

molecules. Mountjoy *et al.* of Roger Cone's laboratory used the polymerase chain reaction with degenerate primers to amplify a sequence from a melanoma line expressing high levels of MSH-R. With this they obtained the full-length sequence, which they found encodes the functional receptor.

The cloned receptor made it possible to see if this receptor is the product of the *e* locus. Mapping the murine MSH-R gene showed that it was very close to, and therefore a candidate for *e*. The final piece of the story fell into place last month, enabling Cone and colleagues³ to determine the sequence and activities of the mutant alleles. The recessive allele has a frameshift mutation between transmembrane domains 4 and 5, which results in a non-functional receptor. So, no α -MSH signal is received and the melanocyte defaults to produce yellow pigment. Three dominant mutations have been characterized, and all are point mutations. One, *Sombre-3J* is constitutively activated to around 60 per cent of hormonally activated levels, whereas another, *Tobacco*, is a hyperactive receptor. These mutants signal even in the absence of α -MSH, and so result in black pigmentation even when the product of *a* is present.

How that product antagonizes α -MSH binding is not known. But an extra dimension to the story ensures that there will be keen interest in finding out. The dominant (yellow) *a* alleles have several effects, which include obesity, resulting in diabetes, and a propensity to develop tumours. So, ectopic expression of *a* leads to these phenomena. Is the MSH-R normally expressed elsewhere, and being abnormally blocked there by the *a* product in the mutants? Probably not, as the recessive *e* mice are not obese nor especially susceptible to tumours. More likely, ectopic *a* expression is interfering with other receptor/ligand complexes elsewhere. If the mutant effect on these complexes results in obesity, their identification may provide clues to the basis of some forms of obesity, and perhaps pointers to pharmacological treatments. Finding where these complexes are is a first step, and that is likely to be achieved using transgenic mice in which the *a* gene is driven with different tissue-specific promoters. □

Ian J. Jackson is in the MRC Human Genetics Unit, Western General Hospital, Edinburgh EH4 2XU, UK.

1. Bultman, S. J., Michaud, E. J. & Woychik, R. P. *Cell* **71**, 1195–1204 (1992).
2. Miller, M. W. *et al.* *Genes Dev.* (in the press).
3. Robbins, L. *et al.* *Cell* **72**, 827–834 (1993).
4. Jackson, I. J. *Bioessays* **13**, 439–446 (1991).
5. Bultman, S. J., Russell, L. B., Gutierrez-Espeleta, G. & Woychik, R. P. *Proc. natn. Acad. Sci. U.S.A.* **88**, 8062–8066 (1991).
6. Mountjoy, K. G., Robbins, L. S., Mortrud, M. T. & Cone, R. D. *Science* **257**, 1248–1251 (1992).

No need to stick to the point

Charles G. Sammis

ONE of the primary goals of earthquake mechanics has been to understand the physical instability that nucleates an earthquake. The hope is that such an understanding will, one, guide the search for physical precursors that might have a predictive value; and, two, relate nucleation to fault structure, helping to identify likely nucleation sites of impending earthquakes. Mechanical models of fault-zone stability are complicated by the observation that natural faults can be geometrically complex and commonly contain a layer of crushed rock or 'fault gouge'. Elsewhere in this issue (*Nature* **362**, 618–621; 1993), C. Marone and B. Kilgore present the first convincing link between the structure of such a fault zone and its frictional stability.

In a series of frictional sliding experiments on simulated fault zones (two sliding rock surfaces separated by a layer of crushed rock) the authors show that the characteristic displacement, a parameter which is important in determining frictional stability, is directly related to the width of shear-localization bands which develop within the gouge layer. As these bands are observable not only in laboratory experiments, but also in natural fault zones that have been exhumed by a combination of tectonic uplift and erosion, Marone and Kilgore's observations represent an important breakthrough in the long-standing problem of how frictional-stability studies in the laboratory should be scaled to model earthquake nucleation on natural faults.

The problem with scaling from the laboratory to the field is that it is not clear how parameters measured for rock-on-rock friction apply to zones of crushed rock. In the laboratory, studies of frictional sliding between rock surfaces have found a stick-slip instability from a velocity-weakening phenomenon, in which the coefficient of friction decreases with increased sliding velocity. Velocity weakening in rock can be understood in terms of the classical asperity model of Bowden and Tabor, in which surfaces are in contact only at microscopic bumps, the asperities.

In the asperity model, velocity weakening comes about because the asperity strength is time dependent. The longer an asperity contact is maintained, the stronger it becomes. At higher sliding velocities, the average lifetime of an asperity is shorter, it is weaker when it breaks and, therefore, the coefficient of friction is slightly lower. In this model, the characteristic displacement is related to the average distance between asperities, and can be thought of as the

displacement required to change a population of contacting asperities to a completely new population having strengths appropriate to the new sliding velocity. The characteristic displacement is therefore the sliding distance required to weaken the coefficient of friction following an increase in sliding velocity.

What is the significance of all this to fault stability? It turns out that the reduction of friction associated with an increase in slip speed and the critical distance over which it occurs define a rheological stiffness. The stick-slip instability requires that the stiffness of the driving system (the laboratory apparatus or the elastic continuum surrounding the fault) be less than this rheological stiffness. In the case of faulting, the stiffness is related to the size of the slipping dislocation patch. Driving stress falls faster with displacement for a small dislocation than for a larger one, hence smaller dislocation patches are stiffer than larger ones. The implication is that a slipping patch must exceed some minimum size to nucleate an earthquake. A larger characteristic displacement corresponds to a less-stiff rheology which requires a correspondingly larger patch for nucleation. If the characteristic displacement is large enough, it is conceivable that the motion on a fault could be accommodated by a series of creep events without the nucleation of earthquakes.

The characteristic displacement measured in the laboratory is of the order of a few micrometres for rock-on-rock friction. If this same value is relevant for faults, earthquakes will be nucleated from very small patches and the chance of observable precursory creep or other pre-failure phenomena is nil. However, as mentioned above, real faults in nature are not well modelled as two rock surfaces in contact. The observation of a layer of crushed rock separating the fault surfaces raises the question of what constitutes an asperity, and what physically determines the characteristic displacement in such systems. Previous laboratory studies of frictional stability in artificial gouge layers found that the characteristic displacement is, in fact, larger in such systems (10–100 micrometres), but no clear dependence on either layer thickness or particle size had been observed which would allow direct scaling from the laboratory to the field.

Marone and Kilgore's principal contribution is the design of a set of experiments that clearly separates the effects of layer thickness, particle size and shear strain on the characteristic displacement.

By also measuring subtle volume changes associated with changes in sliding velocity they argue, convincingly, that the characteristic displacement scales as the thickness of the gouge that actually participates in the deformation — that is, the width of the shear localization bands. Thus armed with a physical interpretation of the characteristic displacement in terms of observable fault-zone structures, the problem of scaling frictional-stability parameters measured

in the laboratory to the field can now be sensibly addressed. How such structures are related to more readily observable fault-zone parameters such as depth, width and total displacement has yet to be determined, but at least the question has been framed. □

Charles G. Sammis is in the Department of Geological Sciences, University of Southern California, Los Angeles, California 90089, USA.

PALAEOLOGY

Ground rules for early birds

Angela C. Milner

UNTIL very recently, our knowledge of the early evolution of birds was handicapped by the paucity of the Mesozoic fossil record and was restricted largely to the 147-million-year-old *Archaeopteryx* from the Upper Jurassic of Bavaria, Germany. But a trickle of discoveries, the most recent of which is reported by Perle *et al.* on page 623 of this issue¹, is now providing tantalizing clues to the complexities of the morphological transformation series of characters leading to the development of powered flight apparatus.

The new specimens, designated *Mononychus*, come from the late Upper Cretaceous of Mongolia (that is, about 75 million years ago). The creature is represented by three-dimensional remains, whereas most other key examples are essentially two-dimensional, crushed and often fragmentary, which makes anatomical interpretation difficult. So *Mononychus* provides a character set of great importance to understanding primitive birds; this set can be interpreted unambiguously and it indicates a transitional position between *Archaeopteryx* and all other birds. However, alongside its primitive bird characters, *Mononychus* possesses a uniquely derived forelimb: it is short and powerfully built, and the hand is reduced to a single digit bearing a robust claw. Clearly, this animal did not fly.

This unexpected find demonstrates how little is known about the radiation of birds in the Mesozoic. It is widely, but not universally, accepted that birds are descended from advanced theropod dinosaurs with a specialized wrist structure (maniraptorans²). *Archaeopteryx*, the earliest avialian (the taxon that includes it and all other birds³) possessed a wing structure identical in many respects to that of modern birds. Impressions of the wings and tail feathers are uniquely well-preserved in the fine-grained lithographic limestone matrix of the famous Solnhofen Limestones of Bavaria. The

primary and secondary flight-feather count in the wing is identical⁴ to that of modern birds, as is the structure of the flight feathers in which asymmetric vanes confer aerofoil characteristics⁵. As far as its skeletal anatomy is concerned, there are few characters that distinguish *Archaeopteryx* from maniraptoran theropod dinosaurs.

What of other recent finds? Lower Cretaceous birds from 135-million-year-old rocks in China (*Sinornis*⁶), and from very slightly younger deposits at Las Hoyas in Spain (*Iberomesornis*⁷, *Concornis*⁸), demonstrate a more derived pectoral condition than *Archaeopteryx* in that they have a strut-like coracoid, furcular process and ulna longer than humerus. All three also share a pygostyle (reduced tail formed from fused caudal vertebrae) for support of a tail feather fan, which is important in flight manoeuvring at slow speeds. *Sinornis* and *Concornis* are more derived than *Iberomesornis* in their possession of a keeled sternum; *Concornis* shares derived characters with modern birds, including fusion of elements in the manus and tibiotarsus. These Lower Cretaceous birds are small — *Iberomesornis* and *Sinornis* are the size of a house sparrow, *Concornis* about twice that — which suggests that a size-filter may have operated as a selection pressure in the development of powered flight. The acquisition of a suite of evolutionary novelties relating to flight and perching apparently preceded 'refinements' of other parts of the skeleton which shifted the centre of gravity and balance forwards towards the forelimbs.

The bird record from the Upper Cretaceous is sparse, but demonstrates the establishment of a range of advanced fliers, secondarily flightless seabirds (hesperornithiforms), a flightless cursorial (running) land bird *Patagopteryx*⁹, and representatives of two modern orders. *Mononychus* postdates most of those occurrences and is evidence of a

hitherto unknown radiation of primitive, thrush-sized cursorial birds. Perle *et al.* offer two equally parsimonious alternatives concerning the acquisition of flight. Either it was primitive for all avialians and lost in the lineage leading to *Mononychus*, or flight arose independently in *Archaeopteryx* and the derived sister group (Ornithothoraces¹) to *Mononychus*. The latter implies that an identical flight-feather structure and complement arose convergently. Because *Mononychus* had a keeled sternum¹, a derived character associated with flight which it shares with all other post-*Archaeopteryx* birds, it is perhaps more likely that it represents a lineage that diverged in late Jurassic or early Cretaceous times and became secondarily flightless. A test of this hypothesis awaits the discovery of further metornithine¹ birds.

Feathers are rarely preserved in the fossil record. In the Lower Cretaceous their only associations with skeletal material are poorly preserved traces in *Concornis*, and the record is meagre in the Upper Cretaceous. However, it is a logical assumption that feathers were present in all birds derived with respect to *Archaeopteryx*, including *Mononychus*, for insulation, if not for flight. Developmentally, feathers and reptilian scales are homologous structures; down feathers must have arisen, initially as means of insulation, in the lineage of maniraptoran theropod dinosaurs from which birds arose. Another find from the Upper Cretaceous of Mongolia, a small theropod dinosaur, *Archaeornithoides*¹⁰, raises the possibility, as has been suggested in some cladistic schemes, that the bird lineage branched off the theropod line before the advent of a range of advanced dinosaurs. Feathers may, therefore, have been widespread among bipedal carnivorous dinosaurs as an insulating outer layer, as well as being universal in birds. □

Angela Milner is in the Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.

1. Perle, A., Norell, M. A., Chiappe, L. M. & Clark, J. M. *Nature* **362**, 623–626 (1993).
2. Schultze, H.-P. & Trueb, L. (eds) *Origins of the Higher Groups of Tetrapods* (Comstock, Ithaca, 1991).
3. Gauthier, J. *Mem. Calif. Acad. Sci.* **8**, 1–56 (1986).
4. Heilmann, G. *The Origin of Birds* (Witherby, London, 1926).
5. Feduccia, A. & Tordoff, H. B. *Science* **203**, 1021 (1979).
6. Sereno, P. C. & Rao, C. *Science* **255**, 845 (1992).
7. Sanz, J. L. & Bonaparte, J. F. in *Papers in Avian Paleontology Honoring Pierce Brodkorb* (ed. Campbell, K. E. Jr) 39–49 (Nat. Hist. Mus. Los Angeles, Sci. Ser. 36, Los Angeles, 1992).
8. Sanz, J. L. & Buscalioni, A. D. *Palaeontology* **35**, 829–845 (1992).
9. Alvarenga, H. M. F. & Bonaparte, J. F. in *Papers in Avian Paleontology Honoring Pierce Brodkorb* (ed. Campbell, K. E. Jr) 51–64 (Nat. Hist. Mus. Los Angeles, Sci. Ser. 36, Los Angeles, 1992).
10. Elzanowski, A. & Welinhofer, P. *Nature* **359**, 821 (1992).