molecular and infrared emissions; these correlations are not too surprising because the infrared luminosity is thought to arise as black-body radiation from warm dust grains mixed within dense clouds of interstellar material.

Sanders et al. consider these observations to be overwhelming evidence that the phenomenon of ultraluminous infrared galaxies is a consequence of collisions between individual galaxies. Furthermore, given that these same galaxies have nuclear quasars, they argue that this process must be fundamentally related to the origin of quasars. They conclude that quasars are spawned by the collision of two gas-rich galaxies, and that the increased frequency of such collisions in a younger, denser Universe naturally explains why quasars were more conspicuous in the past.

These ideas are not completely new, as earlier observers had noted that a surprising number of quasars discovered optically have interacting galaxy companions. What is unique about the hypothesis put forward by the infrared astronomers is their contention that most quasars begin as ultraluminous infrared sources, and that optical observers cannot see them until the intense radiation has driven away the dust cocoon that shrouds the quasar birth. Sanders et al. make some preliminary suggestions as to where their individual galaxies lie in such an evolutionary sequence, and they are undertaking more observations to describe better the transition from infrared to optical quasar.

Now that it is clearly demonstrated that infrared-selected samples can reveal important aspects of quasars, fundamental questions must be addressed. What is the ultimate source of the energy heating the dust to make such ultraluminous infrared sources? How much of this energy arises within the non-thermal nucleus and how much within starbursts inside the molecular clouds around the nucleus? Is a quasar formed where none existed before as a consequence of the galaxy collison, or does a previously dormant black hole in a galaxy nucleus simply flare up as a new supply of gas is dumped into its vicinity? Were all early quasars so shrouded that optical surveys could never find the new quasars in the young (distant) Universe? And perhaps most puzzling, where does all of the dust come from that is necessary to explain the infrared radiation?

For the time being, further progress can only come using ground-based observations to target the galaxies found and sorted by IRAS. No further help from new space observations will come until the launch of the Infrared Space Observatory (ISO), expected in 1992.

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Seismology

The deep roots of continents

Thorne Lay

CONTINENTS are the Earth's most conspicuous structures; their precise role in the dynamic evolution of the planet, however, remains elusive. Early notions of continental drift, motivated by observations requiring large-scale translation of continents, were repeatedly stymied by the lack of a mechanism capable of propelling relatively thin (30 km) continental masses through or over the globally extensive oceanic crust. The subsequent theories of seafloor spreading and plate tectonics, which treat the oceanic plates as the upper thermal boundary layer of a mantle convection system, allow the embedded continental nuggets to drift as the boundary layer circulates. It is conventionally asserted that any thermal or compositional differences between the mantle underlying continents and that underlying oceans vanish below depths of 150-200 km. Lerner-Lam and Jordan', however, now provide strong evidence that relatively fast seismic velocities under stable continental regions extend more than 220 km into the mantle.

There is no question that continents are chemically differentiated, buoyant structures that resist recycling down into the mantle, and hence strongly influence the kinematics of surface plates; but the controversial assertion that the stable continental shields have roots extending as much as 400 km into the mantle has radical implications for the dynamic role of continents in plate tectonics.

Jordan² first advanced the thick-plate model for continents, basing it primarily on observations of seismic body and surface waves that he interpreted as evidence for fast seismic velocities underlying continents to depths of 400 km or more. For many years controversy surrounded this interpretation, and new analyses have only recently enhanced the resolution of the vertical extent of seismic heterogeneity.

The best resolution of the upper-mantle seismic-velocity structure is obtained by analysing groups of seismic waves that bottom at different depths in the mantle, including waves that are multiply reflected off the surface. The waves can either be analysed as discrete body-wave arrivals^{3,4} or as interfering surface-wave overtones^{1,5,6}.

Lerner-Lam and Jordan in their new work adopt the latter approach for fundamental and higher-mode 'Rayleigh' wave arrivals traversing either old oceanic or stable continental paths. The variety of Earth models obtainable from sparse seismic-wave data precludes an absolute determination of separate upper-mantle velocity structures under continents and

oceans. Thus the authors combine a hypothesis-testing procedure with the structure inversions to focus explicitly on the required depth extent of lateral variations between the two types of region. They find that lateral variations in the velocity structure of primary (P) waves can be confined to the uppermost 220 km of the mantle; lateral variations in the secondaryor shear-wave (S) velocity structure, however, must extend deeper, with satisfactory models having significant differences between oceanic and continental regions as deep as 400 km. Similar variations in S-velocity structure have been obtained in previous studies2-5, but the lack of any formal analysis of the resolution has always left the models' reliability uncertain.

Most seismic evidence seems to support the contention that differences of shear velocity between mantle beneath continents and that beneath oceans, extend more than 220 km into the upper mantle. But even having accepted this, the interpretation of this heterogeneity and its dynamic implications is still controversial. Anderson⁷ emphasizes the intrinsic ambiguity of interpreting relative velocity variations, arguing that the mantle more than 200 km under continental shields is normal unmolten mantle, whereas the hotter suboceanic mantle has anomalously low shear velocities because of partial

100 years ago



M. Richard's team proved that it was possible to live at high altitude on Mont Blanc. From *Nature* **38**, 35; 10 May 1888.

melting and other isobaric phase changes. Jordan^{2,8} instead attributes the high

velocities below 200 km under shields to petrologically distinct material which accumulated during the early chemical fractionation of the continents. This compositional root must move with the underlying continental plate and it must resist the erosive effects of thermal convection in the surrounding system. It is also necessary to juggle possible chemical and temperature effects in the deep root to explain the absence of geoid (gravitational) anomalies associated with shields.

Additional evidence for the unusual properties of the deep continental environment have come from thermobarometry studies9 of mantle xenoliths (emplaced rock fragments) and modelling studies of surface heat-flow measurements within and along the margins of continental shields¹⁰. These indicate that low temperatures underlying the upper 200 km of continental shields have persisted for up to 3,500 million years, despite dynamic processes which tend to destabilize thick thermal boundary layers. A thick, durable chemical and thermal boundary layer which formed very early in the continental evolution could explain this. But the interpretation is complicated by the intrinsic tendency of continents to override cool subducting oceanic plates, which provides an alternative mechanism for maintaining long-term lower temperatures beneath continents⁷.

Although continental areas cover only one-third of the Earth's surface, and the stable shield regions are only a fraction of this area, it is still critical to resolve the thickness of the coherently translating surface plates. The maximum depth of the convective return flow in the mantle which accomodates the oceanic motions is not well resolved, and the possibility that continents with 400-km thick keels must be rafted about clearly affects our understanding of both the nature of the return flow and the forces that drive the motions.

How then, is this issue to be resolved? High-precision seismic investigations like that of Lerner-Lam and Jordan' must be undertaken to quantify the global occurrence of high-velocity extensions under shields. But this will not resolve the issues clouding the interpretation of the seismic models. It is clear that temperatureinduced variations are important for lateral variations of seismic velocities

within continental regions. In fact, the most extreme lateral variations in shear velocity in the upper 300 km of the mantle that we know of are found between the Canadian shield and the tectonic belt of western North America. Temperature causes stronger variations in shear velocities than in compressional velocities, and thermally activated processes are also the cause of anelastic attenuation of seismic waves. Thus, modelling of regional variations in seismic attenuation, together with studies of the elastic velocities, could be the key to apportioning the chemical and thermal interpretations of the deep continental root controversy.

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Transcriptional activation

Acid blobs and negative noodles

Paul B. Sigler

THE more that is known about the aminoacid sequences of proteins that participate in transcriptional activation, the clearer it becomes that many of the critical events cannot depend upon the precise geometrical complementarity that we associate with the interactions of globular proteins during molecular assembly, and the binding of substrates, cofactors and haptens. The latest entries in this chronicle of molecular imprecision are the activator domains of the proteins that stimulate

for correct placement and orientation with respect to the start site of transcription. The promoter sequences are a defined distance upstream of the transcriptional start site. Modulating the activity of the incipient transcriptional complexes is a wide variety of transcriptional activator proteins that bind to specific DNA targets called by various names, such as 'enhancers', upstream activating sequences (UASs) or hormone response elements (HREs). The position and polarity of



Fig. 1 A generic transcriptional-regulatory protein. A DNA-binding domain with a welldefined conformation (often dimeric) and a peptide with an excess of negatively charged side chains that has a poorly defined conformation (here, none at all).

transcription by RNA polymerase II. These activating 'structures' (and one must use that term advisedly) are targeted to specific DNA-sequences usually by a specific DNA-binding domain on the same polypeptide. The DNA-binding domains appear to have well-defined structural motifs; by contrast, mutational studies of the activator domains suggest a disquieting picture of a conformationally ill-defined polypeptide that can function almost irrespective of sequence, provided only that there is a sufficient excess of acidic residues clustered or peppered about. Thus, the elegant molecular machinery that so reliably controls expression of eukaryotic polymerase IItranscribed genes relies on nearly shapeless molecular components dubbed "acid blobs" or perhaps more aptly "negative noodles" (Fig. 1).

The function of these activating proteins and their poorly structured acidic domains is to stimulate the formation and/ or action of transcriptional preinitiation complexes. The core of these complexes consists of the promoter-binding proteins on which the RNA polymerase depends

these cis regulatory sequences are not stringently defined with regard to the promoter that they activate. Thus in a geometrical sense, though not in a topological sense, the complete preinitiation complex must have a poorly defined architecture. Moreover, not only are the preinitiation complexes casually defined in spatial terms, but they have a surprisingly indefinite stoichiometry. It is not uncommon to find many enhancer sequences clustered or sprayed over a region of several hundred base pairs upstream or sometimes downstream of the promoter.

In most cases, reiterated sequences work better than just one or two. (Imagine haemoglobin benefiting from having a few extra β -subunits!) Even if we knew nothing about the sequences of the transcriptional activating proteins, this wide latitude of arrangement and stoichiometry argues strongly against any dependence of the activating events on specific and rigid (or even firm) complementary surfaces. One imagines the polymerase II transcription initiation complex before initiation as a convoluted loop of B DNA that brings the activator domains into contact with

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