'Plant mimicry': An enthralling evolution of erroneous exploitation

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ABSTRACT

The term "mimicry" is racking the brain of scientists, novelists, ecologists, evolutionists and lay man readers since this behavior has been observed. Many plants have evolved to appear like other plants, its own parts, inanimate objects, animals, fungi, or most commonly insects. This can have wide ranging benefits including increasing pollination, protection, and imitation and so on.

The present review is a huddle of information about the so called "MIMICRY" in plants viewing grounds of it; predominantly the talk on plants which mimic animals, other plants, inanimate object and fungi. Further, mimicry has been portrayed in diverse way naming "Ant mimicry", "Aphid mimicry", "caterpillar mimicry" on the basis of which object is being mimicked by plants.

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INTRODUCTION

It is widely accepted that mimicry evolves as a positive adaptation. The lepidopterist and writer Vladimir Nabokov argued that although natural selection might stabilize a "mimic" form, it would not be necessary to create it. It may be that much of insect mimicry, including the Viceroy/Monarch mimicry, results from similar self-organizing processes, and thus the tendency for convergence by chance would be high[1].

In evolutionary biology, mimicry is the similarity of one species to another which protects one or both[2]. This similarity can be in appearance, behaviour, sound, scent and location, with the mimics found in similar places to their models[3]. Mimicry occurs when a group of organisms, the *mimics*, evolve to share common perceived characteristics with another group, the *models*. Camouflage, in which a species resembles its surroundings, is essentially a form of visual mimicry. Crypsis is a broader concept which encompasses all forms of avoiding detection, such as mimicry, camouflage, hiding etc[4]. In any case, the signal always functions to deceive the receiver by preventing it from correctly identifying the mimic. In evolutionary terms, this phenomenon is a form of co-evolution usually involving an evolutionary arms race[4]. It should not be confused with convergent evolution http://en.wikipedia.org/wiki/Convergent_evolution, which occurs when species come to resemble one another independently by adapting to similar lifestyles.

Mimics may have different models for different life cycle stages, or they may be polymorphic, with differ-

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ent individuals imitating different models. Models themselves may have more than one mimic, though frequency dependent selection favors mimicry where models outnumber mimics. Models tend to be relatively closely related organisms[4], but mimicry of vastly different species is also known. Most known mimics are insects[3], though many other animal mimics including mammals are known. Plants and fungi may also be mimics, though less research has been carried out in this area[5-7].

The most widely accepted model used to explain the evolution of mimicry in butterflies is the two-step hypothesis. In this model the first step involves mutation in modifier genes that regulate a complex cluster of linked genes associated with large changes in morphology. The second step consists of selections on genes with smaller phenotypic effects and this leading to increasing closeness of resemblance. This model is supported by empirical evidence that suggests that there are only a few single point mutations that cause large phenotypic effects while there are numerous others that produce smaller effects. Some regulatory elements are now known to be involved in a supergene that is involved in the development of butterfly color patterns. Computational simulations of population genetics have also supported this idea[8].

Species resemble each other owing to a shared phylogenetic history or adaptation to a similar abiotic or biotic environment. Among the various adaptations that plants show, deception of other organisms is arguably one of the most intriguing. Traditionally, mimicry has been the primary concept put forward to explain deception. The mimicry hypothesis rests upon the principal assumptions that the model (species that is imitated) and the mimic (species imitating the model) interact with the same receiver individuals, that the receiver mistakes one for the other, and that this mistake has important fitness consequences for the mimic and, often, also for the model[9-13].

Plant community ecology offers tools to study floral colours. For example, the influence of floral colour as a driving force of evolution was addressed[14], who evaluated colour distribution within plant communities. They discovered that rare plants tended to be more distinguishable from the rest of the community than common plants by hymenopteran pollinators, and this would help to secure pollination.

Several authors[15-26] have proposed that mimicry

of various types helps in plant defense. More specifically, Müllerian mimicry was already proposed to exist in several defensive plant signaling systems. The first was for several spiny species with white-variegated leaves[23,27,28]. The second was for some tree species with red or yellow poisonous autumn leaves[29]. The third cases are of a mixture of Müllerian and Batesian mimicry, of thorn automimicry found in many *Agave* species[27].

Aposematic (warning) coloration is a biological phenomenon in which poisonous, dangerous or otherwise unpalatable organisms visually advertise these qualities to other animals. The evolution of aposematic coloration is based on the ability of target enemies to associate the visual signal with the risk, damage or non-profitable handling, and later to avoid such organisms as prey. Typical colors of aposematic animals are yellow, orange, red, purple, black, white or brown and combinations of these[13,30-33].

Many thorny, spiny and prickly plant species were proposed to be aposematic because their sharp defensive structures are usually colorful (yellow, orange, red, brown, black, white) and/or associated with similar conspicuous coloration[13,27,28,34-47].

The mechanisms involved in plant deception, with an emphasis on pollination has been reviewed[48]. They proposed that generalized food deception evolves if plants exploit the innate preferences of pollinators, and thus represents a form of exploitation of perceptual biases (EPB). They contrast this with floral mimicry, which is viewed as a distinct phenomenon that might originate with EPB before selection hones the resemblance between a mimic and a specific model. They argued that EPB in the form of pre-existing bias is not limited to deceptive plants, but rather drives the evolution of floral traits of animal-pollinated plants in general. Further, in their view, EPB is central to the evolution of floral mimicry, which differs from generalized mimicry only in the exploitation of specialized pollinators, leading to a close resemblance between mimics and specific models. Schaefer and Ruxton highlighted the importance of preexisting biases in pollination through the EPB model. They agreed that EPB is an important mechanism for understanding the evolution of floral traits, but suggested that it is more widely applicable to floral evolution, and that it cannot explain the evolution of deceptive flowers. The prerequisites for EPB to select for particular

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plant signals are: (1) pollinators having specific innate preferences; (2) plants being limited in their reproductive success by access to pollinators (i.e. increased pollinator attraction increases plant fitness); and (3) insect perceptual systems predating plant signals, thus the evolution of plant signals exploits pre-existing sensory preferences in the pollinators. There is ample evidence for all three conditions across plant and pollinator lineages. Several studies have shown that plants are often pollinator-limited in their reproductive success[49].

Phylogenetically informed approaches to the evolution of sensory systems in insects and the corresponding signals in plants indicate that insect vision and olfactory systems predated the evolution of floral colour and scent in angiosperms[50,51]. Examples of floral signals influenced by preexisting pollinator bias include the convergent evolution of red colouration in bird-pollinated flowers, which may result from better detection of the colour red in birds, possibly because red serves as an intra-specific communication signal in birds[52]. Floral guides (stripes, dots) might have evolved under innate preferences of bees for radiating stripes, dark centres, and peripheral dots[53]. Yellow spots on flower petals are thought to mimic pollen, selected for by innate preferences of pollinators for the yellow colour of pollen and/or its contrast with petal colours[54]. Patterns of floral scent have recently been shown to converge onto patterns of chemical communication in insects, suggesting that plants have co-opted signals originally used in insect chemical communication for pollinator attraction[51]. Floral traits may thus evolve with the perceptual preferences of pollinators in rewarding as well as deceptive plants, including systems with floral mimicry. Floral mimicry systems differ from generalized deception in their exploitation of specialized pollinators as operators. Such pollinators usually visit only a few floral species or, in sexual deception, court nonspecific females, albeit with preferences for 'allopatric' scent bouquets[55]. In such cases the perceptual filter of the pollinator can be expected to be more finely tuned, so a closer resemblance to the given model will evolve, leading to a classification as floral mimicry.

There is a natural continuum between generalized food deception and floral mimicry: many plants cannot be conveniently assigned to one or other category because the basis for their pollination is a combination of EPB and preferences conditioned by particular food

plants[56]. Proximate mechanisms of floral trait evolution may not differ appreciably between rewarding and deceptive plants. The key to understanding deception in plants can be found among the ultimate reasons driving the evolution of nectar-less flowers. A seeming paradox in deceptive plants is that experimental addition of a reward usually leads to a strong increase in gross pollination success, making deception appear maladaptive[57]. However, pollinators also tend to move between plants more often if flowers are deceptive, thus increasing the rate of outcrossing[57]. Deception may thus represent one of the many plant strategies that reduce inbreeding.

PLANTS THAT MIMIC ANIMALS

Orchid and bee

Through pseudoantagonism, Orchids exploit the territorial behavior 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 bees (*Centris spp.*) may be exploited by some *Oncidium* and *Tolumnia* species[58,59]. This mechanism has not been thoroughly studied and seems to be extremely rare. It was suggested[60] that this interaction may be mutualistic as bees become better territorial defenders with practice. However, no evidence yet supports this hypothesis.

Because of 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*[61] and *Orchis papilionacea*[62], as well as in the African *Disa obtusa* and *Ceratandra grandiflora* species[63,64].

Passiflora flowers and butterfly

The American genus Passiflora is the best-known plant genus with regard to several morphological adaptations suggested to have evolved to reduce herbivory via animal mimicry. The best-studied case is of butterfly egg mimicry by the leaves of several Passiflora species, which has been suggested to reduce egg-laying by Heliconius butterflies, but seems to operate also for other

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plant and butterfly taxa[16,48,65].

Passiflora flowers and caterpillars, slugs, or snails

Another type of defensive animal mimicry in Passiflora genus was noted by Rothschild[66] for the stipules along the branches of *Passiflora caerulae* that resemble caterpillars, slugs, or snails crawling along the stems.

Passiflora flowers and ant or aphid presenting "Ant or Aphid mimicry"

Ant mimicry is not necessarily the sole option of defensive mimicry by means of the dark spots on flowers of *Passiflora*. Such spots may also mimic aphids. Aphid mimicry has already been suggested to defend plants from herbivory because aphids refrain from colonizing plants already occupied by other aphids[22]. In 2009, Lev-Yadun concluded that[67] in the flowers of many *Passiflora* species the coloration pattern raises the possibility of a visual defensive ant or aphid mimicry. While the evolution of such coloration patterns in flowers could be attributed primarily or solely to pollinator attraction, the occurrence of such color patterns on stems and leaves seems to be purely defensive. The physiological functions of anthocyanins (the pigments responsible for the suggested ant mimicry patterns), such as defending the plant from photoinhibition and photooxidation[44], do not explain the dot and stripe patterns. Thus, it is possible that visual ant mimicry by plants is a common phenomenon, the extent of which should be studied globally. When studying the complicated plant–ant relationships, defensive ant mimicry by plants should also be taken into account. The suggested ant mimicry in *Passiflora* adds to the increasing number of cases of apparent defensive plant coloration.

Plants and ant performing "Ant mimicry"

The stems, branches and some of the petioles of *Xanthium trumarium* (Asteraceae) are characterized by scattered conspicuous dark-coloured dots and flecks usually 2–10 mm in size. Dots predominate in some individual plants, flacks in others. Similarly, the petioles and inflorescence stems of *Arisarum vulgare* (Araceae) are covered by many dark flecks. Thus, to the human eye the shoots of these two species appear to be covered by a swarm of ants. Ant swarms are typically made of many moving dark flecks, each varying in size from several mm to over 1 cm. The swaying of leaves, stems

or branches in the wind in combination with the dark spots and flecks, some of which are arranged in lines, may give the illusion that the 'ants' move.

Plants and aphid showing "Aphid mimicry"

The anthers of *Paspalum paspaloides* (Poaceae), a wind pollinated plant, are about 2–3 mm long, dark coloured, and dangle from the green inflorescences, gently moving with the wind. The anthers thus appear to be covered by dark aphid colonies (Homoptera: Aphidoidea, e.g. Aphis, *Toxoptera* and *Macrosiphum*). Similarly, the stems of *Alcea setosa* (Malvaceae) are covered with dark flecks that look like aphids. Many species of aphids tend to aggregate on young stems and leaves of their host plants[68], and two common polyphagous species *Sipha maydis* Passerini and *Rhopalosiphum maidis* (Fitch), both 2–3 mm long, are found on many species of the Poaceae.

Plants and caterpillar presenting "Caterpillar mimicry"

The immature pods of three wild legume species: *Pisum fulvum*, *Lathyrus ochrus* and *Vicia peregrine* (Fabaceae) have conspicuous spots of several shades of red. *Vicia peregrine* has two distinct morphs. Red spots characterize the first, resembling those of L. *ochrus* and P. *fulvum*. Red circles with green centres, the pods characterize the second morph. All these pods mimic the general shape, size and colour of lepidopteran caterpillars ornamented with spiracles or other spots on their sides such as a pieride moth (Pieridae).

Thorny plants resemble green zebras

Two types of conspicuousness of thorns are typical of many plant species originating from several continents and belonging to various families has been showed[37]: (1) colorful thorns and (2) white spots and stripes associated with thorns in leaves and stems. Both phenomena predominate the spine system of the spiniest taxon—the Cactaceae in which about 90% of the species have white markings associated with the colorful thorns. Similarly, most spines in Agave are colored and in about 25% of the species there are stripes along the margins that mark the spines. Dozens of *Aloe* species also have colorful thorns and many *Aloe* species have both colorful thorns and white markings.

In the genus *Euphorbia*, colorful thorns and white or whitish variegation or white markings associated with

thorns also predominate. It was also proposed that multicolored spines have a specific value as they provide more possibilities that some will be visible to herbivores that are color blind to a certain sector of the spectrum. A white signal has a distinct advantage over a colorful one: color-blind animals can see it, and it is more visible to all under low illumination. Thus, vegetal aposematic coloration that communicates between plants and herbivores about being thorny has been proposed[34]. He showed that a very thorny annual rosette species of the Asteraceae in Israel have white markings that resemble a zebra. Such a unique and conspicuous appearance should have a function, which he tried to determine. The significant correlation between the conspicuousness of the white variegation and spinyness enabled the proposition that this is a special case of vegetal aposematic (warning) coloration that communicates between plants and herbivores about being spiny.

PLANTS THAT MIMIC OTHER PLANTS

Orchid shows double floral mimicry

Dactylorhiza sambucina is a non-rewarding orchid, which shows flower colour polymorphism. Natural populations are composed of different proportions of yellow and purple flowered individuals[69] rarely pink[70], which grow in mixed grasslands with different nectariferous species. While it has long been assumed that colour polymorphism is maintained by negative frequency-dependent selection produced by pollinators that over-visit the rare colour morph[71]. There is no field evidence to support this hypothesis[70,72], which indicates that other factors may influence the variable and often unbalanced morph ratio observed in natural populations[70,72].

For example, interactions with rewarding co-flowering plants may influence reproductive success of D. *sambucina*, nonetheless, they have not been thoroughly investigated previously. Moreover, while potential flower mimicry by *D. sambucina* morphs of a putative model species (*Mimulus guttatus*) has been identified[73]. Floral mimicry in *Dactylorhiza* was suggested by[74] who observed that the removal of pollinia from **D.** *lapponica* and *D. traunsteineri* is associated with the presence of large quantities of pollen on their stigmas from re-

warding co-flowering *Pedicularis sylvatica*. Recently, it was demonstrated that in *D. sambucina* there is floral mimicry of the rewarding, dimorphic, putative model species *M. guttatus*[73]. These authors recorded that inexperienced insects visit both rewardless morphs, but learned to avoid them after they gained experience of rewarding plants.

Agave species show weapon (thorn) automimicry

Several dozens of *Agave* species show spine automimicry. In Agave species the developing leaves are strongly pressed against one another. The teeth along the margins press against the surface of the same leaf or another leaf and the pattern of the teeth along the margins is copied and retained along the non-spiny parts of the leaves. In *Agave americana* L., a common ornamental in Israel, the teeth copies are seen in many leaves. The species showing the most remarkable teeth mimicry is A. *impressa*, in which the teeth mimicry is made of white material and is very conspicuous. However, in 2003, the specimens of A. impressa which was seen[27] in Israel were still young and thus smaller than the ones described in[75].

Additional *Agave* species with such teeth mimicry are *A.ferox, A.lophantha, A.macroacantha, A.marmorata, A.parryi, A.triangularis, A.utahensis and A.xylonacantha*[76]. The same type of colorful teeth along the margins and their mimicry by impression is obvious in the American palm *Washingtonia filifera* Wendl. (Palmaceae), a common ornamental and a feral tree in Israel and in *Aloe* sp (Liliaceae). Regular thorn mimicry Colorful thorn-like structures were found in several wild species growing in Israel.

PLANTS THAT MIMIC INANIMATE OBJECTS

Orchid flowers mimic aphid alarm pheromones

Hoverflies (Syrphidae) are important pollinators of flowering plants throughout the world[71] and, furthermore, some species are very efficient predators of aphids[78]. *Episyrphus balteatus* De Geer 1776 (Diptera, Syrphidae) is the most frequently encountered syrphid species at aphid-infested sites in temperate regions of the Northern Hemisphere[79]. While the larvae are aphidophagous (feed on aphids), adults feed on nectar and pollen from flowers[80]. Syrphid larvae are

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unable to disperse far[81] which makes female choice of oviposition site a crucial factor in offspring survival. Females of *E. balteatus* are able to locate plant and aphid species, discriminate between them and adjust their oviposition behaviour according to the performance of their larvae on different host species[82] and aphid colony size[83]. Furthermore, aphid honeydew and aphid alarm pheromone compounds (e.g. (E)-b-farnesene, a- and b-pinene) elicit oviposition in *E. balteatus* females[84,85]. Visual cues are important for the search for host plants and flowers, but do not trigger oviposition behavior[86]. The genus *Epipactis* (Orchidaceae) contains 25–59 species with a predominantly Eurasian distribution[87,88].

Epipactis veratrifolia Don. is exclusively pollinated by five species of aphidophagous hoverflies (Syrphidae), namely *Sphaerophoria ruepellii Wiedemann* 1830, *Sphaerophoria scripta* (L.1758), *Ischiodon aegyptus Wiedemann* 1830, *Eupeodes corolla* (F.1794) and *E. balteatus*. Flies of the genus *Paragus* also visit the flowers, but are too small to carry the pollinia and effectively pollinate the flowers. The flowers produce small amounts of nectar that is presented freely on the labellum. Flowers are not autogamous, and the natural pollination rate is about 15 per cent[89].

E. veratrifolia flowers produce the same compounds as are found in the alarm pheromone of some aphid species, e.g. *M. viciae*, namely aand b-pinene, and b-myrcene[90,91]. The flowers, therefore, appear to mimic the alarm pheromone of aphids, thus attracting hoverflies for pollination. Aphids not only release alarm pheromone when under attack, but continuously release small amounts[92]. Predators can thus use aphid pheromones as faithful cues for locating aphid colonies. Although (E)-bfarnesene is the most commonly used aphid alarm pheromone, several other terpenoids are produced by aphids and also function as alarm pheromones[90,91].

Male hoverflies are often found in the vicinity of the orchids. Males occupy a territory comprising a few plants, in which they try to copulate with females approaching the flowers. Males occasionally visit the flowers in search of nectar and thereby also pollinate them. Hoverfly females approach the flowers in hovering flight, land on the labellum, may lick the exposed nectar droplets and lay an egg on the labellum or in other parts of the flower. During nectar feeding and egg laying, they pollinate the flowers[89]. The fact that females lay eggs on the flowers of the orchid is very interesting as aphidophagous hoverflies normally lay their eggs exclusively in places where aphids are present, because the larvae feed on aphids[93]. Based on this fact and on the aphid-like dark warts in *E. veratrifolia* flowers, it was suggested that the flower mimics the shape and colour of aphids to attract syrphid flies for pollination [89]. However, as volatiles seem to play a key role in host location and oviposition behaviour of syrphid flies[92], which had been reasoned that the flowers would also have to mimic aphid volatiles if they were to achieve pollination by attracting female hoverflies searching for oviposition sites.

The European lady's slipper orchid

Deception in pollination by orchids was first reported by[94], who noticed that some of the species within the genus *Orchid* do not produce any nectar. Interestingly, he observed that those flowers were nonetheless visited by insects. Today, the occurrence of deception in the pollination of many plant species is widely accepted. While it is not limited to orchids[95-97], it occurs in the orchid family at rates unparalleled in any other plant family[98]. It is estimated that about one-third of all orchids deceive their pollinators[60]. However, in many individual species details of the mechanisms by which pollinators are deceived are still lacking. Many studies on the subject call for further research[99-101] and a multidisciplinary approach[102]. The European lady's slipper orchid (*Cypripedium calceolus L.*) is an example which illustrates this deficiency.

Despite the fact that C. calceolus has been studied for well over a century[103], and is native to Europe, its pollination is still poorly understood[104]. Flowers of *C. calceolus* are characterized by a large yellow pouch which is a modified labellum. The pouch has an opening on the top and its rim is covered by a slippery substance. Insects that land on the top of the labellum are very likely to slip inside the pouch where they are trapped. To free itself, an insect has to use one of the two orifices in the back of the pouch. During the laborious process of crawling out, the pollen mass is smeared on the dorsal side of the bodies of visitors with the correct size. The same insect has to fall into another *C. calceolus* flower to ensure pollination. A visitor that is too big has a chance of climbing out of the pouch with-

out touching any reproductive parts of the flower[105-107]. Insects, especially bees, can learn to avoid unrewarding flowers[102,108-111]. Therefore, the discussion on reproduction of *C. calceolus* is dominated by research aimed to discern all the cues that attract bees to the flowers. The discussion on possible attractants is still ongoing and is far from resolved.

Welch analyzed asymmetry of slipper orchid flowers and discovered that various *Cypripedium* species among which *C.calceolus* have tepals all coiling in the same direction[112, 113]. This makes the flowers asymmetrical. The coiling tepals might have a special function in insect deception by distorting floral symmetry. Bees have more difficulty memorizing asymmetrical flowers than symmetrical ones[114,115]. The coiled tepals of rewardless slipper orchid flowers might make it more difficult for bees to recognize and avoid these flowers during foraging. Nilsson brought attention to olfactory cues and suggested that undulating flight patterns of the bees approaching a slipper orchid flower resulted from chemical attraction[105]. The theory of a strong role of olfactory cues in this species gained wide acceptance[116,117]. Most of the olfactory studies so far focused on revealing the chemical composition of the floral fragrance of the European lady's slipper orchid[105,116,117], occasionally comparing it to chemical compounds known to be produced by insects[106]. Such an approach can provide valid information about the possible role of flower stimuli in attracting pollinators.

PLANTS THAT MIMIC FUNGI

Dracula orchid

Dracula is a genus of epiphytic orchid that produces flowers that look and smell like small mushrooms. Most of these orchids exhibit a peculiar morphology of the lip-like lowermost petal of the flower ("labellum") that resembles the reproductive surfaces of gilled ("agaric") mushrooms[118-123]. In some species, such as *Dracula felix*, the outermost portions of the flower (sepals) have a superficial resemblance to the caps and stalks of small mushrooms. Most *Dracula* flowers are produced at the end of long stems and are oriented towards the ground where mushrooms are most abundant[121]. Some of these orchids even produce scents reminiscent of fungi[118,123,124]. Chemical analysis of scents trapped from greenhouse-grown flowers of

Dracula chestertonii show they are dominated by the long-chain alcohol 1-octen-3-ol and other "typical *flavour* compounds of mushrooms"[123,124]. All of these floral traits are thought to function in *Dracula* for deceptive pollination by "fungus gnats" seeking places to lay their eggs[118,121], but the relative roles of the morphological and chemical cues in achieving pollinator visitation are not known. It is quite possible that these flowers combine imitations of multiple resources, such as places to take shelter during heavy rains or meeting places where potential mates can find each other[96].

Rationale: Why mimicry?

Ant mimicry

The hypothesis that visual ant mimicry, in the shape of dark dots and short stripes, occurs in flowers is not exclusive. Such coloration also serves the function of attracting pollinators and leading them to and within the flowers[53,125]. A dual purpose of flower characters for both pollination and defense has been suggested many times for various visual and chemical flower characters[28,126-128].

Batesian mimicry

In Batesian mimicry the mimic shares signals similar to the model, but does not have the attribute that makes it unprofitable to predators (e.g. unpalatability). In other words, a Batesian mimic is a sheep in wolf's clothing. It is named after Henry Walter Bates, an English naturalist whose work on butterflies in the Amazon rainforest (including Naturalist on the River Amazon s) was pioneering in this field of study[129,130]. Deceptive orchids that achieve pollination through the resemblance of their flowers to those of particular rewarding species have been termed Batesian mimics[12,102,131-133]. Mimics are less likely to be found out when in low proportion to their model, a phenomenon known as negative frequency dependent selection which applies in most other forms of mimicry as well. This is not the case in Müllerian mimicry.

Some authors, such as Little[134], have rejected this term on the grounds that Batesian mimicry in animals involves repulsion of predators[135], 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[136]. Batesian mimics often form part of

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pollination guilds involving several rewarding plant species that show convergent evolution to common pollinator(s)[131,137,138]. Dafni & Bernhardt[137] 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 'Mü llerian floral mimicry'[139,140], in reality Mü llerian 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[138,141].

Guild mimicry

Guild mimicry has been reported for the southern Australian genera *Diuris*[142] and *Thelymitra*[143], 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[133] or long-proboscid flies[138,144,145]. The convergence among guild members includes similarities in flowering time, spur or flower tube length, and flower colour[138,146].

Müllerian mimicry

Müllerian mimicry describes a situation where two or more species have very similar warning or aposematic signals and both share genuine anti-predation attributes (e.g. being unpalatable). At first Bates could not explain why this should be so; if both were harmful why did one need to mimic another? The German naturalist Fritz Muller put forward the first explanation for this phenomenon: If two species were confused with one another by a common predator, individuals in both would be more likely to survive[147,148]. Müllerian mimicry is common in aposematic animals but till recently, like other aspects of plant aposematism was almost unknown.

This type of mimicry is unique in several respects. Firstly, both the mimic and the model benefit from the interaction, which could thus be classified as mutualism in this respect. The signal receiver is also advantaged by this system, despite being deceived regarding species identity, as it avoids potentially harmful encounters. The usually clear identity of mimic and model are also blurred. In cases where one species is scarce and another abundant, the rare species can be said to be the mimic. When both are present in similar numbers however it is more realistic to speak of each as *comimics* than of a distinct 'mimic' and 'model' species, as their warning signals tend to converge toward something intermediate between the two[149].

Camouflage mimicry

Camouflage, in which a species resembles its surroundings, is essentially a form of visual mimicry.

Food-deceptive floral mimicry

Food-deceptive floral mimicry is associated with pollinators that use mainly colour, rather than scent, as their primary foraging cue[133,138,144,145]. Nevertheless, even bees can be deceived by mimics that match the flower colour of models, yet differ substantially in floral scent[150,151].

Defensive or Protective mimicry

Defensive or protective mimicry takes place when organisms are able to avoid encounters that would be harmful to them by deceiving enemies into treating them as something else. Cases discussed here entail mimicry of organisms protected by warning colouration. Batesian mimicry, where a harmless mimic poses as harmful; Müllerian mimicry, where two or more harmful species mutually advertise themselves as harmful; and Mertensian mimicry, where a deadly mimic resembles a less harmful but lesson-teaching model. The fourth case, Vavilovian mimicry, where weeds resemble crops, is important for several reasons; and humans are the agent of selection.

Many thorny, spiny and prickly plants are considered aposematic because their sharp defensive structures are colorful and conspicuous. Many of these spiny plant species (e.g., Cacti and *Agave* in North American deserts; *Aloe, Euphorbia* and acacias with white thorns in Africa; spiny plants in Ohio; and spiny members of the Asteraceae in the Mediterranean basin) have overlapping territories, and also similar patterns of conspicuous coloration, and suffer from the evolutionary pressure of grazing by the same large herbivores.

Müllerian mimicry was already proposed to exist in several defensive plant signaling systems. The first was for several spiny species with white-variegated leaves[28,36]. The second was for some tree species with red or yellow poisonous autumn leaves[29]. The third cases are of a mixture of Müllerian and Batesian mim-

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icry, of thorn automimicry found in many *Agave* species[27].

Attraction – Pollination

Epipactis veratrifolia does provide some nectar in its flowers (although very little) and might thus not be a truly deceptive species. On the other hand, the floral signal that attracts the pollinators advertises a different reward (aphids) than actually provided (nectar). Thus, *E.veratrifolia* has to be considered deceptive, at least in terms of pollinator attraction. A similar case has been found in the wasp-pollinated *Epipactis helleborine* and *Epipactis purpurata*, where the flowers mimic volatiles associated with the wasps' prey. But instead of the prey, the wasps get rewarded with nectar[152].

An important question that remains unanswered is the cost to the pollinators when they deposit eggs that cannot develop in the flowers. First-instar larvae of *E. balteatus* are limited in their dispersal[81]. If the larvae do not find a suitable host and consequently die, *E.veratrifolia* does harm its pollinators by reducing their fitness. Harming the pollinator is thought to be evolutionarily unstable and, therefore, very rare[153]. However, detailed data on the survival rate of hoverfly larvae on *E.veratrifolia* are needed to support this hypothesis.

Generalized food deception

Most orchids with deceptive pollination mechanisms exploit the innate food-foraging behaviour of pollinators[154,155]. 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[150,151]. Consequently, Little[134] termed this type as 'mimicry based on naïvete''. Dafni[156] 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[144], 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'[64] 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*[157], *Maxillaria*[157,158], certain species of *Eria*[159,160] and *Dendrobium*[161,162]. The bright yellow tufts of hairs on the lips attract pollen-foraging bees in *Arethusa bulbosa, Pogonia ophioglossoides, Calopogon tuberosus* and *Cephalanthera longifolia*[163-165]. Dummy anthers occur in *Caladenia*[166], Glossodia, *Elythranthera*, and *Eriochilus* species[137].

Imitation

Some flowers offer insects a floral tube in which to rest or sleep, as a hiding place during windy and rainy weather[167], or for thermoregulation, because the temperature in the flower tube may exceed the ambient temperature by up to 3°C during the morning hours[168,169]. In orchids, shelter imitation appears to be confined to the Mediterranean genus *Serapias*, whose extremely dark red-coloured flowers appear to mimic bee nest entrances[168]. Given that bees probably obtain real shelter in the flowers of Serapias[168], the characterization of this system as 'deceptive' is open to debate.

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. Roy & Widmer[12] and Schiestl[95] extended the concept of Batesian mimicry in plants to cover not only food-deceptive floral mimicry, 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[164] 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 behavior[170]. 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[171].

The behavior of the males landing on dark spots on the labellum suggests that the strong, musk-like scent

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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[172]. 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[172]. Orchid flowers that elicit 'pseudocopulation' by male insects possess not only sex-pheromone-like odours, but also visual and tactile cues[170]. The odour plays a key role in the long-range attraction of males to the flower[173-175].

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[176]. 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[177,178]. Sexual deception imposes strong specialisation in orchids as insect pheromones are generally highly species specific[179]. The specialization ranges from species that lure few pollinator taxa[175,179,180] to species pollinated exclusively by one pollinator[181,182].

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