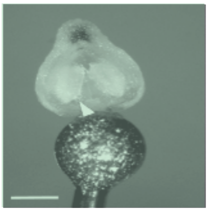
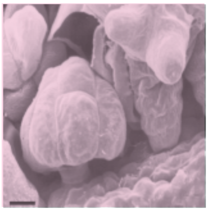
# Content*Select*

John Bryant takes a closer look at some of this month's Original Articles



## Retention of cap promotes safer sex

Readers will be familiar with genetic mechanisms that impose self-incompatibility in many flowering plants. However, despite these and the disadvantages of self-pollination, including inbreeding depression, many plants are actually self-fertile. Investigation of such species reveals the presence of a range of mechanisms that increase the likelihood of outbreeding. **Peter and Johnson (University of Natal, South Africa, pp. 345–355)** point out that, in orchids, the total complement of pollen-packed pollinia can be removed in one visit. Consequently, the total pollen load could be shot in a single inbreeding event. The authors suggest that the rewardless flowers of many orchids deter repeat visits to the same inflorescence; further, in many species, the initial orientation of the pollinia prevents pollination. Only after a long interval, by which time the pollinator is likely to be visiting another inflorescence, does the orientation of the pollinia become suitable for presentation to the stigma. However, study of *Eulophia foliosa* has revealed a very unusual mechanism previously described in only a handful of species. Like many other orchids, *E. foliosa* exhibits deceit pollination. The click-beetle *Cardiophorus obliquemaculatus* is a relatively slow-moving pollinator, staying on an inflorescence for approximately five minutes on average. However, the pollinia removed by the beetles are very unlikely to pollinate another flower in the inflorescence because the exit of pollen is prevented by retention of the anther cap on each pollinium. Typically, this remains attached for about eight and a half minutes; by then the beetle is likely to be on a different inflorescence. The detachment of the anther cap occurs by dehydration and cell shrinkage causing breakage along a defined abscission layer. Thus, anther caps are retained longer under humid conditions. The corollary of this is that there is a greater probability of self-pollination under very dry conditions.



## Do they make sugar?

If a plant lacking a conventional nectary nevertheless produces nectar it is reasonable to ask where the nectar comes from. It is this question that has motivated the research of **Machado *et al*. (Botucatu, Brazil, pp. 357–369)**. The plant in question is *Zeyheria montana*, a member of the Bignoniaceae that grows in the tropical savanna of Brazil. The pollinators are humming birds, attracted to the flowers by copious quantities of nectar. However, *Z. montana* has only a rudimentary, non-functional nectariferous disk round the base of the ovary. It had been suggested previously by this research group that nectar is produced from glandular trichomes also located around the base of the ovary. However, according to the old proverb, the proof of the pudding is in the eating (or, for the humming birds, the drinking). What actually do these trichomes secrete? The authors have shown that the trichomes are present from an early stage in floral development, certainly long before nectar is secreted. Further, new trichomes are initiated through flowering and into fruit set so that trichomes at different stages of development are present at the same time. The timing of secretion from the trichomes is also significant, again occurring from flower-bud stage into fruiting. This is not a pattern expected of nectariferous organs and, indeed, chemical analysis indicates strongly that these glandular trichomes are not substitute nectaries. The majority of the secreted substances are terpenoids, accompanied by alkaloids, while sugars are undetectable. Consistent with this, the authors observe the accumulation of lipophilic substances initially in plastids (the site for terpenoid synthesis) and then movement from the plastids via the endomembrane system to the secretions. The authors thus reject their earlier views of the function of these trichomes and suggest that rather than functioning as nectaries, they are involved in defence of the flower and young fruit.

**Getting a buzz from outbreeding**

For the second time this month I am discussing mechanisms that prevent inbreeding in self-fertile species. The species in question here is *Paraboea rufescens*, a tropical Chinese member of the Gesneriaceae and studied by **Jaing-Yun Gao *et al*. (Yunnan, PR China, pp. 371–376)**. The plant shows two fascinating floral characters. First, it is one of those species that possess mirror-image flowers (i.e. are enantiostylic); in this species the two forms (left-styled, anthers deflected to the right; right-styled, anthers deflected to the left) are borne within the same inflorescence. Secondly, it is buzz-pollinated: the visiting bumblebees rapidly vibrate their indirect flight muscles to induce pollen release from the tip of the anther. The authors have carried out a detailed study of flower morphology and pollination in this species. They showed first that pollination by hand was much more efficient than open-pollination, possibly suggesting sub-optimal numbers of pollinators. However, open-pollinated flowers, although yielding fewer fruit per inflorescence, produced more seeds per fruit. Whether this is related to resource allocation is not clear. Secondly, they confirmed that *P. rufescens* is self-fertile but that autonomous self-fertilization in the absence of pollinators does not occur. When flowers were self-pollinated by hand, there was clear evidence of inbreeding depression in respect of the number of seeds set. Outbreeding is therefore advantageous to this species. The relative positions of anthers and style within an individual flower actually make self-pollination within one flower very unlikely. Indeed, if the pollinator visits another flower of the same enantiomorph, pollen transfer remains very unlikely because pollen is present only on one side of the bee, the side away from the style. However, inbreeding is not completely eliminated in *P. rufescens* because both flower enantiomorphs are present in the same inflorescence. Because of the geometry, a bee moving from one enantiomorph to another may well effect a self-pollination.

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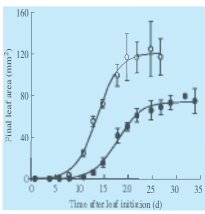


**Shining the light on shade responses in arabidopsis**

One of the current buzz-words in biology is 'systems'. Behind this term lies an approach that many of us have espoused for a long time. We may study molecular or cellular aspects of biology in isolation but there must be a realization that these events are integrated into regulatory and developmental networks that contribute to the life of the whole organism. This is nicely illustrated by the work of **Cookson and Granier (Montpellier, France, pp. 443–452)** on the development of rosette leaves in *Arabidopsis thaliana* (ecotype Landsberg *erecta*). Seedlings were kept in either fully lighted or shaded conditions with all other conditions being identical. The authors then compared the initiation, growth and development of the rosette leaves and the time to bolting under the two conditions. The effects of the shading were seen at several levels. First, leaves were initiated less frequently in shaded than in well-lit plants, an effect that goes right back to the dynamics of the apical meristem. Secondly, the phase of rosette leaf initiation was shorter and this was associated with the timing of the floral transition in the apical meristem, which occurred 3 days earlier in shaded than in fully illuminated plants. Further, those rosette leaves that were formed in shaded plants had significantly less area than those of the fully illuminated plants. This was caused by a reduction in the rates of both cell division and cell expansion, which were only partly compensated for by increases in duration of both these phases. These effects on rosette leaf number and on the area of individual rosette leaves also dramatically reduced carbon gain via photosynthesis, the absolute of rate of which was already reduced by the shade treatment. One wonders how much this factor contributed to the signalling network in this set of responses.

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