EVO–DEVO

How the butterfly got its spots

The eyespots that decorate certain butterfly wings are a recently evolved adaptation to deter predators. Their function is clear, but understanding how they got there — both developmentally and evolutionarily — is a trickier matter. Now, Craig Brunetti and colleagues have found three genes that are turned on in the concentric domains that correspond to the future coloured rings of *Bicyclus anynana* eyespots. Their findings indicate how these genes might contribute to pattern formation and to the spectacular variation in eyespot colour schemes of other butterfly species.

To understand how an eyespot is patterned, Brunetti *et al.* looked for proteins that are present at the right place and at the right time in the developing pupal wing of *B. anynana*. Those that were — encoded by the conserved *distal-less* (*Dll*), *engrailed/invected* (*en/inv*) and *spalt* (*sal*) genes — had very telling expression profiles. All three genes are expressed early on in the centre of the eyespot field; however, a ring of *sal* expression quickly surrounds the central focus, which, in turn, is soon enveloped by an outer ring of *en/inv* expression. What makes this pattern interesting is that the three rings correspond to the three coloured rings of the adult eyespot of *B. anynana*, which comprises a central white spot surrounded by a black then a golden ring (see picture). Looking at a spontaneous mutant, *Goldeneye*, helped to define the relationship between the genes. In *Goldeneye*, the golden ring has expanded into the territory normally occupied by the black ring, which is almost lost. As expected, the expression of *en/inv* in the developing *Goldeneye* eyespot is increased at the expense of *sal*, indicating that the two genes normally antagonize each other's expression.

That the three genes are expressed in other butterfly species with differently patterned eyespots reinforces, and broadens, the model that Dll, En/Inv and Sal operate alone or in a combinatorial manner to determine eyespot rings. Indeed, although the genes can have different spatial distributions in other species, their expression correlates with specific eyespot colour schemes.

The authors propose that Dll, En/Inv and Sal define an intermediate, regulatory step between the morphogenetic signal emanating from the focus of the developing eyespot and the pigmentation genes themselves. Their study shows that the two tiers of information — the regulatory and the pigmentation genes — are very plastic and can evolve independently, so that *en/inv* expression alone can specify gold, black or orange scales, depending on the species. Refining the model will require understanding whether the spatial distribution of regulatory genes depends on threshold responses to the morphogen, on cross-regulatory interactions between genes, or indeed on both, depending on the species.

Tanita Casci

References and links

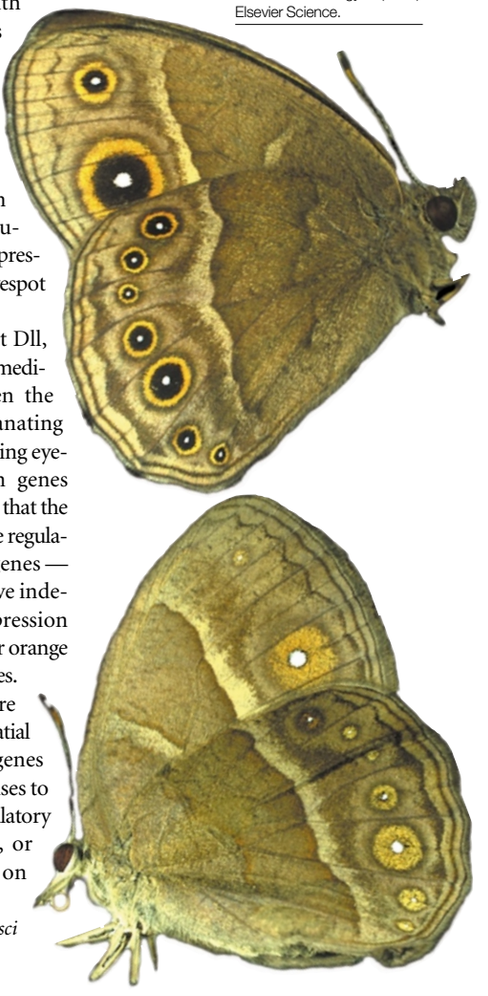
ORIGINAL RESEARCH PAPER Brunetti, C. R. *et al.* The generation and diversification of butterfly eyespot color patterns. *Curr. Biol.* **11**, 1578–1585 (2001)

WEB SITES

Paul Brakefield's lab: http://www.helsinki.fi/science/fragland/ldn_idx.html

Sean Carroll's lab: http://www.molbio.wisc.edu/carroll/

Vernon French's lab: http://helios.bto.ed.ac.uk/icapb/people/v_french.html



The butterfly *Bicyclus anynana*. Wild type, top; *Goldeneye* mutant, bottom. Courtesy of Paul Brakefield, University of Leiden, The Netherlands, and Craig Brunetti, University of Wisconsin–Madison, USA. Reproduced with permission from Brunetti *et al*. *Current Biology* © (2001) Elsevier Science.