thousand base pairs, presumably reflecting variation in the number of repeat units present[7]. The inverted repeats of FB4 differ in this way, with the right-hand repeat being longer than the left, and Potter points out that length variation of this type could be generated by mismatch recombination between repeats of different FB elements. In addition to these gross differences, the two repeats also differ by base substitutions and deletions/additions. The most highly conserved regions are at the extreme ends of FB elements. This is not surprising since these regions must presumably interact with any proteins involved in transposition.

The central region of most FB elements is made up of sequences related to the inverted repeats themselves[7]. FB4 is unusual in that its terminal repeats are separated by about 1,750 base pairs of unrelated DNA containing a potential gene coding for a 148 amino acid polypeptide. Most of this central region may itself be a transposable element since 33 nucleotides at its right-hand end occur as a near-perfect inverted repeat a short distance from the left-hand end (terminal inverted repeats are characteristic of all known prokaryotic and eukaryotic transposable elements).

The mechanism by which *copia*-like elements are able to redistribute themselves around the genome is by no means clear but the many properties they have in common with proviruses[3] suggest that it could involve circular intermediates[9] produced by a transcription–reverse transcription cycle. This is unlikely to be true of FB elements, however, and Potter (p.201) suggests that a transposase similar to those of bacterial transposons is involved and might been coded by the central region of FB4. Against this one has to remember that FB4 is the only FB element known to contain this sequence and its putative gene product might equally well be a transposase for the potential transposable element comprising this region.

The role (if any) of FB elements is unknown. Goldberg *et al.*[10] reported that an FB element lies at one end of one of the very large transposable elements (TE elements) described by Ising[8]. These are several hundred kilobases long and in some cases can be detected cytologically. The DNA involved can include respectable components of the genome, such as the white eye gene (*w*), unlike *copia*-like elements which seem to be genomic parasites. This raises the interesting possibility that any sequence bounded by two FB elements may potentially be transposable.

Inverted repeats can be detected in rapidly re-annealing DNA from many species and one may wonder whether these are similar to FB elements in the same way that endogenous proviruses seem to correspond to *copia*-like elements. In humans, the bulk of inverted repeat structures are comprised of two copies of the 300 base pair 'Alu' sequence in opposite orientation and separated by variable lengths of unrelated DNA[11]. Alu sequences make up a substantial component of human dispersed repetitive DNA and have counterparts in other species[12]. Jagadeeswaren *et al.*[13] have suggested that Alu sequences can themselves transpose but there is no indication that they behave like FB elements. It does not follow that humans and other vertebrates do not contain such elements, however, since even in *D. melanogaster* they make up less than two per cent of inverted repeats. All of this goes to show that there is still much work to be done in the study of repetitive DNA. ☐

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Seamounts and flexure of the lithosphere

from A.B. Watts

MORE than 75 years have passed since the first gravity measurements showed that the Hawaiian islands, in the Pacific Ocean, were associated with large positive gravity anomalies of up to a few hundred mGal. The American geodesists, Hayford and Bowie[1], showed in 1912 that these anomalies could be substantially reduced by taking into account isostasy. The form of isostasy they preferred was the Pratt model, which considered that the islands were locally compensated by lateral variations in crustal density. The model was popular with geodesists since it enabled them to readjust the triangulation system of the US: a task of immense practical importance in mapping and surveying. It was of comparatively little interest, however, to a leading geologist at the time, Barrell, because it did not account for the lateral strength of the crust. Putnam pointed this out to Hayford and Bowie who subsequently amended the Pratt model by extending the compensation from beneath the islands into surrounding regions. They showed that a regional model of isostasy could reduce the gravity anomalies over the Hawaiian islands further than could the Pratt model.

But it was not until 1926, when Vening Meinesz[2] made the first pendulum gravity measurements in a submarine, that it was possible to prove regional, rather than local, isostasy for the Hawaiian islands. The measurements showed that the positive anomalies over the islands were flanked by negative anomalies of up to 100 mGal, which Vening Meinesz first interpreted as a result of downbending or flexure of the crust due to the load of the Hawaiian volcanoes. He used a model of an elastic plate overlying a weak fluid substratum, similar to one developed by Hertz[3] to model the flexure of ice on ponds by skaters. Subsequently, Vening Meinesz demonstrated that a flexure model of isostasy reduced the gravity anomalies over the islands further than could either the Pratt model, favoured by Hayford and Bowie, or the Airy model, preferred by some European geodesists.

Since the development of the concept of plate tectonics the flexure model of isostasy has assumed a special significance. Plate tectonics views the outer layer of the Earth, or lithosphere, as consisting of several large plates which converge, move apart and slide past each other. The plates therefore correspond to the rigid layer argued for earlier, on isostatic grounds, by Barrell and Vening Meinesz. An important assumption of applying plate tectonics to the geological past is that the plates behave rigidly for long periods of time. Thus, one of the objectives of current flexure studies has been to determine the thickness of the rigid layer and whether it varies on long geological time scales.

The numerous oceanic islands and seamounts that occur in the world's oceans have proved particularly satisfactory loads for flexure studies. They are mainly of volcanic origin, form relatively quickly on the plates (as evidenced by the short times between eruptions) and occur in a variety of tectonic settings. Since WW II there have been a number of geological, geophysical and geodetic investigations of seamounts and oceanic islands so there is now a large amount of bathymetry, gravity, geoid and recent crustal movement data for them. By comparing these data with predictions based on elastic plate models it has been possible to estimate the flexural rigidity, and the equivalent elastic thickness of oceanic lithosphere, in different tectonic settings in the oceans[4–7].

Flexure studies at seamounts and

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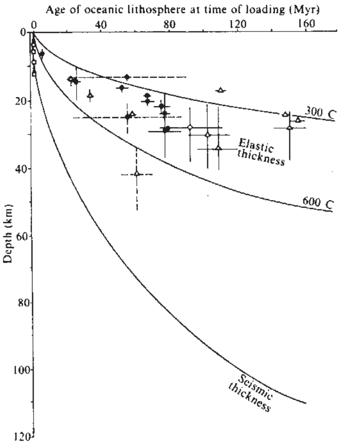
oceanic islands have shown that the elastic thickness of oceanic lithosphere, which is significantly smaller than the seismic thickness, increases with the age of the lithosphere at the time of loading. The large range of ages represented by these features (1–56 Myr) suggest that on loading, the lithosphere rapidly relaxes from its initial short-term (seismic?) thickness to a long-term mechanical thickness. Subsequent relaxation has not been observed, but may occur on very long (> 56 Myr) time scales. The smallest values of elastic thickness (5–8 km) have been determined at features which form on young oceanic lithosphere, such as the western Walvis ridge guyots, while the largest values (17–37 km) have been determined at features which form on old oceanic lithosphere, such as the Hawaiian islands. These variations suggest[8] that as the oceanic lithosphere cools, it becomes progressively more rigid in its response to volcanic loads.

The flexure model, deduced from these studies, is referred to as 'elastic', even though the model parameters actually vary with time. The elastic thickness apparently changes rapidly following loading, approaching an asymptotic value that depends on the plate age. The lithosphere only appears elastic, therefore, after some time has elapsed (∼1 Myr) and, even then, the thickness of the elastic layer is determined by the plate age.

The actual long-term mechanical properties of the lithosphere are, of course, likely to be more complex than would be predicted by an elastic model. A difficulty is that flexure studies only reveal information on the average mechanical properties of the lithosphere. The estimation of elastic thickness from gravity and geoid data, for example, is complicated by uncertainties in the volcanic load and infill densities, the crustal structure before flexure, and the lateral and vertical extents of lithospheric heating at the time of loading. But as Lambeck[9] and others have pointed out, gravity and geoid data are consistent with an elastic model in which the elastic thickness increases with age of the lithosphere at the time of loading. A more difficult problem, though, is that there is no maximum stress a purely elastic plate can store; yet the actual materials of the lithosphere are likely to have some ultimate strength. Goetze and Evans[10] have pointed out, however, that if a more realistic 'yield stress envelope' is used for the lithosphere (based on data from experimental rock mechanics), an elastic core would be expected to develop during flexure that corresponds closely to the elastic thickness determined using the elastic model.

Although an elastic model has been widely used in flexure studies[4–9], it has been criticized by some workers who prefer a viscoelastic (Maxwell) model. A viscoelastic model is characterized by an initial elastic response to a load, followed by a viscous relaxation that rapidly increases with age of the load. Since the model incorporates a form of stress relaxation, the 'equivalent' elastic thickness would be expected to decrease as the load increases in age, the decrease being most apparent for long times (compared with the Maxwell relaxation time) and large loads. But elastic and viscoelastic models produce flexure curves of similar shape. Thus, the best way to distinguish between them is to determine whether the elastic thickness is controlled by the age of the load (viscoelastic model) or by the age of the plate (elastic model).



Estimates of the elastic thickness (or mechanical thickness) of oceanic lithosphere plotted against age of the lithosphere at the time of loading. The solid symbols are estimates from studies by different workers at seamounts and oceanic islands, open symbols are estimates from studies at mid-ocean ridges (squares), river deltas (diamond) and deep sea trench-outer rises (triangles). As the age of most of the features range from a few Myr to several tens of Myr, flexure studies indicate that on loading the mechanically supportive part of the lithosphere relaxes from its short-term (seismic) thickness to a long-term mechanical thickness. The long-term thickness does not appear to change appreciably with time. Thus, flexure is likely to be an important controlling mechanism in the tectonic evolution of geological features in the oceans and continents.

Walcott[4] first suggested, based on the results of flexure studies of continents and oceans, that the elastic thickness of the lithosphere depends on the age of the load, rather than on the plate age. A difficulty with his study, however, was that he did not satisfactorily account for differences in size or tectonic setting of the various geological features used in these studies. Recently, Lambeck[11] accounted for these differences in a study of the Society and Cook Islands in the South Pacific Ocean and argued for a dependence of the elastic thickness on age of these loads, that indicated a Maxwell time of about 10^7 yr for the oceanic lithosphere. The differences in age between the Society and Cook Islands are too small (1.4–3.1 Myr), however, to resolve satisfactorily whether there has been more relaxation beneath the older load (Cook) than the younger load (Society). The best example of a dependence of the elastic thickness on age of load occurs, in fact, along the Hawaiian–Emperor seamount chain; the younger Hawaiian ridge (4–18 Myr) shows the larger elastic thickness (37 km) and the older Emperor seamounts (44–58.5 Myr) the smaller thickness (22 km). But as Watts[8] pointed out, the small values for the Emperor seamounts can be more simply explained by an elastic, rather than a viscoelastic, model since these seamounts were originally emplaced on young, weak, oceanic lithosphere.

This discussion suggests, therefore, that a consensus is emerging from flexure studies at seamounts and oceanic islands favouring the elastic model as the most useful working hypothesis for the long-term mechanical properties of the lithosphere. The model can also explain (with some modification) the topography of the outer rise seaward of deep-sea trenches, the deep structure of large river deltas, the pattern of late glacial rebound due to the receding Laurentide ice caps and the patterns of gravity anomalies over orogenic belts and Precambrian granite plutons. The model is therefore currently enjoying a wide range of applications in geology that include the determination of the tectonic setting (on-ridge or off-ridge) of intraplate volcanoes, the nature of the control on stratigraphical sequences in sedimentary basins and the gravity and geoid effect of deep processes beneath the lithosphere, such as layered mantle convection.

Clearly, the elastic model remains a working hypothesis that needs to be tested in the future. A critical test would be to determine the actual seismic thickness of the crust and lithosphere in the region of a large volcanic load, such as the Hawaiian islands. Recently, two-ship multichannel seismic experiments, using long arrays and repetitive sound sources, have been carried out in the western and eastern Pacific Ocean[12] that have revealed nearly continuous reflections from the 'Moho' discontinuity at the base of the oceanic crust. Similar experiments in the central Pacific, near the Hawaiian islands, offer the most promise, therefore, to test the flexure model of isostasy during the next decade. ☐

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