Flowers interact simultaneously with a variety of insect visitors, including mutualistic pollinators and antagonists such as florivores, nectar robbers and pollinator predators. The plant epidermis produces a range of structures, such as conical or papillate cells, that can help mutualists to grip the flower, while a variety of other structures, such as slippery wax crystals on the flowers or on the stems leading to them, are able to deter non-beneficial insects or behaviors.

Modification of the floral surface can also aid pollination in unusual ways in some highly specialized interactions. In the case of the trap-flowers in species of Arisaema, conical cells aid pollination by being present on the spathe surface, but here they are modified in such a way as to decrease the pollinating insect’s grip. We discuss a variety of these floral structural features that influence insect stability on the plant.

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Structural Modifications of Flower Stems that Deter Nectar Thieves

The pollination relationship between plants and insects is not always simply mutually beneficial. Both sides on occasion cheat, and some plants have modified surface morphology that minimises the consequences of this. One example of insect cheating is robbing of nectar without providing a pollination service. Many plants have defensive structures that limit access to the flowers for potential nectar thieves. As a result of their near-ubiquitous occurrence in most habitats, ants show a range of interactions with plants. While

increases foraging efficiency. However, conical petal cells are found more frequently than initial floral angle would suggest—many flowers that are simple to handle and are held at flat or shallow angles also have conical epidermal cells. While floral color, wettability and temperature, which are also affected by the presence of conical cells, could be more important in these particular flowers than in Antirrhinum, it is also possible that other pollinator slip factors, such as wind; the landing of the pollinator, leading to bending and shaking of the flower; or decreased traction due to rain may cause the increased grip provided by conical cells to be advantageous to many flowers. We suggest that this 'grip' function of floral epidermal cells will be important for a wide range of insect pollinators. While it is evident why pollinators such as bumblebees, which have relatively small tarsal adhesive pads for their size, should rely on grip by their interlocking claws, other flower visitors with relatively larger tarsal adhesive structures such as flies and honeybees should not have a significant problem with smooth flowers. However, contamination of the tarsae by pollen grains might inhibit their adhesive function, so that interlocking by claws becomes more important.

**Figure 1.** (A) *Salvia candelabra* petal conical cells. (B) *Foeniculum vulgare* stem showing slippery wax deposition. (C) *Arisaema jacquemontii* epidermal cells from inside the spathe, pointing downwards and preventing insects climbing out. Scale bar = 100 μm.
there is evidence that some plant species are ant-pollinated, most are pollinated by flying insects, and for these species ants behave primarily as nectar thieves. This can be detrimental to plant fitness in several ways. Nectar-robbing reduces the amount of reward a plant has available for genuine pollinators, potentially resulting in fewer pollinator visits and reduced reproductive output. Ants can also damage flowers or reduce pollen fertility, and have been shown to reduce the rate of visits from flying insects, either by attacking their pollinators or just by their presence. Plants have developed a range of mechanical defences against nectar-robbing ants. Plumbago auriculata, for example, has glandular trichomes on the calyx which exude a sticky substance, acting as a barrier against crawling insects. This means that ants do not have access to the interior of the flower, while flying insects do. The epidermis can also be modified to deter ants. While structures on the petal epidermis positively aid the grip of insect feet, the stem leading to the flowers does the opposite in many species. One example is displayed by Salvia candela. While the petal epidermis produces conical cells (Fig. 1A), which will provide grip for flying insect pollinators, the top of the stem leading to the flower is covered by epicuticular wax crystals (see Fig. 1B). Flower stems covered by wax crystals are found in many different plant families. This wax crystal bloom makes gripping the flower stem difficult for insects such as ants that might rob flowers. Wax particles can also break off and clog the tarsal adhesive structures, further decreasing insect grip. As the waxy surfaces are mostly restricted to the stems, many of the other proposed functions of epicuticular wax crystals (protection against excessive radiation, reduction of transpiration, inhibition of pathogen attachment and self-cleaning ability) are implausible here, suggesting that waxy stems have evolved primarily as climbing barriers against nectar-robbing ants.

Modification of the Epidermis in Trap-Flowers

Cheating is not restricted to animals, but is also practiced by plants. For example, some plants cheat by advertising non-existent rewards, or by trapping and even sometimes killing their pollinators. The genus Arisaema produces kettle-trap inflorescences (consisting of a unisexual inflorescence surrounded by a cup-like spathe) which cheat in this way. While male inflorescences trap and then release the fungus gnats attracted by the strong floral volatiles, female inflorescences trap but do not release the gnats. Having provided a pollination service, the gnats die within the female inflorescence. As with more conventionally pollinated flowers, Arisaema has modified epidermal structures that aid pollination. Analysis of the surface structures of the spathe by scanning electron microscopy (SEM) showed that all of the species studied produced a wax crystal bloom similar to those found on the stem of Salvia candela. While the spathe of most Arisaema species had flat, smooth epidermal cells, two species (A. utile and A. jacquemontii) produce modified conical cells that point straight down into the kettle-trap (Fig. 1C). Similar cells have been found in some carnivorous pitfall traps such as Nepenthes, Darlingtonia, Sarracenia and Cephalotus, and it has been hypothesized that these overlapping downward pointing ‘tooth’ cells might make the slide of the insect into the trap very easy, but could then block any escape upwards. Vogel and Martins suggest that the presence of these cells is a trait that aids in insect capture, as downward-pointing conical cells are also found in kettle traps of the related genus Arum, which capture more ‘alert’ insects than fungus gnats. The presence of trapped insects may also provide an incentive for more predatory insects to enter the trap, potentially damaging the flower in the process. For example, in the genus Ceratopteris, which also produces trap flowers, evidence has been found that ants prey on the trapped pollinators. Modification of the epidermis appears to prevent this in Arisaema, where a thick layer of epicuticular wax is observed around the outside of the base of the inflorescence below the spathe (Whitney H.M., personal observation). Flowers therefore appear to produce a range of epidermal structures within and around an inflorescence that either optimize pollination or discourage damaging non-pollinating visitors.

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