

disks — sacs of embryonic epithelium. An imaginal leg disk cultured in 20-hydroxyecdysone produces an adult leg in 18 hours (J. Fristrom, University of California at Berkeley): this does not involve cell proliferation, merely elongation of individual cells driven by ecdysone-dependent contraction of an actin-myosin ring. The actin and myosin genes are not directly affected by ecdysone; the hormonal effects are mediated by genes of the Broad-Complex.

The action of ecdysone and TH are countered by juvenile hormone (JH) and prolactin respectively, the balance of the two hormonal systems being important in determining the timing of the onset of metamorphosis. For instance, JH regulates the synthesis of the cuticle proteins in the moth *Manduca sexta* (L. Riddiford, University of Washington, Seattle). It has no effect on the ecdysteroid-induced expression of genes required for new cuticle at moults associated with growth but prevents activation of genes specific for the transition to pupa or adult. The effects of 20-hydroxyecdysone on the cuticular protein genes are indirect. A possible mediator of the ecdysteroid induction is MHR3, an orphan steroid receptor, which may regulate stage-specific cuticular protein genes but has no effect on at least one of the genes for enzymes required for cuticular sclerotization after ecdysis. A putative JH receptor has been identified, but JH action remains a grey area.

In *Xenopus*, prolactin abolishes transcription of both early and late genes, those for the TH receptor and for keratin and albumin. It also has growth-promoting and osmoregulatory effects, implantation of pellets impregnated with prolactin in the larval spleen (from which blood drains to the liver) resulting in marked tail growth in *R. catesbeiana* (C. Nicholl, University of California at Berkeley). The hepatic factor that synergizes with prolactin, named synlactin, has not yet been purified. Insulin-like growth factor (IGF-I) can mimic synlactin in one biological assay, but it has not been found in frog serum (although an IGF-binding protein has).

So where does that leave us? The genes that respond to hormonal signals are being identified and the tissue-specific responses can be explained in terms of expression of hormone receptor isoforms and the requisite transcription factors. But the differences between the processes of metamorphosis in insects and vertebrates suggest that similar events are not mediated by homologous gene products. Kafka might not have been surprised. □

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Sorting out natural stone stripes



MUNDANE geomorphic processes have an uncanny ability to create remarkable patterns in the world around us. Bedforms such as ripples or dunes formed under flowing air or water, beach cusps, evenly spaced rills on hillsides, and meanders in rivers are just a few examples. On page 142 of this issue, B. T. Werner and B. Hallet use computer cellular automata to model the development of sorted stripes of stones, shown above from near the summit of Mauna Kea, Hawaii. Along with sorted circles, these are among the most striking patterns in arctic and alpine landscapes. In none of these cases is there an external template to impose the pattern, which instead must be entirely self-organized, bringing investigation of them into an arena of more general interest in physics and chemistry.

In the past, perturbation methods have been applied to such studies to find the fastest-growing perturbation. But the fastest-growing initial perturbation is not always equivalent to the final wavelength, because the pattern becomes strong enough for local finite-amplitude effects to dominate the physics. As many interesting geomorphic problems involve the rearrangement of individual grains and are the result of independent motions modulated only by local conditions, others have turned to cellular-automaton techniques. In these, the complex physics is boiled down to a simple set of rules that is applied to every grain in the system. Individual grains, represented by pixels on the screen and perhaps coloured to represent different grain sizes, are moved from one position to another according to these rules. The power of the technique is that subtly different rules may be easily tested to reveal the relative importance of one or another feedback in creating the patterns.

The sorted stripes that Werner and Hallet investigate form on unvegetated arctic and alpine hill slopes subject to

periodic freezing. Under these circumstances, stones larger than several millimetres become separated from the frost-susceptible fine-grained domains to create a pattern of stone stripes aligned up- and downslope. On lower slopes, the same physics apparently creates sorted nets. Hallet brings to bear considerable experience in both theory and observation of periglacial phenomena, while Werner has helped to pioneer the application of cellular-automata and grain-dynamics techniques to geomorphology. The process they finger as the cause of sorted stripes is ice needling, wherein tiny pillars of ice, sometimes several centimetres long, form beneath the surface grains on cold, clear nights. When the needles thaw, the grains are lowered back to new positions on the surface, typically downslope.

Several feedbacks operate in the growth of the stone stripes. Most important is the differential frost heave in fine- and coarse-grained domains. Ice needling transports the coarser grains — the stones — on average perpendicular to the local contour, expelling them from the fine-grained domains. But the coarser domains are less susceptible to heaving, so that ice needling is less likely to drive the stones back. Subtle perturbations in an otherwise random walk therefore lead to this strikingly regular textural pattern. In the absence of a mean slope, the simulations produce sorted nets, passing yet another test against the natural landscape. The authors not only match the statistics of the stripe spacing, they also point to new measurements that may pinpoint the physics more tightly; downslope motion of grains should be faster within the fine domains, for example.

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