian species *Caladenia patersonii* pollinated by tiphiid males (Stoutamire, 1983). However, sexual deceit in this species appears to be mixed with generalized food deception, as the flowers are pollinated also by other insects of both sexes, including bees and syrphid flies searching for food (Stoutamire, 1983).

Orchid flowers that elicit 'pseudocopulation' by male insects possess not only sex-pheromone-like odours, but also visual and tactile cues (Bergström, 1978). The odour plays a key role in the long-range attraction of males to the flower (Kullenberg, 1961; Peakall, 1990; Schiestl *et al.*, 1999). During pseudocopulation the pollinia become attached to the male's head or abdomen and are transferred to a flower of another plant during the next copulation attempt (Borg-Karlson, 1990). The pheromone-like odour of orchids is often even more attractive for male insects than that of their own females, but males can learn to avoid areas containing orchids or females can increase their attractiveness by walking away from the orchid colony (Wong & Schiestl, 2002; Wong, Salzmann & Schiestl, 2004). Sexual deception imposes strong specialisation in orchids as insect pheromones are generally highly species specific (Paulus & Gack, 1990). The specialisation ranges from species that lure few pollinator taxa (Paulus & Gack, 1990; Schiestl *et al.*, 1999, 2000) to species pollinated exclusively by one pollinator (Schiestl *et al.*, 2003; Schiestl, Peakall & Mant, 2004).

True sexual deception is found only in the orchid family, although exploitation of mate-seeking behaviour through petal ornamentation that resembles insects has been reported in plants belonging to other families (Johnson & Midgley, 1997; Johnson & Dafni, 1998). Unrelated orchid genera that exploit mating behaviour of pollinators by mimicking attraction cues of female insects evolved independently in Europe, Australia, Africa and South America. Pseudocopulation is found in Europe only in the genus *Ophrys* (Kullenberg, 1961; Paulus & Gack, 1990; Schiestl *et al.*, 1999), while in southern Australia at least ten orchid genera (Coleman, 1928; Stoutamire, 1975, 1983; Peakall, Beattie & James, 1987; Peakall, 1990; Dafni & Bernhardt, 1990; Bower, 1996; Schiestl *et al.*, 2004), in South America five genera (van der Pijl & Dodson, 1966; Dod, 1976; Singer, 2002; Singer *et al.*, 2004), and the Central American genus *Lepanthes* (Blanco & Barboza, 2001, 2005) are involved in sexual deception. Sexual deception has also been reported in two African *Disa* species (Steiner, Whitehead & Johnson, 1994).

III. FLORAL DECEPTION – A PRIMITIVE OR DERIVED FEATURE?

Nectar rewards have traditionally been thought to be an ancestral condition within the orchids with the nectarless condition having evolved more recently (van der Pijl, 1966; Dressler, 1981; Dafni, 1987; Dafni & Bernhardt, 1990; Aceto *et al.*, 1999). Burns-Balogh, Szlachetko & Dafni

(1987), for example, suggest that within the subfamily Neottioideae, the more primitive groups (Limodorinae, Neottinae) offer nectar as a reward for pollination whereas the more advanced group (Cephalantherinae) exhibits mimicry and deceit.

The first fossil plant, *Eorchis miocaenica* that shows a typical orchidaceous flower and fruit is dated back to the Eocene (Mehl, 1984). The family Orchidaceae was formerly included in the Liliales (Darwin, 1877; Dahlgren, Clifford & Yeo, 1985), due to possession of certain morphological characters, including the presence of perigonal nectaries, a character otherwise rare in monocots (Rudall *et al.*, 2000; Smets *et al.*, 2000). However, recent molecular analyses suggest that Orchidaceae represents the earliest-diverging asparagoid lineage (Fay *et al.*, 2000) with close relationships to the nectarless family Hypoxidaceae (Rudall, 2002). The two families have epigynous flowers that lack septal nectaries. Assuming that orchids do indeed belong to the Asparagales, the absence of septal nectaries may be associated with the secondary development of perigonal nectaries (Rudall *et al.*, 2000; Smets *et al.*, 2000).

Dressler (1993) speculated that the 'primitive' orchid or orchid ancestor would have had inferior trilocular ovaries (a three-chambered ovary surrounded by and joined to the basal parts of the flower), six free stamens with eventual stamen/staminodial fusion to the style, basifixed anthers with introrse dehiscense (anther attached at its base to apex of filament, dehiscing longitudinally inward), and fleshy fruits with small seeds. Rudall & Bateman (2002) added mycorrhizal associations, which allowed the development of the characteristic 'dust seeds', and emphasised the importance of epigyny and syncarpy, which are pre-requisites for gynostemium formation. According to both molecular (Cameron *et al.*, 1999; Kocyan *et al.*, 2004) and morphological analyses (Freudenstein & Rasmussen, 1999), the apostasioid orchids (genera *Apostasia* and *Neuwiedia*) appear to be the basal clade in Orchidaceae. Both genera are nectarless, using pollen as a reward (Garay, 1960). *Neuwiedia* has resupinate flowers (i.e. the flower is twisted 180° around its flower stalk to position the lip on the bottom), a poorly developed labellum, and is pollinated by *Trigona* bees. *Apostasia* has non-resupinate *Solanum*-type flowers with fused anthers and an actinomorphic perianth lacking a recognisable labellum (Kocyan & Endress, 2001). The flower morphology of this sister group to all other Orchidaceae represents the buzz-pollination syndrome (i.e. flowers need high-frequency vibrations to release their pollen from the anthers), which is often associated with lack of nectar reward to pollinators (Rudall, 2002). The most parsimonious conclusion from cladistic analyses is thus that the first orchid ancestors were nectarless pollen-rewarding plants (Bateman *et al.*, 2003). Nevertheless, the independent loss of nectar in both of the basal apostasioid and cypripedioid lineages cannot be fully excluded as a possibility. Moreover, some recent analyses using nuclear and plastid genes do not support the basal position of Cypripedioideae and, instead, indicate that an ancestor to the Vanilloideae, which contains both nectarless and nectariferous species, diverged to give rise to the Cypripedioideae and remainder of the Orchidaceae (Rudall &

Bateman, 2002; Kocyan *et al.*, 2004). In this case, nectar production would be likely to have been lost and regained independently in different clades (Aceto *et al.*, 1999; Cozzolino *et al.*, 2001; Bateman *et al.*, 2003).

In the case of sexual deceit, Ames (1937) and Meeuse (1973) suggested that pollinators were originally rewarded by food. Kullenberg & Bergström (1976a) postulated that chemical attractants of insects are ancient in evolutionary terms and that the scent was already present before the loss of reward occurred and before the labellum acquired a female-like structure (Kullenberg, 1961, see also Schiestl *et al.*, 1999). Such a transitional step is recorded in *Diuris pedunculata*, an Australian species that contains nectar and attracts only males of *Halictus lanuginosus* (Coleman, 1932). Bergström (1978) speculated that the early forms of sexually deceptive orchids were pollinated by both male and female bees. Further evolution towards exclusive pollination by males could easily promote loss of reward due to the male's weak feeding instinct (Faegri & van der Pijl, 1979). None of the sexually deceptive species that elicit 'pseudocopulation' in their pollinators is known to offer an edible reward (Dafni & Bernhardt, 1990). However, the existence of species that exploit both food and sexual drives suggests that sexual deception could also evolve from food deception (Vogel, 1972; Bino *et al.*, 1982; Stoutamire, 1983; Dafni & Bernhardt, 1990; Nilsson, 1992; Kores *et al.*, 2001).

IV. FITNESS BENEFITS OF FLORAL DECEPTION: GENERAL HYPOTHESES

The widespread occurrence of floral deception within Orchidaceae, despite its apparent evolutionary lability, suggests that it confers fitness advantages under some circumstances. There are two general hypotheses as to how deception could increase fitness in plants. The first is that deception allows reallocation of resources from rewards to fruit production and future flowering. The second is that deception results in pollinators visiting fewer flowers on a plant, thereby promoting outcrossing.

(1) The resource-limitation hypothesis

The resource-limitation hypothesis assumes that sexual reproduction (flower production and fruit set) is limited primarily by resources (Lloyd, 1980; Stephenson, 1981; Calvo & Horvitz, 1990; Calvo, 1993; Mattila & Kuitunen, 2000). Resources available for seed development may be restrictive both within and between seasons (Meléndez-Ackerman, Ackerman & Rodriguez-Robles, 2000). Elevated fruit set within one season may be at the expense of future growth, probability of flowering, reproduction or survival (Lovett-Doust & Lovett-Doust, 1988; Snow & Whigham, 1989; Ackerman & Montalvo, 1990; Bartareau, 1995). This is not a strict rule, however, as certain species, like *Cypripedium acaule*, show long-term symptoms of resource limitation only after exceptionally heavy fruiting episodes (Primack & Stacy, 1998). Some orchid species,

Table 2. *Efficiency of pollen transport in rewarding and rewardless orchids*

Species	Pollen vector	Pollinium type	Self-pollination (% of pollen transfer)	Mean pollen transfer distance (m)	Reference
Rewarding					
Aerangis ellisii	Hawkmoths	Solid	30	*c*.5	Nilsson *et al.* (1992*a*)
Comparettia falcata	Hummingbird	Solid	85	—	Salguero-Faría & Ackerman (1999)
Disa cooperi	Hawkmoths	Sectile	29–52*	2.7–10.6	Johnson *et al.* (2005)
Epipactis helleborine	Wasps	Sectile	40	—	Light & MacConaill (1998)
Microtis parviflora	Ants	Sectile	70	0.22	Peakall & Beattie (1991)
Platanthera bifolia	Moths and hawkmoths	Sectile	23–38*	—	Maad & Reinhammar (2004)
Prasophyllum fimbria	Bees and wasps	Sectile	22	8	Peakall (1989)
Rewardless					
Caladenia tentactulata	Wasps	Sectile	<10	17	Peakall & Beattie (1996)
Cypripedium calceolus	Bees	Soft	0	5.2	Tremblay (1994)
Calypso bulbosa	Bumblebee	Solid	18–37*	15	Alexandersson (1999)

* Values for two years of study of same population.

e.g. nectariferous *Spiranthes spiralis*, exhibit not only a cost of fruiting, but also a cost of flowering (Willems & Dorland, 2000).

Profuse production of nectar can consume a substantial fraction of a plant's photosynthetic production during the flowering period. Estimates of nectar production costs in terms of the daily amount of photosynthates vary from 3.3 % in short-lived flowers to 37 % in long-lived flowers (Southwick, 1984; Harder & Barrett, 1992). Pyke (1991) was the first to demonstrate that nectar entails a cost to a plant in terms of growth and/or reproduction. Indirect evidence for the cost of nectar is that it is often reabsorbed after pollination, presumably for allocation of carbohydrates to fruit production (Burquez & Corbet, 1991; Koopowitz & Marchant, 1998; Luyt & Johnson, 2002; Stpiczynska, 2003).

Reproduction in non-rewarding orchids is often severely pollen-limited, even over a lifetime (Calvo, 1993; Tremblay *et al.*, 2005). Thus it is hard to understand why resources in these orchids are not allocated to a component of pollinator attraction such as nectar. One possibility is that allocation to the floral display (size of inflorescence, its colour, scent etc.) is even more important for alleviating pollen-limitation than nectar. Plants with larger floral displays increase the number of pollinator approaches due to a strong long-distance attractiveness (Sih & Baltus, 1987; Hessing, 1988).

(2) The outcrossing hypothesis

Plants that reward their pollinators experience higher visitation rates, more flowers probed per visit, and longer duration of pollinator visits (Hodges, 1981; Klinkhamer, de Jong & de Bruhn, 1989; Harder & Barrett, 1995; Johnson & Nilsson, 1999; Johnson *et al.*, 2004). However, this behaviour also tends to result in higher levels of pollinator-mediated self-pollination, both within and among flowers (de Jong, Klinkhamer & van Staalduinen, 1992; Klinkhamer,

de Jong & Metz, 1994; Snow *et al.*, 1996; Barrett & Harder, 1996; Rademaker & de Jong, 1998; Barrett, 2003; Johnson *et al.*, 2004) (Table 2).

The absence of nectar in many orchids may serve to reduce levels of pollinator-mediated geitonogamy, as pollinators tend to visit fewer flowers on such plants (Dafni & Ivri, 1979; Nilsson, 1980, 1983*a*; Ackerman, 1986; Dafni, 1987; Johnson & Nilsson, 1999). Significant increases in self-pollination have been shown to result from experimental supplementation of artificial nectar to flowers of the deceptive species *Anacamptis morio* (Johnson *et al.*, 2004). Other experiments with labelled pollen in orchids also tend to be consistent with this hypothesis (Tables 2 and 3). In rewarding species, *Comparettia falcata* and *Microtis parviflora*, more than 70 % of pollen transfers were involved in self-pollination (Peakall & Beattie, 1991; Salguero-Faría & Ackerman, 1999).

In general, self-pollination has negative consequences for plant fitness. Firstly, it reduces pollen export and fewer ovules are successfully fertilized by outcross pollen, processes known as pollen and ovule discounting, respectively (Holsinger & Thomson, 1994; Herlihy & Eckert, 2002). Secondly, self-fertilization reduces levels of genetic variation (Charlesworth & Charlesworth, 1995) and may cause inbreeding depression (*ID*) characterised by lower reproductive output and lower viability of offspring (Andersson & Waldmann, 2002). Even though orchids are typically self-compatible, the seed set and seed quality is normally greatly reduced after self-pollination (Tremblay *et al.*, 2005). Inbreeding depression is typically caused either by the expression of lethal deleterious recessive alleles that were formerly masked by the heterozygous state or by the loss of heterozygote advantage (Charlesworth & Charlesworth, 1987; Barrett & Charlesworth, 1991).

The relationship between inbreeding and inbreeding depression is likely to depend on the characteristic rate of selfing. Jain (1976) suggested that when self-pollination is common, plants might not suffer from inbreeding

Table 3. *Effects of nectar supplementation on pollinator behaviour (number of flowers probed and time spent per inflorescence or flower) and pollen transfer (number of pollinaria removed, amount of pollen involved in self-pollination and number of massulae deposited per stigma). The symbols indicate a significant increase (+), decrease (−), non-significant effect (NS) or trait that was not measured (NM)*

Species	no. of flowers probed	Probing time	no. of pollinia removed	Self-pollination	no. of massulae deposited	Reference
Barlia robertiana	+	NS	−	NS	NS	Smithson & Gigord (2001)
Anacamptis morio	+	+	NS	NS	NM	Smithson (2002)
Anacamptis morio	+	+	+*	NM	NM	Johnson & Nilsson (1999)
Orchis mascula	+	+	NM	NM	NM	
Anacamptis morio	+	+	+	+	NM	Johnson et al. (2004)
Disa pulchra	+	+	+	+	+	Jersáková & Johnson (2005)

* Significant in one of two populations studied.

depression because most of the recessive deleterious alleles have already been purged from the population. Husband & Schemske (1996) compiled data on 79 populations of 54 species of plants and found a negative correlation between inbreeding depression and selfing rate. Thus if deceptive orchid species regularly experience high levels of outcrossing, one would expect to find a higher cost of selfing in deceptive species than in rewarding ones. Inbreeding depression is most often expressed in the early stages of seed development (Levin, 1984). Our survey of published breeding system data for 46 orchid species (Table 4) revealed that the percentage of seeds with viable embryos is significantly lower in capsules resulting from self- than cross-pollination for both rewarding and rewardless species, respectively (*t*-test for dependent samples: $t = -5.22$, d.f. = 28, $P < 0.00001$; $t = -3.67$, d.f. = 16, $P < 0.002$). However, the level of inbreeding depression [measured as $ID = (C-S)/C$, where C and S represent percentage of seeds with embryos of cross- and self-pollinated capsules, respectively Johnston & Schoen, 1994], does not differ between rewarding and rewardless species (*t*-test for independent samples: $t = 0.68$, $P = 0.498$, 17 rewardless and 29 rewarding species). Though not significant, the mean level of apparent inbreeding depression appeared higher for rewarding orchids than for rewardless ones (0.34 *versus* 0.26, respectively). Regardless of nectar production, the higher costs of selfing could be associated with a particular group of pollinators, especially with insects promoting outcrossing. We found a non-significant trend for the type of pollinator to influence the cost of selfing (one-way ANOVA, $F_{5,40} = 1.54$, $P = 0.197$), with the level of inbreeding depression decreasing in the series: flies – butterflies and moths – bees and bumblebees – hummingbirds – wasps – ants.

Observations of pollinator behaviour on orchids and artificial rewardless flowers suggest that pollen dispersal distances may be greater in deceptive species due to the tendency of pollinators to depart from unrewarding patches, and conversely to remain in rewarding ones (Peakall & Beattie, 1996; Alexandersson, 1999; Keasar, 2000; Smithson and Gigord, 2003; Renner, 2005; Table 2). Thus inbreeding may result not only from geitonogamous pollination, but also from pollination between neighbouring

individuals (biparental inbreeding: Vekemans & Hardy, 2004). This idea has been recently supported by several studies showing the fine-scale genetic structure of orchid populations (Machon et al., 2003). In rewardless *Cephalanthera longibracteata*, relatedness between plants growing closer than 3 m was comparable to that expected for half sibs and first cousins (Chung, Nason & Chung, 2004). Similarly in rewardless *Dactylorhiza praetermissa*, hand-pollination between plants growing less than 10 m from the mother plant resulted in a lower proportion of seeds with embryos and decreased germination rate than for pollination between plants growing at more than 20 m distance (Ferdy et al., 2001).

V. FITNESS BENEFITS OF FLORAL DECEPTION: ORCHID-SPECIFIC HYPOTHESES

Non-rewarding flowers have evolved independently in many plant families; however, the vast majority of deceptive species belong to the orchid family. There have been a number of hypotheses for the concentration of non-rewarding species in the orchid family.

(1) Low-density hypothesis

The low-density hypothesis was raised for the first time by Macior (1971). Orchids often occur in small, scattered populations, which may reflect the limited availability and ephemeral nature of their habitats (Ackerman, 1986; Nilsson, 1992). With individual plants so scattered, even rewarding plants are unlikely to encourage foraging constancy in pollinators (Heinrich & Raven, 1972; Ackerman, 1986; Dafni & Bernhardt, 1990). Given that rewards may have little fitness benefit under such circumstances, resources used for their production may be better transferred to other traits that increase fitness, such as a larger floral display (Schemske, 1980) or longer blooming period (Proctor & Harder, 1995). We need further studies which test the relationship between plant density and selection for floral rewards.

Table 4. *Effect of self- and cross-pollination on the percentage of seeds with embryos in rewarding and rewardless orchids*

| Species | Pollinator | Seeds with embryos (%) | | Reference |
		Self-	Cross-	
Rewardless species				
Caladenia tentactulata	Thynnine wasp	74	73.7	Peakall & Beattie (1996)
Cleistes divaricata	Bees, bumblebees	64	89	Gregg (1989)
Dactylorhiza praetermissa	Bumblebees	91	89.3	Ferdy *et al.* (2001)
Dactylorhiza sambucina	Bumblebees	43	75	Nilsson (1980)
Disa atricapilla	Wasps	82.2	94.7	Steiner *et al.* (1994)
Disa draconis	Long-tongue flies	65.3	93.2	Johnson & Steiner (1997)
Disa ferruginea	Butterflies	36.4	86.4	Johnson (1994)
Disa pulchra	Long-tongue flies	48.2	96.6	Johnson (2000)
Diuris maculata	Bees	94	82	Beardsell *et al.* (1986)
Epidendrum ciliare	Moth	79.3	74.5	Ackerman & Montalvo (1990)
Orchis mascula	Bees, bumblebees	59.8	75.1	Nilsson (1983*a*)
Anacamptis (Orchis) morio	Bumblebees	10.1	35.2	Nilsson (1984)
Orchis spitzelii	Bumblebees	54	86.9	Fritz (1990)
Pleurothallis fabiobarrosii	Flies	32.8	95.7	Borba *et al.* (2001)
Pleurothallis johannensis	Flies	20.7	93.5	Borba *et al.* (2001)
Xylobium squalens	Trigona bees	74.7	82.3	Pintaúdi *et al.* (1990)
Leporella fimbriata	Ants	50	40.3	Peakall (1989)
Mean $\pm$ S.D.		57.6 ± 24.0	80.2 ± 17.8	
Rewarding species				
Brownleea galpinii ssp. *major*	Long-tongue flies	1.4	79.7	Johnson *et al.* (2003*a*)
Bulbophyllum involutum	Milichiid flies	52.7	71.2	Borba *et al.* (1999)
Bulbophyllum ipanemense	Milichiid flies	44.4	47	Borba *et al.* (1999)
Bulbophyllum weddellii	Milichiid flies	68.3	54.4	Borba *et al.* (1999)
Catasetum viridiflavum	Euglossine bees	67.8	98.3	Tremblay *et al.* (2005)
Comparettia falcata	Hummingbirds	97.2	95.8	Salguero-Faría & Ackerman (1999)
Cynorchis uniflora	Hawkmoths	36	61	Nilsson *et al.* (1992*b*)
Goodyera oblongifolia	Bumblebees	40	60	Kallunki (1981)
Goodyera oblongifolia	Bumblebees	52.7	83.8	Ackerman (1975)
Goodyera pubescens	Bumblebees	77	64.5	Kallunki (1981)
Goodyera repens var. *ophioides*	Bumblebees	36	63.5	Kallunki (1981)
Goodyera tesselata	Bumblebees	88	79	Kallunki (1981)
Listera cordata	Fungus gnats	88.5	94.2	Meléndez-Ackerman & Ackerman (2001)
Listera ovata	Beetles,wasps	89.3	97.7	Nilsson (1981)
Microtis parviflora	Ants	83	89	Peakall & Beattie (1989)
Mystacidium venosum	Hawkmoths	37.1	99	Luyt & Johnson (2001)
Platanthera bifolia	Hawkmoths	43.8	84.2	Nilsson (1983*c*)
Platanthera chlorantha	Hawkmoths	23.9	73.5	Nilsson (1983*c*)
Platanthera ciliaris	Butterflies	66	76	Gregg (1990)
Platanthera lacera	Moths	67	47	Gregg (1990)
Platanthera leucophaea	Hawkmoths	29	50.5	Wallace, 2003
Platanthera stricta	Bumblebee, moths, flies	45	82	Patt *et al.* (1989)
Pleurothallis adamantinensis	Flies	29.3	95	Borba *et al.* (2001)
Pleurothallis ochreata	Flies	30.7	96.4	Borba *et al.* (2001)
Pleurothallis teres	Flies	2.8	92.1	Borba *et al.* (2001)
Satyrium bicorne	Moths	14.8	66.1	Ellis & Johnson (1999)
Satyrium coriifolium	Sunbirds	29.3	65.6	Ellis & Johnson (1999)
Satyrium erectum	Bees	14.5	57.9	Ellis & Johnson (1999)
Vanilla claviculata	Euglossine bees	63	88	Tremblay *et al.* (2005)
Mean $\pm$ S.D.		48.9 ± 26.8	76.3 ± 16.8	

(2) Pollinia-removal hypothesis

This hypothesis is based on the notion that orchid pollinia can be removed or deposited in a single visit, thus obviating the need for rewards that encourage multiple visits by pollinators. However, orchids as a group suffer higher pollen removal failure than other monocot species with granular pollen (reviewed by Harder, 2000). The generally high removal failure for orchids is apparent from a sample of 53 orchid species, for which an average of 48.3% of flowers fail to have any pollinia removed (Harder, 2000). This removal failure is most likely a consequence of low

levels of visitation to orchid flowers, as Harder (2000) noted that complete removal failure occurs significantly less often for plant species that reward their pollinators and receive frequent visits (34.6%) than for deceitful species (63.6%).

Pollinia are not specific to Orchidaceae: similar structures have evolved independently in the non-related family Apocynaceae with radially symmetrical flowers and relatively promiscuous pollination systems (Ollerton & Liede, 1997). The asclepiad Apocynaceae have five solid pollinia per flower, thus the flower needs to be visited more than once to maximize pollen transfer. This could be a reason why most asclepiads provide pollinators with abundant nectar. Only a few genera such as *Ceropegia* and *Stapelia*, pollinated by carrion flies, have rewardless flowers (Vogel, 1961; Meve & Liede, 1994).

A recent version of the pollinia-removal hypothesis suggests that deception actually increases the rate of removal of pollinia from flowers (Smithson & Gigord, 2001). Although decreased pollinia removal was associated with nectar addition in one study (Smithson & Gigord, 2001), other studies have shown either no effect of nectar addition on pollinia removal (Smithson, 2002) or a positive effect of nectar on pollinia removal (Johnson & Nilsson, 1999; Harder, 2000; Johnson *et al.*, 2004; Table 3). It is possible that the decreased pollinia removal in *Barlia robertiana* flowers when nectar is added (Smithson & Gigord, 2001) represents an artefact of changes in pollinator probing position or in the effectiveness of the viscidium.

(3) Transport efficiency hypothesis

The reduced transport loss achieved by adhesive attachment of pollen to pollinators may be a key innovation that enabled the evolution of deceit pollination in orchids (van der Pijl & Dodson, 1966; Dressler, 1990; Paulus & Gack, 1990). Among animal-pollinated species, the fate of transported pollen depends fundamentally on whether pollen travels as independent grains or in aggregations. Pollen fates in species with granular pollen are characterised by low levels of removal failure and high levels of transport loss – usually less than 1% of pollen reaches a stigma (Harder, 2000). Orchids, by contrast, experience much higher removal failure, but their ability to glue pollinia onto pollinators greatly reduces transport loss; for 11 orchid species 9.6–36.9% of removed pollen dispersed successfully (Harder, 2000). Thus, one may hypothesize that by having fewer transport losses orchids may have less cause to provide rewards to induce foraging constancy in pollinators. This idea seems to be supported by a recent survey (Harder, 2000), although it unfortunately included few deceptive species: the percentage of pollen reaching stigmas in deceptive orchids (range 5–13%, mean = 9%, N = 2) was similar to that in rewarding orchids (range 3–22%, mean = 11.4%, N = 9; t-test for independent samples: t = −0.42, d.f. = 9, P > 0.680).

(4) Limited pollen-carryover hypothesis

Angiosperm pollen may be dispersed in different ways, either as single units or united in various manners (clumps, tetrads or multiples of tetrads; Knox & McConchie, 1986; Pacini & Franchie, 1998). Type of dispersal pollen unit has important consequences for pollen carryover (i.e. the fraction of pollen carried over from one flower to the next). If orchids have limited pollen carryover, which renders them prone to geitonogamous self-pollination, then selection may favour deception as this discourages pollinators from visiting many flowers on a plant (see Section IV.2).

In orchids, pollen carryover differs according to the degree of cohesion of pollen in the pollinium, which may be soft, sectile (comprised of sub-units known as massulae) or hard (Burns-Balogh & Bernhardt, 1985; Johnson & Edwards, 2000; Pacini & Hesse, 2002). Hard (solid, compact) pollinia, the most common type among orchids (Dressler, 1993), are deposited as an entire unit on the stigma. Soft (mealy) and sectile (massulate) pollinia disintegrate on the contact with the sticky stigmatic surface into smaller pollen loads, which may be deposited sequentially over several flowers. One would therefore expect that pollen carryover would be limited in orchids with solid pollinaria, and be more extensive in orchids with sectile or mealy pollinia.

Pollen carryover should be higher in orchid species with mechanisms that allow insects to visit a long sequence of flowers before pollination occurs. Mechanisms that may increase pollen carryover include: (a) bending movement of pollinaria, (b) shrinking of the pollinium, (c) retention of anther cap, (d) protandry, and (e) sequential flowering (Catling & Catling, 1991; Johnson & Edwards, 2000).

Johnson & Nilsson (1999) and Johnson *et al.* (2004) allowed insects carrying freshly removed sectile pollinaria to visit a sequence of emasculated virgin flowers to evaluate pollen carryover in the deceptive species *Orchis mascula* and *Anacamptis morio*, and the rewarding species *Platanthera chlorantha*. The average number of flowers receiving pollen from a single pollinium was 6.6 for *O. mascula*, 7.7 for *A. morio* and 13.8 for *P. chlorantha*. The fraction of pollen carried over from flower to flower was 0.67 for *O. mascula*, 0.72 for *A. morio* and 0.87 for *P. chlorantha*. Nectar addition to flowers of *A. morio* had no effect on the pollen carryover (Johnson *et al.*, 2004). Johnson & Nilsson (1999) thus concluded, at least for orchids with sectile pollinia, that pollen carryover is not restricted and in combination with other mechanisms that promote outcrossing may not pose a serious problem for geitonogamy and pollen discounting.

Johnson & Edwards (2000) suggested the pollen carryover of hard pollinia may also be extensive due to imperfections in the pollen-transfer process, as captured pollinators were carrying large loads of solid-type pollinaria. To draw general conclusions on pollen carryover and its evolutionary consequences, the actual levels of pollen carryover in orchids with hard-pollinia must be examined in future research.

VI. IS FLORAL DECEPTION EVOLUTIONARILY STABLE?

Non-rewarding orchids are, on average, less fecund than their rewarding counterparts (Dafni & Ivri, 1979; Gill,

1989; Neiland & Wilcock, 1998; Tremblay *et al.*, 2005). Direct observations indicate very low pollinator visitation rates, and as a consequence production of fruits is much lower in deceptive than in rewarding species. For example, the average fruit set in 29 European rewarding and in eight rewardless orchid species was 63.1 and 27.7%, respectively (Neiland & Wilcock, 1998). Johnson & Bond (1997) found strikingly similar fruit set values in South African orchids: 64.8% in 12 rewarding species and 25.2% in 21 nectarless species. This trend was recently confirmed by a broad survey of the orchid family (Tremblay *et al.*, 2005): a per cent fruit set in non-rewarding species (median $\pm$ S.E. $= 20.7 \pm 1.7$; $N = 130$) is roughly half that of rewarding species (37.1 ± 3.2; $N = 84$).

Given that nectar-deception is evolutionarily ancestral in orchids and yet associated with very low levels of fruit set, it is difficult to explain why mutations for reward production would not rapidly spread to fixation (Gill, 1989). There have been a number of documented instances of nectar-rewarding species evolving within deceptive lineages (*cf.* Johnson *et al.*, 1998), so lack of mutations is unlikely to suffice as an explanation for the apparent stability of the deceptive strategy.

Johnson *et al.* (2004) argued that genetic load and pollinator abundance would have major influences on the fate of mutations for nectar-production. When pollinators are very rare, mutations for nectar production should spread within a population even when there are high levels of genetic load. This is because the benefits from having more flowers pollinated and exporting pollen would outweigh the costs in terms of inbreeding depression, pollen discounting and resource usage. On the other hand, when pollinators are very common, mutations for nectar production would be unlikely to spread through a population because the marginal gains in seed production and pollen removal would be outweighed by the loss of fitness through inbreeding depression, pollen discounting and resource use. Another factor that may slow rates of fixation is the scenario of 'auto-mimicry' whereby pollinators would not easily be able to distinguish between rewarding and non-rewarding plants using visual cues (Renner, 2005), though the use of spatial cues is a possibility (Bell, 1986).

VII. CONCLUSIONS

(1) The orchid family is exceptional for its unusually high frequency of non-rewarding species compared to other plant families. Generalized food deception is the most common mechanism of pollination in non-rewarding orchids (reported in 38 genera) followed by sexual deception (18 genera).

(2) Of the many hypotheses that have been put forward to explain the evolution (or persistence) of deception in orchids, the promotion of cross-pollination has received the most theoretical and empirical support. The higher seed quality and more efficient pollen export that results from cross-pollination in deceptive orchids would be particularly beneficial when pollinators are common. When visitation

rates to deceptive orchids drop below a certain threshold at which these advantages are outweighed by very low seed quantity, then selection should favour reward production or autogamy.

(3) The evolution of deception in orchids cannot be explained by a single hypothesis because the conditions that favour rewarding or non-rewarding strategies are highly context dependent. In this review we have identified pollen packaging, genetic load, population density and pollinator abundance as key variables whose role in the evolution of deception needs to be explored further.

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