Orchid diversity: an evolutionary consequence of deception?

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The Orchidaceae are one of the most species-rich plant families and their floral diversity and pollination biology have long intrigued evolutionary biologists. About one-third of the estimated 18 500 species are thought to be pollinated by deceit. To date, the focus has been on how such pollination evolved, how the different types of deception work, and how it is maintained, but little progress has been made in understanding its evolutionary consequences. To address this issue, we discuss here how deception affects orchid mating systems, the evolution of reproductive isolation, speciation processes and neutral genetic divergence among species. We argue that pollination by deceit is one of the keys to orchid floral and species diversity. A better understanding of its evolutionary consequences could help evolutionary biologists to unravel the reasons for the evolutionary success of orchids.

Pollination by deceit: how it all began

The Orchidaceae are among the most species-rich plant families and are renowned for their spectacular floral diversity and intricate adaptations to pollinators (Box 1). The great interest in orchid pollination dates back to Darwin, who devoted an entire book to orchid pollination biology [1]. Arguably, the most fascinating aspect of orchid biology is pollination by deceit (see Glossary), which was discovered by Sprengel in 1793 [2]. His observation that some orchids never carried nectar in their spur was met with disbelief by Darwin, but it was eventually established that some orchids successfully attract pollinators although they never provide a reward. Later, Pouyanne and Coleman independently discovered that some orchids, such as the Mediterranean *Ophrys* [3] and the Australian *Cryptostylis* [4], are pollinated by sexual deceit [5]. To date, this pollination strategy has been documented exclusively in orchids.

Food deception (i.e. attracting pollinators by mimicking rewarding signals) has evolved repeatedly in different angiosperm groups, but is typically restricted to a few species per family [6]. By contrast, one-third of orchid species are estimated to be food deceptive, and another presumed 400 species are sexually deceptive (i.e. attracting pollinators by mimicking the mating signals of the

female) [7], suggesting that pollination by deceit in orchids is an evolutionarily highly successful strategy.

Numerous theories have been proposed to explain the evolution of deception in orchids and these theories have been widely discussed [8]. It is currently an open question as to when pollination by deceit evolved in orchids. Phylogenetic evidence suggests that deceit pollination is either ancestral in orchids, or evolved early in their evolutionary history (Box 2). This inference is supported by the observation that numerous mechanisms are found throughout the Orchidaceae to promote pollination success under conditions of pollinator limitation, as is typically observed in deceptive orchids, including extreme pre-pollination floral longevity, prolonged viability of excised pollen, extended stigma receptivity and delayed development of ovules [9,10]. The suggestion that

Glossary

Anthesis: the period during which a flower is fully open and at its most receptive state.

Autogamy: a form of self-pollination, in which a flower is fertilized by pollen from the same flower.

Food deception: pollination strategy in which flowers ignal the presence of a food reward to pollinators without providing this reward. This strategy is based on the general resemblance of the non-rewarding species to nectar-rewarding species and exploits the innate food-searching aptitude of pollinators. A special case is Batesian floral mimicry, where the non-rewarding species strictly resembles a specific co-occurring rewarding species [5].

Geitonogamous pollination: a form of self-pollination, in which a flower is fertilized by pollen from another flower of the same plant.

G_{st}: a measure of population differentiation that ranges from zero to one. Low values indicate that little of the variation is proportioned among populations, whereas high values indicate that much of the variation is distributed among populations.

Pleiotropy: a gene that has a large effect on one trait also affects the expression of other traits.

Oligogenic: a quantitative trait is under oligogenic control if it is controlled by few genes, in contrast with a polygenic trait, where many genes are involved in its phenotypic expression.

Pollinarium bending: the pollinaria of many orchid species, only after having been removed from the flower by a visiting pollinator, start to bend downwards shortly thereafter. Although the freshly removed erect pollinarium is not in a position to deposit the pollen onto a receptive stigma, it can do so once it has bent down.

Pollination by deceit: the plant that is being pollinated provides no reward (e.g. nectar or pollen) to the pollinator, although it attracts the pollinators using signals that are typically associated with a reward (such as spur and nectar guides).

siRNA: small interfering RNA (siRNA) are short RNAs that mediate messenger RNA (mRNA) degradation [61] and can be used experimentally to 'silence' a targeted gene.

Sexual deceit: flowers mimic mating signals of female insects and are pollinated by deceived males while they attempt to copulate with the flower [18]. To elicit the male mating behaviour, the flowers provide a series of key stimuli. Floral odour signals, more so than visual or tactile ones, are of primary importance for successfully attracting pollinators [63].

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Box 1. The unique morphology of orchid flowers

The complex 'inventions' of orchid flowers have always attracted biologists. Orchid flowers are typically zygomorphic, with an outer whorl of three sepals, and an inner whorl of three petals, as is typical for monocots (Figure I). Sepals are often differentiated in a 'dorsal' or 'medial' sepal that is large and showy, and two 'lateral' sepals. The two lateral petals flank the greatly enlarged third petal, better known as either lip or labellum, which corresponds to the top petal. Just before the flower opens, it rotates 180°. This unique process is called 'resupination' and is necessary to position the labellum on the bottom of the flower, where it often serves as a landing platform for pollinators.

In orchids, there are no stamens with free filaments as in other plants; instead, there is a reduction in the number of floral parts and the male and female reproductive organs are fused into a single structure, the column or gynostemium, which is located at the centre of the flower. At the top of the column is the anther, and below the sticky stigma. The rostellum, a beaklike structure, separates male and female organs and acts as a barrier to prevent self pollination.

Unlike most other plants, orchid pollen is typically derived from a single stamen and pollen grains stick together to form pollinia. Pollinia are connected directly or through a short stalk (stipe or caudicle) to the sticky foot-like viscidium. This structure is termed the 'pollinarium' and becomes attached to the pollinator [10].
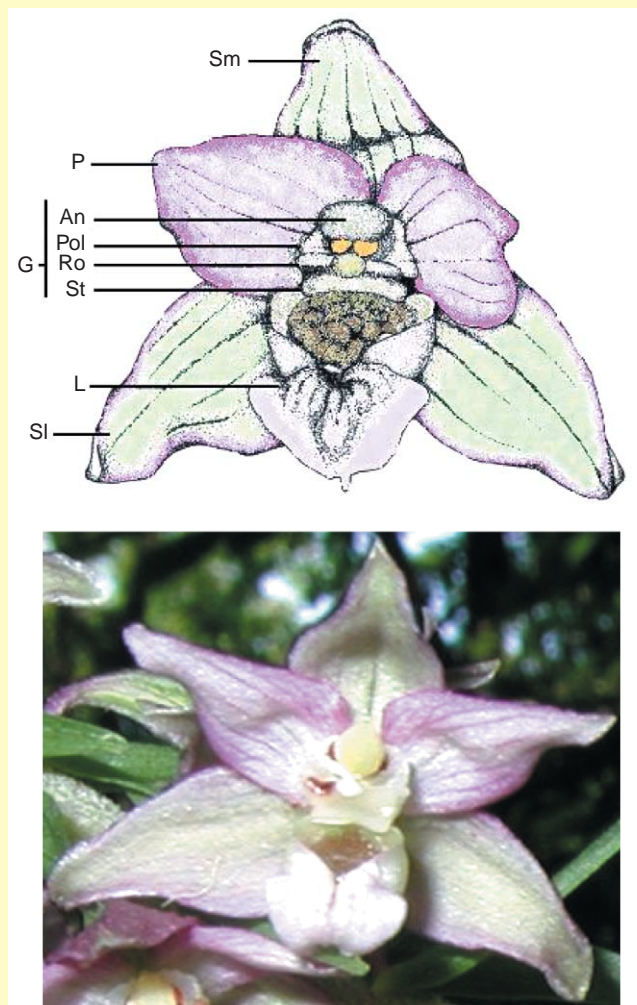

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Figure I. Flower of the nectar-rewarding orchid *Epipactis helleborine*. Abbreviations: An, anther; G, gynostemium; L, labellum; P, petal; Pol, pollinia; Ro, rostellum; Sl, lateral sepal; Sm, median sepal; St, stigma.

deception evolved early in orchid history should not only affect discussions about the evolution of deception, but it should also emphasize the need for understanding the evolutionary consequences of deception, because these might reveal how the spectacular ecological diversity seen in modern orchids has evolved.

Deception and orchid mating systems

The pollination strategy of an orchid (reward pollination versus food or sexual deception) strongly affects its mating system. Although autogamy in not infrequent [11], orchids show several mechanisms to promote outcrossing. Darwin discovered pollinarium bending in some orchids and interpreted it as a contrivance to avoid self-pollination [1]. Experimental evidence has confirmed that this mechanism reduces the chances for geitonogamous pollination and thus promotes outcrossing [12,13].

Pollinarium bending is particularly important in orchids carrying a nectar reward. Here, pollinators spend more time per flower and visit more flowers per inflorescence compared with rewardless flowers, which can lead to increased rates of geitonogamous pollination [13,14]. The time interval that elapses between pollinaria removal and cessation of bending reduces this chance of geitonogamous pollination occurring. In deceptive orchids, pollinators rapidly depart after a rewardless visit, reducing the optimal time span for the pollinarium to attain a horizontal position. As expected, pollinarium bending is significantly faster in the deceptive *Anacamptis morio* and *Orchis mascula* than in the rewarding *Platanthera chlorantha* [12]. To demonstrate conclusively the adaptive value of pollinarium bending in combination with different pollination strategies, direct comparisons of pollinarium bending times between sister species with contrasting pollination strategies are needed.

Orchid population structure is further influenced by pollinator behaviour. Whereas pollinators foraging in a patch of rewarding plants tend to visit neighbouring plants, deceived pollinators often immediately leave the patch [15], especially if it is of sexually deceptive orchids [16–18]. This contrast in pollinator behaviour affects not only the chances for outcrossing, but also the frequency and distance over which gene flow through pollen occurs and has left its distinctive signature in the genetic population structure of the orchids. Genetic differentiation among populations (as estimated by G_{st}) is higher for rewarding orchids compared with deceptive orchids, suggesting that pollinator-mediated gene flow among populations is higher in deceptive orchids (Figure 1). Frequent gene flow among populations reduces the chances for local genetic drift and studies of sexually deceptive Australian and European orchids have found high levels of genetic diversity that translate into large effective population sizes [16,19].

The advantage of outcrossing

High genetic diversity within populations and weak genetic differentiation among populations are compatible with high outcrossing rates in deceptive orchids. These come at a fitness cost when compared with rewarding orchids. Evidence suggests that low fruit set in food- and

Box 2. Phylogeny and the origin of pollination by deceit

The pollination strategies of ancestral orchids are an unresolved enigma. Orchids are a sister group to Asparagales, most of which have septal nectaries and are rewarding, but many extant orchid lineages are nectar-less. Among primitive orchids, Apostasioideae offer pollen as a reward, as do Hypoxidaceae, which are one of the potential Asparagales sister families to the orchids, together with Blandfordiaceae. Vanilloideae and Cypripedioideae, the two other primitive orchid groups, are mainly pollinated by deceit [64]. These lines of evidence indicate that the absence of nectar might represent the primitive condition in orchids (Figure I). Whether ancestral orchids offered pollen as a reward or were already pollinated by deceit is an open question.

Irrespective of whether ancestral orchids were deceptive, it is well established that deception has evolved in many species, and several times independently in the major orchid clades [32]. The direction of evolutionary change between reward pollination, food deception and sexual deception is an active research area. Dafni [36] proposed a scenario for Mediterranean Orchidinae in which food-deceptive and sexually deceptive orchids evolved independently from a nectariferous ancestor. However, phylogenetic analyses [51,65] and the mapping of pollination strategies onto phylogenetic trees for Orchidinae [22] have not supported this hypothesis, suggesting instead that food deception is the ancestral and predominant pollination strategy in this tribe, and that reward pollination evolved more than once independently from food deception [22] as previously suggested [20]. Sexual deception also evolved from food deception in the large and diverse genus *Ophrys* and independently in *Orchis galilaea* [22]. Similarly, it has been shown for the South African genus *Disa* that nectar-rewarding and sexually deceptive species evolved from food-deceptive ancestors [23]. In South America, sexual deception evolved independently in the genera *Trigonidium* [66], *Mormolyca* [67] and probably in Oncidiinae [33]. The most spectacular radiation of sexually deceptive orchids occurred in Australia, where this pollination strategy has evolved several times and occurs in nine genera [68]. It is presently unknown whether reward pollination or food deception have ever evolved from sexual deception.
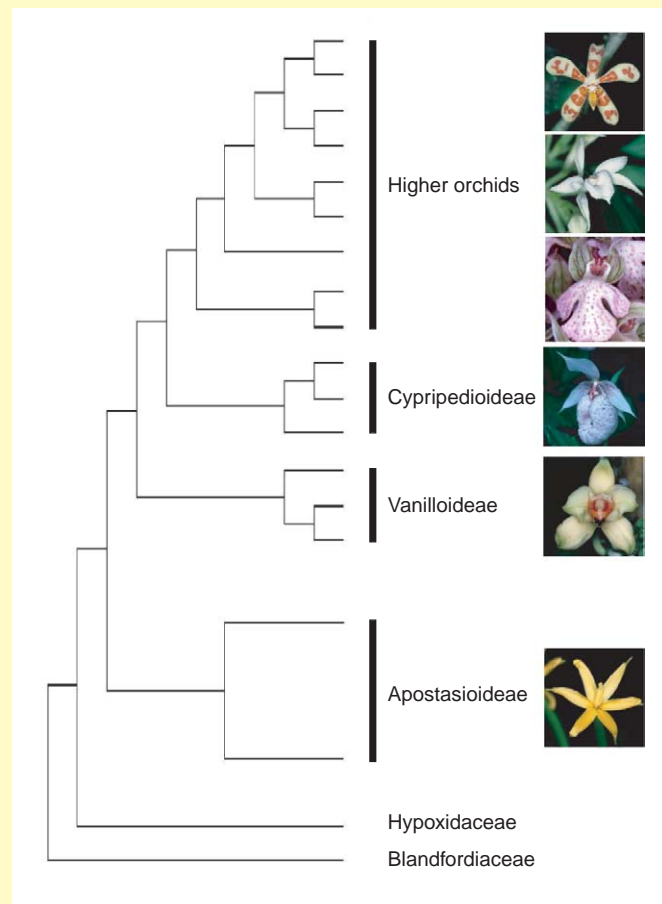

Figure I. The phylogenetic relationships among the major clades of the family Orchidaceae and its closest relatives, based on plastid DNA sequences. Reproduced, with permission, from [69].

sexually deceptive orchids is a consequence of severe pollinator limitation [20,21]. Some nectar addition experiments have shown that pollinator limitation can be alleviated if orchids provided some kind of reward [13,14]. The fact that rewarding orchids have repeatedly evolved from food-deceptive species [22,23] shows that secondary nectar production has evolved in some instances under natural conditions. However, removal of pollinator limitation might not necessarily be advantageous for the plant. Two independent studies of the food-deceptive *Anacamptis morio* found that nectar addition increased the rate of geitonogamous pollination [13,14]. Increased geitonogamy could lead to higher inbreeding rates if cross-pollination is not positively affected by the presence of the reward. If inbreeding depression is severe, the advantage gained by producing more fruits in rewarding flowers is offset by the lower fitness of seeds resulting from geitonogamous pollination. Additionally, geitonogamous self-pollination further compromises male function by reducing the amount of pollen available for export to other plants (pollen discounting), also as a result of the limited carryover of orchid pollinia [12,13].

Not all studies have demonstrated that nectar addition leads to geitonogamous pollination. Some have been

inconclusive [14] whereas others have shown no effect. For instance, in *Barlia robertiana*, no increase in the rate of geitonogamous pollinations was observed with nectar addition [24].The difference between the early flowering *B. robertiana* and the later flowering *A. morio* might be a consequence of differences in pollinator efficiency or identity and in the increased availability of nectariferous plants later in the season; this highlights the importance of considering ecological factors when trying to understand the fitness consequences associated with reward and deceit pollination [25]. Additional experimental tests of this fundamental topic are needed and should be combined with the application of molecular markers to identify the frequency of fruits produced through geitonogamy and outcrossing, respectively, in natural and manipulated populations of rewarding and deceptive orchids.

Costs of reproduction can represent an important constraint on the evolution of life-history traits and such costs have been repeatedly demonstrated for orchids [26]. High fruit production during one year can reduce reproductive performance during subsequent flowering periods in terms of a reduced probability of flowering and smaller plant size [27]. Under this condition, an
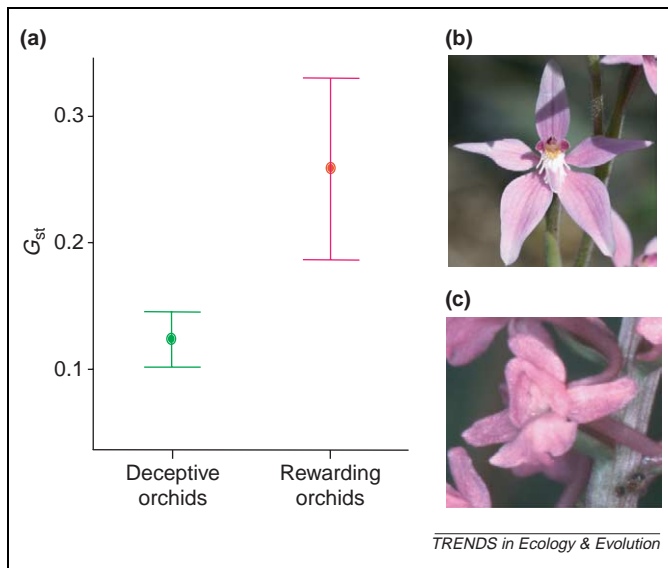
Figure 1. Population genetic consequences of differences in pollination strategy. **(a)** A comparison of levels of mean genetic differentiation (G_{st}) among rewarding and deceptive orchid populations, based on a summary of published allozyme data [58], reveals that populations of rewarding orchids have significantly higher mean G_{st} values than do deceptive orchids (Mann–Whitney U-test, $P<0.001$, error bars represent standard error). This indicates that levels of gene flow are higher among populations of deceptive orchids, assuming no significant difference in seed dispersal or seed quantity between rewarding and deceptive orchids. Similar results were obtained using another independent summary of published allozyme data with slight differences in G_{st} calculation [72]. **(b)** An example of a food-deceptive orchid, *Caladenia latifolia*. This orchid is pollinated by native bees searching for food. **(c)** An example of rewarding orchid, *Gymnadenia conopsea*. This nectar-rewarding orchid is mainly pollinated by moths.

evolutionary successful strategy could be to maximize the number of outcrossed fruits over a limited number of fruits produced.

Arguably the most crucial stages in the life cycle of orchids are the embryo and seedling stages, because an intimate association with an appropriate mycorrhizal partner must be established for survival [10]. Although this association has been known for a long time, scientists have only recently started to investigate it in detail [28]. At present, the mechanisms of cellular signalling among orchid roots and fungal partners are as unknown as the importance of seed fitness for the successful establishment of the fungal association. If seed quantity were of prime importance at this stage, selection would act to increase fruit set, possibly at the expense of seed quality, but available evidence indicates that outcrossed seeds, or possibly the avoidance of inbred seeds, are crucial for fitness [16,29–31]. The connection between outcrossing and seed quality needs further investigation. Currently, the difficulties associated with germinating orchid seeds and growing seedlings to maturity hinder detailed analyses of the fitness differences between selfed and outcrossed seeds and plants, and make estimating the strength of inbreeding depression on later life-history stages time consuming [31].

Given that most orchids are perennial and produce hundreds or thousands of minute, dust-like seeds per capsule [10], and owing to the apparently high cost of reproduction, a lower but continuous fruit set can represent the best balance to guarantee reproductive success during the lifetime of an orchid, provided that

seeds are of high enough quality. Consequently, low fruit set in deceptive orchids should not be regarded as a failure [21], but rather as an evolutionary consequence of a complex pollination strategy that maximizes outcrossing.

Deception and reproductive isolation

The spectacular floral diversity of orchids has often been attributed to their intricate and intimate interactions with their pollinators, and pollinator specificity has been considered as the main ethological, prezygotic reproductive isolation mechanism among orchid species [21,32,33]. Based on available data, it has been estimated that 60–70% of orchids have a single pollinator species [11], but most observations on pollination system specificity have been carried out in several rewarding tropical orchids that are visited by one or a few species of euglossine bees [34]; there are relatively few observations available for most species of deceptive orchids. A notable exception are the sexually deceptive orchids that have been intensively studied and where it has been shown that the highly specific attraction of male pollinators is sufficient to maintain orchid species boundaries, even among sympatric, co-flowering species [19,35]. At present, however, it is unclear whether high pollinator specificity in deceptive orchids is either the exception or the rule. This depends largely on the pollinator specificity of food-deceptive orchids, which represent most deceptive orchids.

Food deception [5] is a pollination strategy that can attract a guild of locally available pollinators [8,36]. Consequently, sympatric food-deceptive orchid species might share pollinators, which could lead to hybridization and the breakdown of species boundaries [37]. Molecular and SEM analyses of orchid pollinaria found on pollinators indicate that substantial pollinator sharing occurs among sympatric, co-flowering food-deceptive orchids [38,39], which frequently flower in sympatry in the Mediterranean region. Although countless hybrid combinations have been described, real hybrid zones are surprisingly rare [36], except in the genus *Dactylorhiza*, and typically consist of only a few early-generation hybrids [40,41], which suffer low fertility [42]. A similar case has been found in two Australian sexually deceptive *Chiloglottis* species that share the same pollinator [43].

A recent comparative analysis of karyotype differences between orchid species pairs that either have the same or different pollinators found that species that share pollinators, such as food-deceptive orchids, have significantly more divergent karyotypes than do species that are pollinated by different, specific pollinators [37]. These karyotype differences are due to chromosomal rearrangements, which might affect chromosome pairing and lead to abnormal segregation or recombination during meiosis in hybrid progeny [42,44]. This result accords well with the observed low fitness of hybrids [42,43], and indicates that, in food-deceptive orchids, where pollinator specificity is weak or absent, late postzygotic reproductive barriers exist [37].

These results call for a reassessment of the importance of pollinator specificity for prezygotic reproductive isolation in orchids. More detailed analyses of the amount of pollinator sharing among co-flowering orchid species,

especially food-deceptive species, and experimental tests of crossing barriers are needed. Only if these approaches are combined can we hope to assess conclusively the relative importance of pollinator-mediated pre-mating versus post-mating reproductive barriers in orchids.

Deception and speciation

Speciation is a timely and hotly debated issue [45] and has long been of great interest in orchid research [32]. In particular, the highly specific sexually deceptive orchids have been proposed as potential examples for sympatric speciation [46]. Because of pollinator specificity, slight differences in biologically active floral odour compounds in the sexually deceptive Mediterranean *Ophrys* spp. [46], or shifts between structurally similar odour components in Australian sexually deceptive *Chiloglottis* spp. [35,47], are sufficient to attract different pollinator species. If these odour components have a simple genetic basis, slight changes in gene expression could potentially result in the attraction of a new pollinator species and lead to reproductive isolation between the ancestral form and the new form. In this situation, the genes underlying the phenotypic (odour) differences also confer reproductive isolation through pleiotropy. Because of the dual role of pollinators, sympatric speciation can occur without initial establishment of linkage between mating and fitness loci [48]. For sympatric speciation to occur, alleles underlying floral odour differences would have to be under sufficiently strong disruptive selection to become established in the presence of gene flow [49]. The initial establishment of a new lineage could be facilitated because orchids produce several flowers and, with few notable exceptions, are self-compatible [11].

Although such a scenario sounds appealing, it remains to be tested. At present, strong empirical evidence for sympatric speciation, with the exception of polyploid speciation, is scant and is lacking for plants [45]. Although the absence of convincing evidence does not indicate the nonexistence of the process, it shows that the problem of sympatric speciation in sexually deceptive orchids must be investigated further. Experimental manipulations of floral odour, combined with a detailed assessment of the strength of assortative mating, based on molecular markers, could provide a promising research avenue.

In food-deceptive orchids, speciation either involves shifts to new pollinators or the evolution of postzygotic isolation mechanisms [37]. Evidence for pollinator shifts comes from South African *Disa* spp. [50], where speciation is associated with repeated shifts between various specialized pollination systems [23] and from Mediterranean food-deceptive *Anacamptis* spp. and *Orchis* spp. [22,51]. Such pollinator shifts are expected to involve numerous changes in floral morphology, colour, periodicity or odour, to attract a different functional pollinator group consistently [52]. As a consequence, more genetic changes are expected to be required for reproductive isolation to evolve, compared with sexually deceptive species. Interestingly, pollination strategies are correlated with neutral genetic divergence among species (Box 3).

In several Mediterranean food-deceptive species pairs that grow in sympatry, have similar flower shape, overlapping flowering periods, and share a common pool of pollinators, postzygotic isolation mechanisms have evolved [37]. These are based on numerous karyotype changes between sister species that lead to reproductive isolation. The numerous morphological or karyotypic changes required for pre-zygotic and post-zygotic reproductive isolation, respectively, in food-deceptive orchids suggest that speciation occurs predominantly in allopatry [37,50]. Whether allopatric populations have diverged sufficiently to ensure species cohesion is determined upon secondary contact. In this case, only species pairs that are separated by sufficiently strong isolating mechanisms survive the challenge of sympatry [37] and remain reproductively isolated.

By contrast, evidence for gene flow across species boundaries has been found, using neutral markers, among sympatric sexually deceptive *Ophrys* species [19]. At the same time, biologically active floral odour compounds that are responsible for the highly specific attraction of pollinators remain strongly differentiated [46]. These results might indicate that few genes are involved in reproductive isolation among sexually deceptive orchids, and that large parts of the genomes are open for gene exchange, which effectively reduces genetic differentiation among species at neutral loci [49]. At present, we know nothing about the genetic basis of odour variation in orchids and only recently has the genetic architecture of their sophisticated flower organization begun to be investigated [53]. Results from other plant groups, however, indicate that floral trait differences between species often have an oligogenic basis [54,55], and that directional selection drives phenotypic diversification [56] and, thus, speciation.

Recently, alternative models for orchid speciation have been proposed. The first is based on floral mutations and suggests that radical phenotypic shifts could lead to attraction of different pollinators and, thus, to instantaneous sympatric speciation [57]. This hypothesis needs empirical demonstration, for instance by testing whether flower mutants successfully and consistently attract new pollinators. The second is a drift–selection model [11], which suggests that a low proportion of reproducing individuals and low gene flow among populations lead to genetic drift that, combined with local episodic selection, could account for orchid diversification.

Although it has recently been suggested that drift has no central role in speciation [45], the drift–selection model might be appealing in the case of tropical, epiphytic orchids that often grow in small and scattered populations, and are pollinated by highly specific pollinators. In temperate orchids, however, populations are often large, harbour substantial genetic variation, and are often connected by substantial amounts of gene flow [58]. Here, drift is unlikely to be of relevance in speciation.

Perspectives

The time is ripe to investigate the mysteries of orchid diversity with greater scrutiny. Ecological and molecular studies on orchids must be done simultaneously to transgress the inherent limitations of both fields. For example, ecological research and natural history might

Box 3. Pollination strategies and genetic divergence

Pollination strategies are correlated with the level of neutral genetic divergence among orchid species. In Mediterranean and Australian sexually deceptive orchids [35,68,70], molecular phylogenies are largely unresolved and branch lengths are short for most taxa, whereas phylogenetic resolution is often better in closely related clades of food-deceptive orchids (Figure I) [51,65]. Genetic distance, estimated from neutral nuclear ribosomal ITS sequences, between species is smaller among sexually deceptive species than among food-deceptive species.

If this pattern is not due to differences in evolutionary rates among food and sexually deceptive species, respectively, it could be explained by the hypothesis that speciation occurs faster in sexually deceptive orchids than in food-deceptive orchids. Alternatively, the pattern might be a consequence of hybridization in sexually deceptive orchids. Interestingly, it has been proposed that hybridization can generate the raw material for rapid adaptive radiation [71]. Further phylogenetic analyses based on independent genes and tests for rate variation among groups with different pollination strategies are needed to identify the processes underlying the correlation between neutral genetic divergence and pollination strategies.
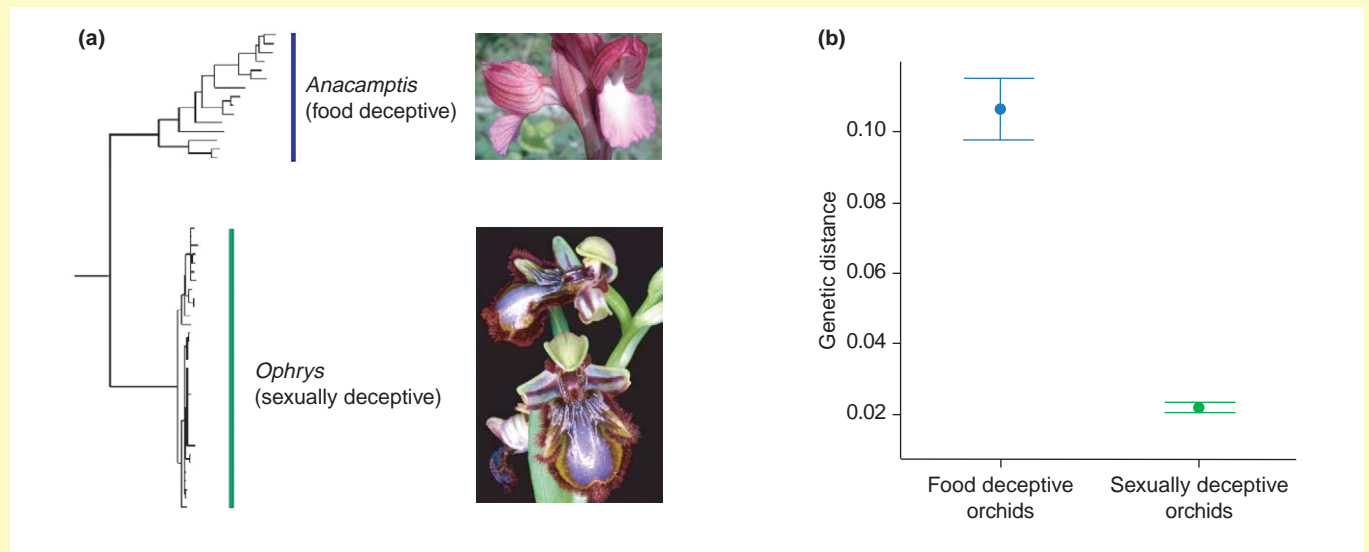

Figure I. Comparison between the clades of **(a)** Mediterranean food-deceptive *Anacamptis* (blue bar) and closely related sexually deceptive *Ophrys* (green bar) reveal that **(b)** mean pairwise genetic distances are significantly smaller among members of the sexually deceptive clade (Mann–Whitney U-test, p<0.001, error bars represent standard error). Comparison based on nuclear ribosomal ITS1, 5.8S and ITS2 sequences. (a) Reproduced, with permission, from [65].

reveal why radiations have been concentrated in particular geographical regions and particular lineages, and molecular research could unravel the genetic basis of these radiations.

The apparent widespread specificity of orchid pollination biology has lured many pollination biologists into believing that the evolution of pre-mating reproductive barriers is necessary and sufficient to drive orchid speciation. New evidence for gene flow across species boundaries, pollinator sharing and the existence of post-mating barriers, however, calls for more-detailed studies that combine pollinator observations, experimental crossing experiments and the use of molecular markers to assess the strength and direction of pre- and post-mating reproductive barriers. This will further help us to better understand the evolutionary consequences of hybridization, a phenomenon that is so pervasive in this plant group [32].

To date, the molecular genetic basis of reproductive barriers among orchids is largely unexplored. In contrast to most other flowering plants, where ovules are fully developed at anthesis, ovule development in orchids is induced by pollination [10]. The molecular events triggered by pollen–stigma interactions leading to ovary development are better understood [59] and might enable isolation of candidate genes for post-mating reproductive isolation. We also need to develop the tools to map loci involved in reproductive isolation to their chromosomal location to assess the genetic architecture of reproductive barriers in orchids, and to test the role of chromosomal change in orchid speciation, as achieved for *Helianthus* spp. [44] and *Drosophila* spp. [60].

The hypothesis of sympatric speciation in sexually deceptive orchids should be tested experimentally using current molecular techniques. Targeted down-regulation of key odour genes, for example through siRNA [61], could be used to assess the strength of selection acting on new odour variants. One complementary population genetic approach would be to infer the history of orchid speciation from multilocus DNA sequence data that can be used simultaneously to estimate ancestral population sizes, migration rates and divergence times [62].

Progress in our study of orchid evolution has been hampered by the paucity of suitable molecular markers available compared with model organisms, such as *Drosophila*. Given that orchids represent one of the most successful and diverse plant families worldwide, attract great interest from plant biologists and the general public, and have great conservation and economic value, the development of genomic resources is an imperative. Only if we look at deception not merely as a pollination strategy, but in the larger context of orchid biology and integrate information ranging from seed establishment to ovule development, will we be able to unravel the mystery of orchid diversity.

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