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My favourite flowering image

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Abstract

Choosing a favourite image is very difficult to do, not least because different images are important to us for different reasons. I have decided to focus here on an image that is not only intrinsically beautiful, but that also emphasizes the importance of looking and seeing properly when trying to understand the world around us. For me, this image, the adaxial surface of the petal of Veronica caucasia, exemplifies how looking at things in different ways can provide unexpected insights into the way nature works.

Key words: Cell morphology, epidermis, iridescence, petal, pollination.

The image I have chosen is a scanning electron micrograph (SEM) I took a few years ago of the adaxial surface of the petal of Veronica caucasia (Fig. 1). It was part of a survey of petal cell morphology among relatives of Antirrhinum. The cells in the image are conical-papillate (or just 'conical') in shape, like those of Antirrhinum. Fifteen years ago, looking at Antirrhinum flowers in a novel way showed us that this cell morphology has a significant effect on flower colour. The mixta mutant of Antirrhinum was selected for study in Cathie Martin's laboratory at the John Innes Centre because its petals were paler in colour than those of wild-type flowers, a phenotype that you might expect to be attributable to a change in pigment content. However, looking at the flowers on the SEM (and therefore, ironically, in monochrome) showed us that the colour difference was due to a change in petal cell shape, with the mixta mutant petals lacking the conical form of wild-type petal epidermal cells (Noda et al., 1994). The colour difference is a trick of the light, caused by increased focusing of light into the pigmented vacuoles of conical cells, compared with flat ones, and thus more absorption of light by the same amount of pigment (Gorton and Vogelmann, 1996). But it took the step of looking at the petals in a different way (under the SEM) to make this link.

Over the last 15 years much of my research has focused on understanding the adaptive significance of the conical cell form. Having discovered the visible effect of these cells on flower colour by looking at the flowers in a different way, I have also had to learn to look at floral morphology in an entirely new way, to understand the role of the cells. Just because a colour difference between two flowers is perceptible to the human eye, it may not be to the insect pollinator of the flower. The compound eyes of insects have different photoreceptors to the simple eyes of mammals, and see colours very differently as a result (Giurfa and Nunez, 1989; Chittka et al., 1994). But even if a colour difference between two flowers is visible to a pollinator, it may be of no significance whatsoever, unless either it makes the flower visible from a greater distance or is a cue that can be learned in association with a particular reward.

A very fruitful collaboration with bee vision and cognition expert Lars Chittka, at Queen Mary University London, has helped me to look at petal conical cells in a whole new light to solve this problem. Through a number of experiments investigating the responses of both wild and caged bumblebees to mixta mutant and wild-type Antirrhinum flowers, it has been possible to show that conical cells do make flowers more attractive to pollinators (Glover and Martin, 1998; Comba et al., 2000), that the colour difference that we perceive between conical-celled Antirrhinum flowers and the flat-celled mixta mutant is visible to bees (Dyer et al., 2007), but that those bees have no intrinsic preference for one colour over the other and that neither colour increases flower visibility at any particular distance (Dyer et al., 2006, 2007). It turns out that the colour difference which first showed us what conical cells can do to a flower is both visible to and learnable by pollinators, but is actually of no real interest to them.

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However, although the difference in colour is of no intrinsic interest to bees, because it can be learned it can be treated as a cue if it is usually associated with a real reward. There is plenty of evidence that pollinators, including bees, can learn to link particular colours with things like ease of handling or increased reward. For instance, Waser and Price (1983) showed that the white form of *Delphinium nelsonii* was less popular with hummingbird and bee pollinators than the blue form, not because the animals had any intrinsic preference for blue but because the white nectar guides were invisible on a white background, which meant that it took the animals longer to find the nectar in a white flower. We are currently exploring a number of options for how conical cells could provide a reward, including the ideas that they make the flower easier to grip and so improve handling efficiency, or that they increase intrafloral temperature, perhaps affecting nectar secretion or concentration, or even perhaps providing a direct metabolic reward in cold weather conditions. These different possibilities might all apply to different flowers in different habitats, and might explain the prevalence of conical cells in the petals of flowering plants.

If we look again at the image of the petal epidermal cells, we can see that there is another interesting aspect of petal cell morphology here, that we have ignored so far. It is too easy to focus on the obvious gross morphology of the cells, and not to properly observe that they are covered with a star-shaped pattern of cuticular ridges or striations. This detailed surface structure is again highly variable among flowering plants: some have smooth petal epidermal cells, some have cells with star-shaped cuticular patterns, some have apparently random patterns of cuticle distribution, and others have long narrow lines of cuticular striations. So do these different patterns have different functions, and if so, what are they?

It turns out that the cuticular striations, if arranged in a sufficiently ordered way in long lines, can have exactly the same effect as the long lines of ridges and troughs in a compact disc (CD)—they can generate iridescence. Iridescence is the phenomenon of a surface appearing as different colours when viewed from different angles. It is a form of structural colour—that is, it can only be produced through specialized structures which reflect particular wavelengths of light. Chemical pigments cannot generate iridescence. The ordered cuticular striations on a tulip petal (and on the petals of many other species) have similar amplitude and frequency to those of a CD, and, allowing for the not entirely flat surface of a petal compared to a CD, generate measurably very similar iridescence (Whitney et al., 2009). This iridescence is more easily visible to the human eye if the surface structure of the petal is replicated in colourless epoxy, without the confusing signal of the petal pigment beneath. These replica surfaces can be studied optically, and the iridescence described in detail.

Ironically, these optical studies have shown us why we hadn’t really noticed the iridescence on the real flowers—because it is primarily in the ultraviolet part of the spectrum. Of course, the human eye cannot detect ultraviolet, so the vast majority of petal iridescence is invisible to us. But to a pollinating insect it should be a very strong signal indeed. This was tested by training caged bumblebees to associate a reward with an iridescent epoxy disc (cast either from a CD or from a tulip adaxial petal surface), and to associate a punishment (bitter-tasting quinine solution) with a non-iridescent disc, even though both types of discs had one of a range of pigment colours incorporated. The bees were easily able to disentangle the ‘changeable’ cue of iridescence from the static cues of colour, and could clearly see the iridescence without any difficulties (Whitney et al., 2009).

So the surface detail on petal epidermal cells can also play a very significant role in final flower appearance, by interfering with light reflection and generating structural colour. Of course, the ability of the surface structure to do this depends on how ordered it is. The star-shaped pattern of the cuticle on the *Veronica caucasia* petal cannot generate iridescence because the ridges are not separated by gaps of the right size. However, they will certainly have some influence on the behaviour of light, if only to act as a scattering mechanism to evenly distribute all wavelengths leaving the petal surface.

Further optical analysis of the behaviour of light leaving different petal surfaces will help us to work out how petal microsculpturing of various sorts affects the way flowers look, not only to us but to the insects that pollinate them.

So this particular flowering image is important to me because it has taught me to look at both the bigger picture and the fine detail, to look in colour and in monochrome, and to look with my eyes, but also with the eyes of the primary target of the flower—the insects that pollinate it. Of course, it is also a very pretty picture, which is another good reason to count it as my favourite flowering image!

References


