range of the mantle transition zone, where phase changes should occur in downgoing slabs. Modeling shows that in fast-subducting cold slabs, the transformation cannot keep pace with the descent, so metastable olivine should persist well below the equilibrium phase boundary in wedge-shaped regions bounded approximately by the 600°C isotherm (*7, 19*). Deep earthquakes are assumed to occur by a shear instability, known as transformational faulting, observed in the laboratory for metastable materials under stress. This model is consistent with the variation in earthquake depths between and along subduction zones.

The recent earthquake observations (*1–3*) pose a problem for both models, in that the large fault zones appear to cut across the predicted narrow wedge of material below 600° to 800°C. The idea of a temperature-controlled process is hard to abandon, however, because deep earthquakes occur only in those slabs that are relatively colder. It thus seems likely that the fault areas indicate slab temperature structures more complicated than the simple models of essentially parallel isotherms in undeformed slabs. The high seismic energy release below about 600 km (*20*), earthquake mechanisms (*21*), and images of slabs from seismic tomography (*22*) suggest that slabs deform because of interaction with the 670-km discontinuity, a major change in physical properties at the base of the transition zone.

The figure shows a possible such schematic model for the Bolivian earthquake (*23*). The slab is presumed to have a more complex thermal structure because of variations in the age of the subducting plate over time and thickening as a result of slab deformation, causing a widened cold "pod." Large deep earthquakes could occur in this region, either because of metastability or another temperature-controlled process. The real geometry is presumably more complicated and varies both within and among slabs.

Complex and variable deep slab thermal structure is plausible for several reasons. Although simple thermal models vary only slowly along strike for a given slab, the deep seismicity is quite variable. Deep seismicity has distinct clusters and gaps where later large earthquakes can occur (as was the case for the Bolivian earthquake) (*23*). Tomographic images of deep slabs also vary along strike and show more complexity (*22*) than simple thermal models predict (*11*). In addition to mechanical perturbations to the slab, some of this variability may reflect metastability because latent heat release would perturb thermal structure (*7, 24*). These variations in both temperature and metastability would cause complex density variations and would thus affect slab stresses and driving forces (*7*). If the wedges were large enough and continuous, the resulting buoyancy might contribute to deflecting the slab to a near-horizontal attitude (*1*), as observed in some cases (*22*), although not for the Bolivian earthquake region.

To date, ideas about subduction have evolved as seismological data have improved. Deep earthquakes showed that subducting slabs exist, indicated that they were colder than their surroundings, suggested that stresses in slabs result largely from the higher density, and now imply that slabs are complicated and variable. Simple slab models will need to be revised to reflect this complexity and then tested against observations from recent and future deep earthquakes. The fact that large deep earthquakes are rare (the last one comparable to the Bolivian earthquake occurred in 1970) will help ensure that the issue of what causes deep seismicity remains open for some time.

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Springs for Wings

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Flying insects beat their wings very fast, up to 1000 cycles per second in the extreme case of a tiny midge. It has long been suspected that their beating is sustained elastically like the vibrations of a tuning fork, that kinetic energy lost by the wings as they are halted at the end of one stroke is stored in springs that recoil elastically to provide the kinetic energy for the next (*1*). It has been frustratingly difficult to demonstrate or disprove this, but in this issue Dickinson and Lighton (*2*) present clear evidence that elastic mechanisms are important for flying fruit flies.

Elucidation of this mechanism is important for understanding insect flight, because it makes a big difference in how we calculate the amounts of work that the wing muscles must do. They must perform aerodynamic work in each wing stroke to overcome the aerodynamic drag on the moving wings. In addition, they must do inertial work to give kinetic energy to the wings as they accelerate at the start of each stroke. If the wings are halted by muscles acting as brakes, their kinetic energy would be degraded to heat and be lost. If, on the other hand, the wings are halted by springs, their kinetic energy can be stored for reuse in the next stroke. If we can calculate these work requirements and also determine the metabolic energy cost of flight, we can estimate the efficiency of the muscles. If there is perfect elastic storage in springs well-matched to their task, the muscles have only to do aerodynamic work, and

$$\text{efficiency} = \frac{\text{aerodynamic work}}{\text{metabolic energy consumption}}$$

If, on the other hand, there is no elastic storage

$$\text{efficiency} = \frac{\text{(aerodynamic + inertial) work}}{\text{metabolic energy consumption}}$$

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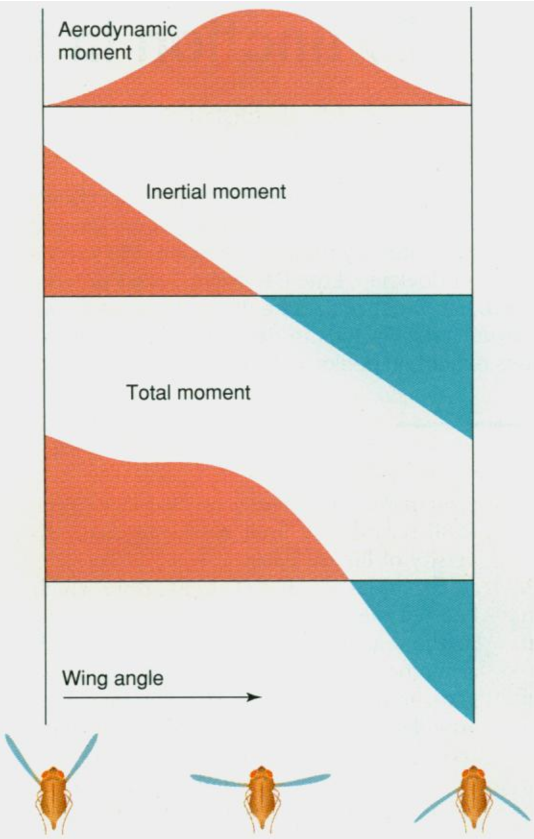

Work done during a wing stroke of a flying insect. The moments that the muscles must overcome to move a wing are plotted as a function of the angle through which the wing moves. The aerodynamic moment is largest in midstroke when the wing is moving fastest. Work done against it is shown in red. A positive inertial moment is needed to accelerate the wing, followed by a negative one to halt it. Positive work (red) is needed, followed by negative work (blue) (a muscle doing negative work is acting like a brake). The total moment is shown at the bottom. Positive work is needed during most of the stroke, and negative work at the end. If there is perfect elastic storage, the muscles have only to do the work against the aerodynamic moment (**top**). If there is no elastic storage, they must do the larger amount of work against the total moment (**bottom**).

[In these equations the total (aerodynamic plus inertial) work is not simply the sum of the aerodynamic work and the inertial work, because some of the kinetic energy taken from the wings late in the stroke can be used to do aerodynamic work (see figure)].

Most data have been obtained from studies of insects beating their wings as if flying while glued to a wire, which keeps the insects where the experimenter wants them. Aerodynamic and inertial work are calculated from the observed wing movements, and the metabolic cost is calculated from oxygen consumption. The accepted method for assessing the role of elastic mechanisms is to calculate the two efficiencies given by the equations above and see which is plausible (*1*, *3*, *4*).

Experiments on mammalian muscles working at near-optimum rates have generally given efficiencies of 15 to 25 percent (*5*) (note that we are concerned with net efficiency, that is, net work divided by metabolic energy cost). There are indications that smaller animals tend to have less-efficient muscles (*4*), but there seems to have been only one determination of insect wing muscle efficiency that did not depend on assumptions about the importance of elastic mechanisms. That calculation gave a value of 6 percent, which may or may not be typical (*6*). Calculations of efficiency from measurements of the oxygen consumption of flying insects (using the above equations) have generally given values in the ranges 4 to 10 percent (assuming perfect elastic storage) and 10 to 30 percent (assuming no storage) (*3*, *4*). Neither of these ranges seemed impossible, in the light of our limited knowledge. Dickinson and Lighton (*2*) have reached a clear conclusion by choosing a fruit fly, an insect for which estimated inertial work requirements are about 10 times the aerodynamic requirements. Thus, the two equations give very different estimates of efficiency. For perfect elastic storage they give an efficiency of 9 percent, which is physiologically plausible. For no elastic storage they give 54 percent, far outside the plausible range. It seems clear that most of the kinetic energy of the wings must be carried over from one stroke to the next, by elastic storage and recoil. Dickinson and Lighton estimate that 90 percent of the energy is stored, but the doubts about muscle efficiency and about the aerodynamic work needed to sustain the highly unsteady airflow around the beating wings make it unwise to be too precise.

The question remains, where are the springs? The elastic properties of the cuticle of the thorax may be important (*1*), but it seems likely that in many insects the principal springs are the muscles themselves. In their classic experiments, Machin and Pringle (*7*) demonstrated the spring-like behavior of wing muscles of the fibrillar type possessed by flies, beetles, bugs, bees, and wasps. More precisely, the muscle cross-bridges may be the springs. The short-range elastic properties of frog muscle have been attributed to cross-bridges (*8*). The wing muscles of wasps performing tethered flight have been observed through a window cut in the cuticle of the thorax (*9*). These observations showed that the muscle fibers lengthen and shorten by only 2 percent in each wing beat cycle. This makes it conceivable that cross-bridges remain attached throughout the cycle, which would enable them to be effective energy-saving springs, storing the kinetic energy of the wings for reuse in the next stroke.

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