From Cinderella's dilemma to rock slides

Jay Fineberg

A mixture of two different types of grain can undergo spontaneous stratification simply by being poured. This surprising behaviour may be significant in fields from pharmaceuticals to geology.

When Cinderella's (or Ashiepattle's, according to the brothers Grimm) wicked stepsisters threw her lentils into the ashes of her cooking fire, salvation came in the form of the friendly birds who helped her to sort them. But had she read the report by Makse *et al.* on page 379 of this issue[1], she might have come to a different solution to the problem of how one can go about separating two different species of intermixed granular materials. The answer may be as easy as pouring the mixture into a box. In the reported experiments, both the stratification and segregation of a mixture of two types of grain is observed to occur spontaneously as the mixture is poured into a narrow box.

Granular media show a rich variety of surprising, and at times counter-intuitive, phenomena[2,3]. One might think, for example, that externally shaking or rotating a system composed of different types of particles would tend to induce disorder or randomize its components. In granular media the opposite occurs, as the vibration[4] or rotation[5] of two types of randomly mixed grain will cause them to segregate and thus *increase* the system's order.

A granular species can be described by the size and frictional characteristics (geometry, roughness and molecular attraction) of the grains composing it. The frictional characteristics can be characterized by the medium's 'angle of repose', the minimum slope for which gravitationally induced flow (or grain motion) can occur. Makse *et al.* prepare a random mixture of two different grain types and simply pour them into one side of a narrow container. As the slope of the 'sandpile' formed steepens, the mixture will flow.

When the angle of repose of the grains having a larger characteristic size is greater than that of the smaller component, the flow causes spontaneous stratification of the medium to occur, and alternating layers composed of large and small particles are formed, with the smaller and 'smoother' (lower angle of repose) grains found below the larger and 'rougher' grains (Fig. 1). The authors also find that within the layers, size segregation of the grains occurs, with smaller grains tending to be nearer the top of the pile. When the medium is chosen so that the larger grains are the 'smoother' of the two, there is no layering, and only segregation is observed.

The appearance of spontaneous grain stratification may have important implications in both industrial and geological processes. Many industries depend on the processing and transport of granular materials. In light of this work, the assumption that, on transport, an initially well-mixed compound will remain well mixed, may need to be re-examined. The potential ramifications of stratification by means of flow may be especially important in certain applications in the pharmaceutical industry where the precise concentration of the components of a given mixture may be crucial.

The same process may also play a part in unravelling the long-standing geological puzzle of long-runout rock slides. Long-runout rock slides result from a catastrophic event such as an earthquake, explosion or meteor impact that releases a large rock mass down a mountain slope. As the name implies, the resulting landslide has the

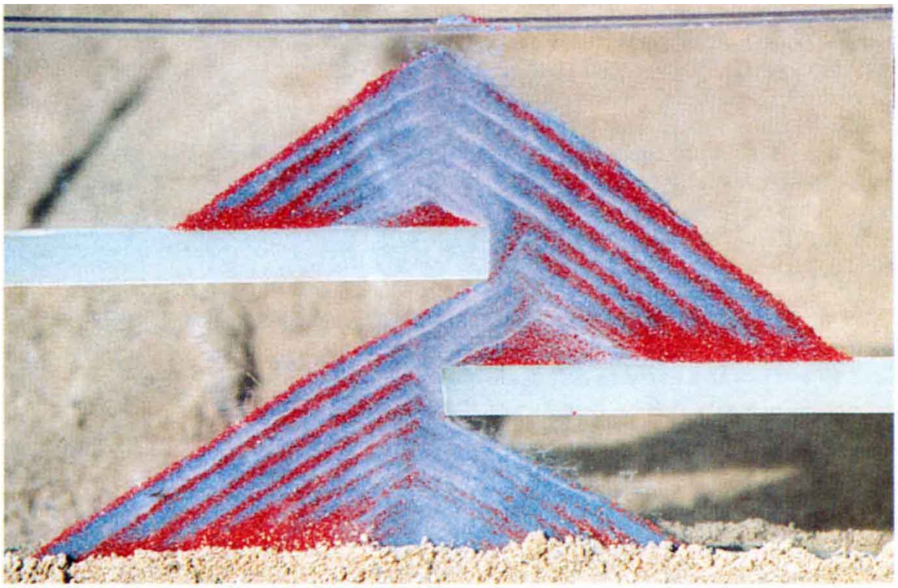

Figure 1 **Spontaneous strata. Layers formed by a mixture of two types of grain, poured into a narrow container.**

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Figure 2 **The long-runout rock slide that wiped out the town of Frank in Alberta, Canada, in 1903. After an initial one-kilometre fall, the slide travelled more than four kilometres across the valley below, and was finally stopped by the opposite slope. (Photo: National Geophysical Data Center, Boulder, CO; prepared by Allen M. Hittelman, Patricia A. Lockridge and Patrick J. Hayes.)**

curious property that it does not stop at the bottom of the slope that drives it, but continues to slide over huge distances until arrested. Events of this nature are not uncommon, and have been known to destroy entire towns that happened to lie in their path[6] (Fig. 2). These huge rock slides are characterized by abnormally low effective friction coefficients (defined here as the ratio of the initial fall height to the runout length), on the order of 0.1.

The origin of this low effective friction has been the subject of much speculation. Proffered explanations include an effective 'air bearing' formed by the air trapped beneath the rock mass[7] and the 'acoustic fluidization' of a narrow zone beneath the rock layer by high intensity sound generated by the rock slide[8]. Recent simulations[9] based on a granular model using an ensemble of smooth monodisperse disks qualitatively agree with observed flows, but many issues remain outstanding.

How, for example, can a rock slide that obviously consists of an ensemble of particles of diverse sizes and degrees of roughness be mimicked by such a simple model? An explanation may be provided by the observations of Makse *et al.* Their results suggest that the spontaneous stratification of large and small particles, with the selection of smooth smaller particles at the bottom of a given layer, may provide an overall lubrication effect, as the best 'ball-bearings' are preferentially shifted to the bottom of the pile. In cases where acoustic fluidization occurs, this effect would tend to increase the fluidization of the medium.

As in the above example of long-runout rock slides, understanding the properties of granular materials is important. Although the subject of much active research, no underlying fundamental theoretical description of these materials yet exists. Experimental observations, such as those described by Makse *et al.*, help to provide the foundation upon which a theory for the rheology of granular materials can be based. ☐

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1. Makse, H. A., Havlin, S., King, P. R. & Stanley, H. E. *Nature* **386,** 379–382 (1997).
2. Jaeger, H. M. & Nagel, S. R. *Science* **255,** 1523–1531 (1992).
3. Jaeger, H. M., Nagel, S. R. & Behringer, R. P. *Rev. Mod. Phys.* **68,** 1259–1273 (1996).
4. Knight, J. B., Jaeger, H. M. & Nagel, S. R. *Phys. Rev. Lett.* **70,** 3728–3731 (1993).
5. Zik, O., Levine, D., Shtrikman, S. G. & Stavans, J. *Phys. Rev. Lett.* **73,** 644–647 (1994).
6. McConnel, R. G. & Brock, R. W. *Can. Dept Inter. Annu. Rep. 1902–1903* pt 8 (Rept Supt. Mines, Appendix, 1904).
7. Shreve, R. L. *Science* **154,** 1639–1643 (1966).
8. Melosh, H. J. *Nature* **379,** 601–606 (1996); *Am. Sci.* **71,** 158–165 (1983).
9. Campbell, C. S., Cleary P. W. & Hopkins, M. *J. Geophys. Res.* **100,** 8267–8310 (1995).

Developmental biology

Chick limbs, fly wings and homology at the fringe

Stephen J. Gaunt

It was from a school textbook[1] that I first understood how the limbs of different vertebrates are assumed — on the basis of their shared pentadactyl anatomy — to be derived from a common ancestral structure. All vertebrate limbs are therefore classed as being homologous. With regard to the wings of birds and insects, the textbook was clear: "the wings of a bird and those of an insect serve the same function, but they cannot possibly be said to have originated in the same way, nor is their structure in any way comparable". For this reason, bird and insect wings are said to be analogous, but new studies reported by Rodriguez-Esteban *et al.*[2] on page 360 of this issue and Laufer *et al.*[3] on page 366, now lead me to think again.

The new papers report that molecular mechanisms for the formation and growth of the *Drosophila* dorsoventral wing margin are conserved — at least in part — at the margin of the vertebrate (chick) limb. In both of these structures, the dorsoventral boundary forms at the junction of the dorsal cells, which produce a protein called fringe, and the ventral cells, which do not. Fringe protein is encoded by the *fringe* (*fng*) gene in *Drosophila*, and the *radical fringe* (*r-fng*) gene in vertebrates. In the case of the vertebrate limb, the *r-fng* expression boundary (generated as described in Fig. 1) results in the development of the apical ectodermal ridge (Fig. 2), which produces signals that are essential to maintain growth at the distal tip of the developing limb.

From work on *Drosophila*[4,5], it seems that fringe can serve as a boundary-determining molecule by inducing another protein, Serrate, which in turn triggers the expression (probably through the Notch receptor) of genes that are involved in wing growth and patterning on both sides of the dorsoventral boundary. Rodriguez-Esteban *et al.*[2] and Laufer *et al.*[3] now show that the vertebrate homologues of these genes (*Serrate-2* and *Notch-1*) are expressed with *r-fng* in the apical ectodermal ridge. This indicates that the whole of this signalling pathway may be largely conserved between insects and vertebrates.

The fringe mechanism is not the only signalling pathway that is conserved in both *Drosophila* wings and vertebrate limbs. But it does seem, so far, to be the pathway that is functionally the most closely conserved. Although other pathways show similarities in their relative modes of action in the *Drosophila* wing and the vertebrate limb, there are also some important differences. For example, in both structures, related members of the *hedgehog*/*TGF-β*/*patched* signalling pathways are concerned with anteroposterior patterning[6,7], but only in the vertebrate does this pathway lie upstream of *Hox*-gene activation[8]. Moreover, whereas expression of the *engrailed* gene confers posterior identity in the *Drosophila* wing[9], its vertebrate homologue *Engrailed-1* is required for ventral identity in the vertebrate limb[10]. And *wingless* (a *Wnt* gene) may be necessary for proximodistal-axis specification in *Drosophila* appendages[11], but its homologue *Wnt-7a* is required for dorsal specification in the vertebrate limb[12,13] (Fig. 1).

How are we to interpret this conservation — albeit an imperfect conservation — of the patterning mechanisms within both vertebrate limbs and insect wings? One possibility is that the two structures are homologous, both being derived from a

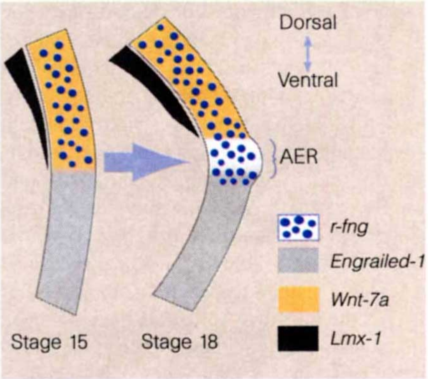

Figure 1 **Dorsoventral patterning and formation of the apical ectodermal ridge (AER) during the development of vertebrate limbs involves the coordinated expression of a number of genes, shown here. During the development of *Drosophila* wings, the dorsoventral margin forms at the juxtaposition of *fng*-expressing and non-expressing cells. Rodriguez-Esteban *et al.*[2] and Laufer *et al.*[3] now show that a vertebrate homologue of this gene (*r-fng*) functions in a similar way to regulate development of the AER at the dorsoventral margin of the vertebrate (chick) limb. Expression of *r-fng* is restricted to dorsal ectoderm partly through repression by the *Engrailed-1* expression domain in ventral ectoderm, and *r-fng* may pattern the dorsoventral boundary — as in *Drosophila* — through *Serrate* and *Notch* homologues[2,3]. Expression of *Engrailed-1* also confines *Wnt-7a* to the dorsal ectoderm[10], and *Wnt-7a* induces *Lmx-1* in the adjacent dorsal mesoderm[12,13]. *Lmx-1* and *Engrailed-1* regulate dorsal and ventral mesodermal patterning, respectively[10,12,13].**